

Mammals

PROCEEDINGS OF THE FIRST INTERNATIONAL REINDEER AND CARIBOU SYMPOSIUM

9-11 AUGUST 1972

UNIVERSITY OF ALASKA

FAIRBANKS, ALASKA



Edited by:

JACK R. LUICK

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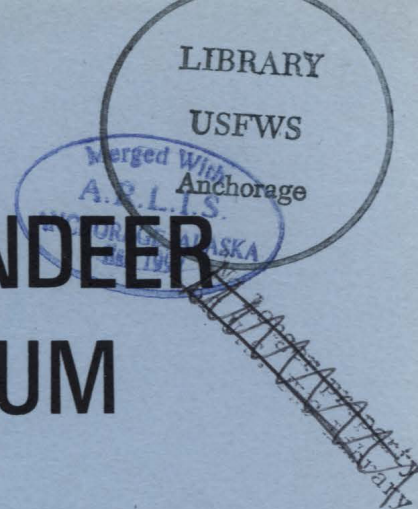
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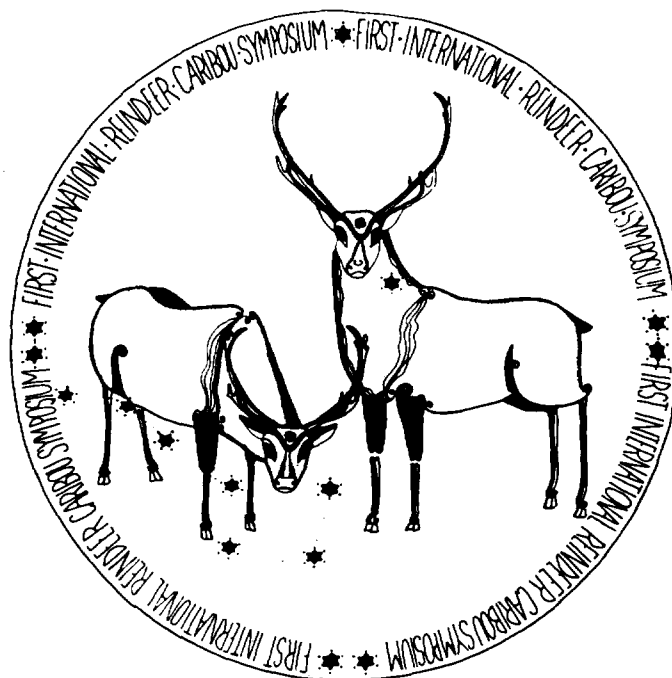
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OPENING REMARKS

An International Reindeer/Caribou Symposium, *raison d'être*

Laurence Irving
Professor Emeritus and Advisory Scientific Director
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska

It is a very special pleasure for me to assure you of the appreciation that the people of this area feel that you experts from many lands meet with us to discuss the most interesting animal of the northern world.

People and reindeer/caribou have left traces of their very ancient association in northern lands. An implement for scraping skins, fashioned from the tibia of a caribou, found at Old Crow Flats in arctic Yukon Territory, was ascribed by W. N. Irving after apatite dating to the work of a human artisan 27,000 years ago. The workmanship shows that the ancient artisan possessed both the hardware and software with which to utilize caribou in that North American ice-free refuge when Wisconsin ice caps still covered so much of North America. From a single relic we can conclude that a society of people was making use of a population of caribou. Those hardy ancients lived in a time when mammoths, horses, camels and large fierce carnivores still existed. These are now extinct, but fortunately for the ancient Americans and for us reindeer and caribou have survived.

Caribou have provided meat, skins for clothing and shelter of exceptional warmth and lightness, and implements made from bones and antlers for the indigenous northern Americans. The fur trade that led to early exploration and exploitation of northern American lands was provisioned from caribou. There is no sign that these earlier Americans were purposively conservative, yet the caribou persisted through the intense period of the fur trade before a marked decline in their numbers occurred.

In North America there are several distinguishable kinds of caribou. In each of these populations there were herds that differed in migratory programs. These local variations in habit of caribou required that the dependent people adopt modes of life to fit their local herds of caribou. These systems developed and maintained a variety of small human societies with specialized cultures pertaining to the local environments and to the habits of their local caribou.

I recall my impressions during some September days 25 years ago when I first watched caribou moving over the tundra near Umiat. Groups of hundreds were moving at their easy but not slow pace westward. Occasionally they paused to feed in their dainty manner. Now and then the sensible adults lay down to ruminate while the calves cavorted in play. I had never before seen numbers of large wild herbivores except in a state of watchfulness or alarmed flight, and I did not realize that most of their natural lives could be spent in such leisurely manner.

The first snow had fallen and summer had ended. I reflected that these caribou should be busily nourishing themselves in preparation for the approaching arctic winter. Now I know that by this date their coats of fur were well prepared and that in their unhurried way they had already acquired substantial reserves of fat.

Then it occurred to me that wild caribou operated quite differently from the familiar domesticated herbivores that feed so intensively. Our domesticated animals are selected for exaggerated appetites, that will produce meat, hides and milk for our use. A wild population

is content with the satisfaction of its own basic needs. Not having abandoned its program of living to human guidance, the wild population must have time in which to perform the many explorations and social activities that order its temporal and geographical operations.

There is just enough study of the physiology and biochemistry of a few ruminant animals to foreshadow great additions to useful basic science from investigations of the caribou and reindeer that live in such varying circumstances about the northern parts of the world.

The natural history of the species *Rangifer*, which is so diverse in North America, its behavior and migrations are of the greatest biological interest and are of essential practical importance for northern people. The physiology and biochemistry of the operation of these large ruminants is required information before artificial selection can seek for genetic characters by which to modify and improve the domestic stock to suit various environments and uses. Among the highly variant American caribou there seem to be available an assortment of characters which, if physiologically defined, could lead to designs for new combinations of characters that would be very useful in domestication.

This Congress assembles experts from many lands to exchange information about their common and differing knowledge of *Rangifer*. The different ways in which people and *Rangifer* are related reveal the diverse manners in which the two species operate in the world's northern environments. Through association in this meeting we look forward to the sociable enjoyment of each others company as we further collaboration around the northern world.

**PLENARY SESSION: POTENTIAL IMPACT OF ACCELERATED NORTHERN
DEVELOPMENT ON CARIBOU AND REINDEER POPULATIONS AND ECOLOGY**

REMARKS OF THE CHAIRMAN

David R. Klein
Alaska Cooperative Wildlife Research Unit
Fairbanks, Alaska

I am sure that all of you here are aware of the accelerated development of the North which is now underway and which is the result of increasing world demand for mineral resources as well as events which have taken place in the North in the past decade or two. Certainly the recent discovery of large reserves of oil in the Arctic has focused attention on the North. In Scandinavia there is rather widespread hydroelectric development and mining exploration and development which is changing the ways of life in northern Finland, Sweden and Norway. Associated with this circumpolar development is the construction of roads, railroads, pipelines, power lines and numerous other activities of man which in turn have an impact on caribou and reindeer and their environment. There are increased numbers of people in the North — resident populations as well as tourists and transient workers. The indigenous people are undergoing a change from subsistence hunting and fishing and semi-nomadic animal husbandry to cash economies and higher standards of living, higher at least if they are measured in terms of per capita cash expenditures. These changing ways of life are associated with the emergence of conflicting resource uses and they have resulted in increased pressures on reindeer and caribou. For example, in Scandinavia approximately 1,500 reindeer are killed annually in Finland by accidents on the highways and around 2,000 are killed by trains in Sweden each year, the numbers depending very much on snow conditions. Also in Scandinavia rather extensive flooding of some range lands has occurred as a result of hydroelectric developments, and other range lands are altered as a result of intensive forestry practices as discussed by Mr. Erickson this afternoon. All of these influences have resulted in increased pressures on the reindeer in Scandinavia through alteration of migration routes, loss or changes in range lands or direct impact on the animals.

In the Soviet Union I recently learned that a gas pipeline constructed on the Taimyr Peninsula of north-central Siberia and laid on the surface of the ground had resulted in the obstruction of the migration of wild reindeer. The construction of ramps over the pipeline to facilitate the movement of reindeer across it has as yet proved unsuccessful. When I was in Leningrad in May I talked to Professor Andreev, a noted scientist who has spent a number of years studying the lichen range lands of Siberia, and he told me of the problem around the industrial city of Norilsk in north-central Siberia where atmospheric pollutants from nickel refineries have caused the deterioration of the lichen range in the surrounding area.

In Canada and Alaska oil discoveries have focused attention on the North and have posed numerous ecological problems, many of which relate to caribou and to a lesser extent reindeer. We heard this afternoon about the possible threat of interruption of migrational movements of caribou by the construction of pipelines and roads. We know that in the North there has been harassment of caribou with the use of aircraft, and particularly by helicopters. This activity is often the result of eagerness to view wildlife and is well intentioned, but it is done in ignorance of the possible problems that it may cause. Again, there is concern throughout the entire polar regions, but particularly in the Canadian and Alaskan Arctic and Scandinavia, over the increased fallout from atmospheric pollution, generated in this case from industrial areas further south rather than from the atmospheric

testing of atomic bombs as was the case a decade ago. We know that atmospheric pollution can be detrimental to lichens which are of vital importance for reindeer and caribou.

It is obvious that we need to understand more about the particular problems that will be facing reindeer and caribou populations as a result of northern development in the future, and one of the objectives, perhaps the primary objective of this panel, is to exchange information and experience on an international basis about these problems so that we can benefit from each other's experiences, and where questions remain unanswered hopefully we, in our own countries, can direct research toward answering them.

THE SCANDINAVIAN VIEWPOINT

Loyd Villmo
State Reindeer Consultant
Tromsø, Norway

The subject we are about to discuss this evening is a very important one. Our generation, more than any before it, seems to have the tendency to over utilize all of the resources in nature. Sufficient notice has not been taken of the lack of balance this creates in nature and of the resulting repercussions on the environment. Desires to improve the public welfare have stimulated an increasing resource utilization without ecological costs being sufficiently appreciated and studied. Only in the last decades have investigations given us more knowledge of the Arctic ecosystem and of reindeer ecology.

To attempt to summarize the Scandinavian viewpoint on the announced subject in the brief time available is difficult, because the subject is large and comprehensive. The information which I will present is drawn from conversations with a number of reindeer herders in Norway and Sweden about their experiences with domesticated reindeer and from my own observations during the last 12 years working with many of these problems. I believe that experiences in Finland are similar to our's in Norway and Sweden.

Initially, I would like to try to briefly answer the question of how reindeer react to physical obstructions and disturbances within their range areas. Each species of animal is adapted to live in a particular environment. Within an ecosystem each species occupies an area where the available nutriment approach the animal's optimum requirements. This is also the case with reindeer. Reindeer require different seasonal pastures and thus must migrate from one area to another. When physical obstructions or disturbances occur along their path of movement or within seasonal range areas, complications in the ecosystem result. For example, when an impoundment is constructed to create an artificial lake in a reindeer pasture allotment or in a calving area, losses of essential range components result and the migratory routes of the reindeer may be disrupted as well. Similarly, movements may be interfered with if a river is changed by constructing a hydroelectric project, or if a road is built through a range land. All of these examples represent different levels of interference between the animals and their environment. Reindeer moving along their migratory routes or the females arriving at their calving area may be confused if they find something strange in otherwise familiar surroundings. Under such circumstances the reindeer may seek new range lands, new migratory routes or different calving areas where their particular life requirements can be fulfilled. As a result the herd strays. They may move to other range lands where they are not permitted to graze or where they become mixed with other herds of reindeer. With certain types of land development such as impoundments, the loss of pasture land is irreversible. In other cases, such as electric power lines or roads, the situation may stabilize after some years as most of the reindeer become adjusted to the obstruction. The length of time required for adjustment to roads depends, to a large extent,

on the traffic and the degree of tameness of the reindeer. I believe wild reindeer require a longer period of adjustment to such disturbances than is true of domestic reindeer. However, the alarm reaction of the reindeer to new obstructions is much greater if the reindeer are moved by the herder than when the animals are roaming free.

Observations along roads with moderate traffic indicate that some reindeer will graze closely adjacent to them. Nevertheless, a break in their grazing will occur with each passing car. The result for the reindeer is that they either get too little feed or they need longer grazing periods. In the latter case, they have a shorter time for resting. In addition, the degree of utilization of pastures close to roads is generally much reduced over areas where no disturbance occurs.

In the last decades, rapid industrialization and increased human populations in northern Norway, Sweden and Finland have led to the corresponding proliferation of roads and railroads within the range areas of reindeer. Some of these roads are main highways and some of them are built in connection with forestry, mining, hydroelectric projects, and so forth. The construction of such roads or railroads always results in a loss of pasture. The loss will be most critical if the area influenced is a pasture which is an essential seasonal component of the total pasturage available to a given herd. In addition, there is a zone of disturbance along each road and railroad (Fig. 1). The well traveled highways and railroads



Fig. 1.—A road recently constructed through reindeer range in Finnmark, Norway. Excessive destruction of vegetation has resulted from careless construction practices. The loss to reindeer range in the area has been substantial.

have been obstructions to the free movement of wild reindeer as well as of domesticated ones. The roads make it easier for people to enter the range lands. These 'tourists' also bring with them their dogs, which can be dangerous for the animals and especially for the pregnant females in the spring. Numerous reindeer are killed by cars and trains, particularly during wintertime when there is deep snow, because the reindeer move along the roadways where travel is easier. Snow fences, deep cuts through rocks and banked or drifted snow act as barriers and prevent the animals from leaving the roadway when vehicles approach. Trains cause the greatest loss of reindeer, accounting for up to 200 reindeer annually in Norway,

and in Sweden, up to 3,800 annually.

Mining of various kinds has, in both Norway and Sweden, resulted in substantial loss of reindeer pasture, and has created obstructions and disturbances which have led to changes in the traditional migration routes and modification of grazing habits (Fig. 2).

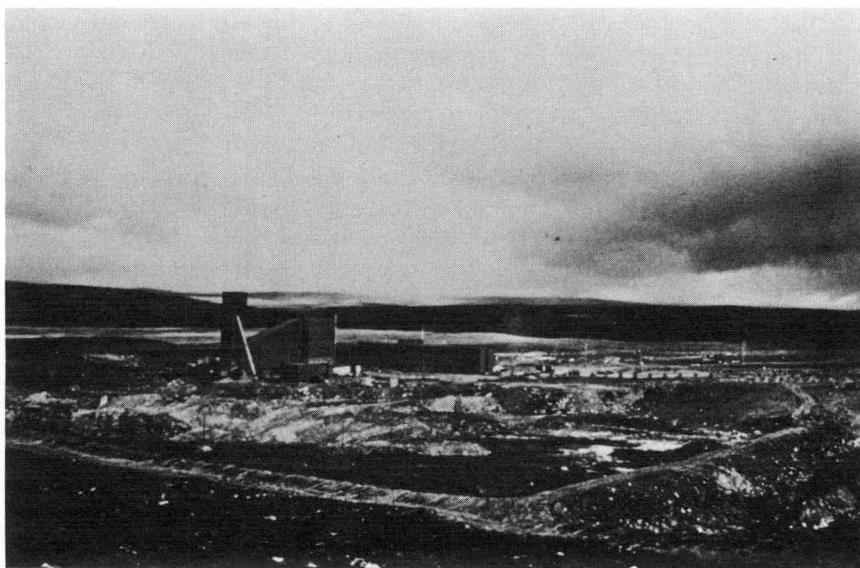


Fig. 2.—A copper mine in the tundra range lands of Finnmark. Such activities not only physically remove rangelands from use by reindeer but they also are a source of air pollution that may affect the growth of lichens in surrounding areas.

Air pollution in connection with factories has in some places damaged both forest and reindeer pasturage, although up to now this effect has been quite localized.

The purpose behind the regulation of watercourses can be to supply population centers or industry with water, but more often it is done in connection with the production of electric power. Construction of impoundments is done to increase the water level in an existing lake or to make an artificial lake. Either practice often results in the loss of some of the best pastures which are most commonly found along the watercourses. Migration routes and access to grazing grounds may also be obstructed. In reindeer husbandry the flood plain often found at the head of lakes is used for various work, as for example in the earmarking of calves. This headland is lost if the water level is increased.

In impoundments for hydroelectric purposes water is stored during summer when runoff is greatest and electric power consumption is low, and it is utilized during winter when consumption is high but precipitation as rain is limited. Such regulation can have a great influence on the ecology along the watercourses. Lowering rivers during the dry season leads to a decrease in the ground water level. This has an effect on vegetation growth and plant succession but its magnitude is still unknown. Rivers at one time acted as natural obstructions discouraging the reindeer from crossing from one range area to another. When rivers are dry during summer, when water is being stored, they no longer serve this function. Now, we get extended movement of the herds which is not desirable for a rational utilization of the total range land and requires more intensive efforts by the herders.

During the winter period of release of reservoir water a completely different situation exists. The temperature of the water released from the bottom of reservoirs is usually so

high that ice will not form on the rivers for some distance downstream from the power plants. Shelves of shore ice do form however, and these together with the open water create an effective obstruction for the movement of reindeer. The reservoirs themselves also interfere with traditional movements of reindeer in winter. Safe ice may be delayed in forming and this means that the moving of the reindeer between summer and winter ranges will, at the least, be delayed. During the period of release of water from the reservoirs, ice along the shore will often break and slant down to the floating ice, forming veritable death traps for the animals. In some cases shelves of ice remain attached along the stream banks and lake edges after the water level is lowered, making passage by reindeer impossible. On occasion when the water level in rivers or in narrow parts of lakes is lowered, the ice does not follow the water, but remains suspended in the air. There have been cases where groups of reindeer have walked out on such ice and perished when they broke through.

The climate along regulated watercourses will be more or less changed. The extent of this modification and its impact on the local ecology have been very little investigated. During summer, I believe the influence is not great. On the other hand, during the cold season, considerable fog forming over the open water may condense as ice on the adjacent forest and lichen pastures, making the forage unavailable or less palatable to the reindeer. Certain hydroelectric developments may involve the lowering of water levels in existing lakes when water is diverted to adjacent drainage systems. This practice also has ecological effects. If the water level in such lakes is lower than normal during the entire summer the ground water level around the lake will be correspondingly lowered. This may create drought conditions in the vegetation types surrounding the lake. Another consequence is that rivers and streams flowing into such lowered lakes erode new beds which may cause landslides. While the lowered water level in lakes and rivers may open new migratory routes for reindeer these are often less desirable than the old ones because of the problems created by the eroding stream beds.

Occasionally water is taken through pipelines from reservoirs high in the mountains down to hydroelectric power stations in the valleys. These pipelines may obstruct migration routes and also may prevent rational utilization of range lands (Fig. 3).



Fig. 3.— Pipelines in conjunction with a hydroelectric power development in Norway. Such structures have proved to be complete obstructions to the movement of reindeer.

The many large electric power lines constructed through reindeer pasture lands in recent years are a new obstruction and disturbance to reindeer. The disturbance starts when the workers are constructing the power lines. The effect on the reindeer, however, is greatest when the power lines cross calving areas or other critical range units. Tracked vehicles used to transport construction materials and personnel cause disturbance to the range lands. In summer they damage pasturage, particularly the lichen, which require many years to recover. Experience suggests that after some years reindeer become adapted to power lines, although it is still not clear how much the power lines influence the reindeer. Reindeer herders claim that it takes three to seven years for the reindeer to become accustomed to power lines. Among other things, the length of this period will depend on the tameness of the animals and their longevity, or length of time for population turnover. Power lines have a direct impact on range lands through the damage caused to vegetation in their construction and maintenance, but there is also an indirect loss of range values in a broader zone along the power lines until the reindeer become habituated to them. The unusual noise generated by the power lines seems to frighten the reindeer. The noise varies considerably with weather conditions and in a strong wind it can sound very much like thunder. It is also possible that frequencies beyond the range of the human ear may be involved. When herders are attempting to move a reindeer herd across a new power line which is generating noise we know that the reindeer react to the sound and are reluctant to pass under the lines. The reaction is much greater if the reindeer are moved by the herders than when the animals are roaming free.

In Finnmark we have experience from an electric power line in the Tana Valley. There the power line passes through a forest area which also includes the migration routes for several reindeer herds. The reindeer have to be moved through this area in the spring and again in the autumn. Although it has been 10 years since the power line was built, the herders have difficulty in moving the reindeer beneath the power line. The animals, on approaching the power line, stop and start to mill. In this case the herders cannot determine whether it is the power line itself or the right-of-way cleared of trees which alarms the reindeer.

Experience with wild reindeer in Norway suggests that when an electric power line crosses a traditional range land, the traditional movements are disrupted. In certain cases where power lines have been constructed through forest areas having deep snows in winter, the reindeer, after a number of years, have learned to move along the power line right-of-ways where wind packed snow will support them. This characteristic may be either of advantage or disadvantage to the herders depending upon the intended direction of movement of the herd.

Increasing tourism has also brought with it hotels, ski lifts and huts within the reindeer range land. This increases the traffic of people on foot, skis and snowmachines and they are often accompanied by dogs. This increased activity is injurious to reindeer, particularly at calving time. Also reindeer moving along trails are disturbed and dispersed, which leads to an increased loss of animals.

The consequences of the impact of accelerated northern development on reindeer in Scandinavia obviously vary with the activity involved. Lost range land from water impoundments, road construction, etc. cannot be compensated for. We can, however, do something to lessen the impact from obstructions and disturbances by increased work on the part of the herders and increased use of capital in building extensive fences, local working corrals, bridges and huts for the herders. This requires a greater amount of working capital and leads to higher working expenses and less income for the owners of the reindeer. With wild reindeer the amelioration of ecosystem disturbances cannot be accomplished through application of money and manpower. The whole complex of problems seems to be

too little investigated. We trust too much on belief and too little on knowledge. With the rapidly increasing development that we have today in the northern areas, it is urgent to provide more knowledge about the ecological consequences of such development. Inasmuch as many modifications of nature caused by this development are irreversible their impact on the ecology of reindeer are cumulative and will continue to be so into the future.

CANADIAN CARIBOU AND NORTHERN DEVELOPMENT

R. D. Jakimchuk
Renewable Resources Consulting Service Ltd.
Edmonton, Canada

In the spirit of a panel discussion I hope in my remarks to initiate discussion. I have a very short time and I hope in that period I will be able to raise the hackles of my Canadian colleagues with some of the things I say. I admit to shamelessly plagiarizing other people's ideas and publications for some of my points as well as making a few of my own contributions.

First, I would like to address myself to the question of Canadian caribou and northern development, prior to getting into the general area of the potential impact of industrial development on caribou. Dr. Klein outlined very well some of the ramifications of developments in the circumpolar region. We have had several years of development in Canada, and in fact these have had their impact on caribou populations. We are now experiencing an era of burgeoning development, one that is accompanied by new technology. Developments such as roads, highways and pipelines were mentioned earlier. These will not only bring technology but will also bring people to the Canadian north in even greater numbers than we have experienced up to now.

In one respect we have a unique problem in Canada. We have mainland caribou populations that tend to gather our attention because of their large numbers, and because they have been intensively studied. But perhaps equally important are the insular populations *Rangifer tarandus pearyi*, probably the most unique subspecies of the genus in the world. This caribou is one we know very little about, and yet it is in the midst of a great flourish of human activity in the high arctic islands where the ecosystem is even less productive than at this latitude. I believe Dr. MacPherson in a paper a year ago quoted that the carrying capacity for a Peary caribou is one per 100 square miles as opposed to one caribou or reindeer per square mile in the MacKenzie grazing reserve. So with this background I would like to get to what I consider to be some key points that will be open to further discussion.

There are habitat considerations. At the present time I consider Canadian mainland caribou habitat to be beneath carrying capacity and I am sure my colleagues will agree with me. We have seen in the literature that lichens are not absolutely vital to the maintenance of caribou populations, so I don't really think that a key point is habitat destruction with respect to mainland populations. I think the reverse is true with the Peary caribou, which as the dominant herbivore on some high arctic islands, occupies a very exclusive niche — little rich pockets of greenery that other people here know much better than I do. So in habitat considerations, I would say that in Canada our main concern should be directed towards the Peary caribou.

In considering potential impact of development on caribou, I think one has to consider the vulnerable periods — the most vulnerable periods in the life cycle of the species. As I said previously, we don't know too much about Peary's caribou, but there is considerable literature on the other subspecies, both in Canada and the United States as well as in

Eurasia. I don't have time to go through all the arguments so I will just have to raise the point and leave the arguments for later. I consider the vulnerable period to be the spring migration because of the stress factors; i.e., stress on cows at a time when their nutritional requirements are high and when stress might predispose calf mortality. I consider recruitment and survivorship to be key issues in the maintenance of caribou populations. The spring migration, calving and post calving periods are the most vital periods of the year: it is in these areas where one might find trigger factors that could very dramatically affect a population, as opposed to other factors such as human disturbance in general which might just cause minor changes over a period of time. I consider the question of synchrony to be very important — not only the obvious need to return to a traditional calving ground, but synchrony during the period of the rut. We have just had a brief indication in the last paper today that there might be a problem if, for example, a highway or a development of some kind could disrupt breeding at a key time of the year. The obvious synchrony of calving is a reflection of some kind of a synchrony at rut and I don't think we know very much about this factor. So there is a potential impact there of man's development if these behavioral patterns are altered.

I think it is quite apparent now from what I have said that I believe the key issue is behavior. I think the key issue is whether caribou behavior is traditional or whether it is random or nomadic. This knowledge will determine the significance of environmental interactions and the reaction of caribou to alterations of their environment. I have already indicated the key impacts in terms of the annual cycle. In Canada, the Porcupine herd is presently subject to the impact of accelerated northern development. We have a highway under construction through their winter range. This highway bisects their migration routes and it also probably falls within their rutting range as well. Of the five major herds in Canada this is I think the most susceptible population at this time. I have already mentioned the importance of Peary's caribou.

Now, I have emphasized a few of the problems, or perhaps raised a few questions. I feel I should close by giving suggestions as to what I think some remedial measures might be; perhaps it is a prognosis for the future. I think that quantitative research such as is being carried out by Ken Child is required. Research such as my firm is carrying out on the impact of noise levels, the significance of which was referred to by Mr. Villmo, is required. We have to have quantitative data if we are going to deal with these questions. I think developments such as highways, pipelines, and so on, and the influx of people are going to create man-caribou problems, and perhaps problems of excessive exploitation. Now, the obvious solution to that is enforcement; increased enforcement capabilities for management of the resource. Land use planning is something that should become more than a lip word in the development scheme. There are things that can be done to avoid conflict. For example we shouldn't construct facilities in the middle of calving grounds during the calving period. There is the question of timing and spacing of certain activities, The timing of overflights over caribou during vulnerable times. I think now of the cow-calf relationship. I think it is important that these relationships not be disrupted. If they are, over a period of time drastic effects could take place on populations through what I would call trigger effects.

In terms of habitat, we have the question of fire for example. But I don't think anyone has demonstrated that fire has ever decimated a caribou population so we won't worry about that. Now, getting onto a prognosis, I have almost decided that maybe I shouldn't make one. But let me just say this — I do believe we have a considerable amount of information that we can apply and I think we should apply it. I personally think with public awareness at current levels, with the capabilities of government, industry and the academic community to come up with information, I don't foresee catastrophe for Canadian caribou populations. However, in all honesty, with increasing northern development I see a gradual

attrition over a period of time that will probably reveal itself in the start of the next century. Attrition of our caribou and our capabilities to maintain them at current levels.

ALASKAN PROBLEMS AND PROSPECTS

James E. Hemming
U. S. Bureau of Land Management
Anchorage, Alaska

I plan to take a slightly different approach in discussing Alaskan problems and prospects for caribou and reindeer. We should first take a brief look at the history of reindeer and caribou in Alaska in order to better understand the problems of the future. Alaska has a land area of about 586,400 square miles, including about 478,000 square miles of habitat that is suitable for caribou and reindeer. There are 13 caribou herds in Alaska, totaling over 600,000 animals, and approximately 31,000 reindeer that are restricted pretty much to the west coast and offshore islands in Alaska.

During the last century, caribou ranged from the highlands of interior Alaska to the north and west coast, including the Alaska and Kenai Peninsulas. However, by the late 1800's, many ranges in northwestern Alaska had been abandoned, apparently due to a natural decline in caribou numbers. The loss of animals from coastal areas worked hardship on the native people of the area. As a result, the United States Government imported about 1,200 reindeer from Siberia between 1892 and 1902. Reindeer were established at various coastal locations between Barter Island and the Alaska Peninsula and on several offshore islands in the Bering Sea. The government employed Siberian Eskimos and Laplanders to teach Alaska's Natives techniques of reindeer husbandry. However, it was difficult for many of the Native people to make a successful transition from subsistence hunting to herding. By the mid-1930's, there were over 600,000 reindeer in Alaska. Both Natives and whites alike struggled to have limitless numbers of animals, and they succeeded. By the late 1930's, reindeer ranges had been severely depleted, and for this and other reasons the industry collapsed.

In 1937, the U. S. Congress passed legislation that restricted reindeer ownership in Alaska to aboriginal people. A few years later, Mr. Sidney Rood, who was then general reindeer supervisor for the government reindeer service in Nome, referred to the collapse of the reindeer industry and stated: "Company 'management' became nothing more than rounding up, once or twice per year, as many wild, scattered reindeer as laborers could locate." Methods of breaking sled deer, constant herding, training of herding dogs and selective breeding had been largely forgotten. For the past 40 years, reindeer herding has continued predominantly on a subsistence basis.

The historical record strongly suggests that expansion now for commercial production would require sweeping changes in management practices. Problems of slaughter, marketing and transportation that have plagued Alaska for some time would have to be overcome. I believe that leasing of additional state or federal lands for reindeer production at this time, within existing wild caribou ranges, would be very difficult to justify. Unless reindeer ownership laws are modified and modern techniques of animal husbandry are adopted, there is really little hope for an economically viable reindeer industry in Alaska.

Wild caribou populations in Alaska have fluctuated widely over the last century. Individual herds have undergone natural patterns of increase, decrease and shifting that were not necessarily synchronous between populations. The arrival of whalers and miners in the late 1800's resulted in a very large demand for meat and skins. Native people were able to obtain firearms for the first time. Caribou were soon overexploited in some areas, and

totally extirpated in a few places like the Kenai Peninsula and Nunivak Island, but the total impact of hunting did not appear to alter significantly the total caribou population in Alaska. It may, however, have caused some herds to shift ranges due to continual disturbance. For many years there was no control over hunting. More recently, government regulations were adopted to prevent overexploitation. Management plans, based on research that has been conducted for about the last 22 years in Alaska, are being developed that can be implemented whenever hunting pressures become great enough to control caribou numbers. At the present time, annual harvests from most herds are below the annual increment.

There has been a steady rise in Alaska's human population since World War II. This has resulted in a sharp increase in recreational hunting. Between 1965 and 1970, hunting license sales increased from 50,000 to 60,000. Conversely, subsistence hunting activity by Alaskan Natives has begun to decrease. From 1959 to 1969, the number of working dog teams decreased by over 50 per cent as villagers replaced dogs with snowmachines. As a result, Eskimo and Indian hunters no longer needed to kill large numbers of caribou for dog food, and the range and mobility of snowmachines made the task of finding enough animals to feed a family much easier. The net result was an estimated reduction in the annual subsistence caribou harvest of 60 per cent. Therefore, the large caribou herds of northern Alaska are probably impacted less by hunting today than at any other time in recorded history.

The speakers that preceded me covered most of the major areas of concern about modification of caribou habitat. However, I feel it is important to emphasize that wildlife habitat is either retained or taken out of production. There is no middle ground. When animals are displaced from their habitat, they die. I firmly believe that the key to maintaining a viable caribou population in Alaska is to retain very large areas of suitable habitat that allow unrestricted movement. Less than 2 per cent of the land in Alaska today is devoted to agriculture, mining, industry and residential use, and thus far, caribou have not been greatly affected by existing disturbances. However, future growth and development will undoubtedly alter the status of caribou because under these pressures it is difficult to retain large land areas without modification. The greatest potentials for inhibiting caribou populations are man-made barriers that may restrict seasonal movements, such as roads, railroads, surface pipelines and fences. Attendant development, such as mining, oil exploration and development, grazing of domestic livestock and settlement will reduce carrying capacity or eliminate habitat.

The ground transportation system in Alaska is currently limited to two railroads and approximately 6,700 miles of roadway, including residential streets. Therefore, travel over much of the State is still limited to airplanes, boats or snowmachines. Proposed transportation projects include a pipeline road which would extend from the Yukon River to the Prudhoe Bay oilfields, a railroad or road to the copper mines at Bornite in the Kobuk Valley and a road from Anchorage to Bristol Bay. Long range plans projected by the Alaska Department of Highways would, whenever economically feasible, connect to the highway system all towns with a population of 1,000 or over. Travel on existing highways and railroad systems is relatively light, especially during migration periods, and so far has not caused measurable effects on caribou movement. However, as we heard earlier, an expanding human population will undoubtedly result in increased traffic on both roads and railroads, and we may one day reach a time when caribou movements will be affected by traffic on these structures.

The giant oil discovery on the Arctic Coast, estimated to exceed 10 billion barrels of oil, brings with it a number of potentials for problems in the future. There are many other areas of the state that also have good potential for oil and gas. These include the eastern and

western Brooks Range, the Yukon-Kuskokwim Delta, the Alaska Peninsula, scattered locations in interior Alaska, plus offshore areas in the Gulf of Alaska, the Bering Sea, the Chuckchi Sea and the Beaufort Sea. Oil exploration in the 1940's and 1960's resulted in many examples of habitat degradation. Surface vehicle use on permafrost areas caused the greatest problem. However, state and federal regulations were adopted in 1969 to control the types of surface vehicles employed and the methods and times of their use. Proper enforcement of these regulations should eliminate this problem in the future. But, even with good regulations, the development of oil or gas takes habitat out of production whenever access roads, drilling pads, airfields and camps are constructed. The land area involved in such activities today is perhaps insignificant, but, as I mentioned earlier, the potentials for oil development in other parts of the state are great, and we will face a gradual loss of caribou habitat in the future.

Perhaps the greatest immediate threat from gas and oil development is the potential for restricting movements. A 48 inch diameter pipeline has been proposed to transport oil from a complex of feeder lines on the Arctic Coast to the city of Valdez on the south coast. This line would traverse the known ranges of three caribou herds, the Nelchina herd of southcentral Alaska and the Arctic and Porcupine herds of northern Alaska. Currently, studies are underway to evaluate the behavioral responses of caribou and reindeer to this type of structure, and Mr. Child will elaborate on that project shortly.

Ultimately, and perhaps very soon, human population growth will be stimulated by oil associated activities. It will become increasingly difficult for resource managers to prevent alteration of large tracts of land. Hunting pressures can also be expected to increase. Hunting in itself, provided there are suitable regulations and enforcement, should not be a problem. However, the impact of large numbers of hunters with various types of all-terrain vehicles moving into remote areas where no road systems now exist can damage caribou habitat, particularly when vehicles are used during the snow-free period.

Mining is presently at a low level in the State and employs only about 700 people. There are a number of known mineral deposits in Alaska, and certainly potentials for development are good, but the costs of transportation and development are very high and have precluded development of most known deposits. Agriculture in Alaska has remained almost undeveloped. The livestock industry (excluding reindeer) is limited to southcentral and southwestern Alaska, where slightly over 30,000 cattle, sheep and horses occur on 31 ranches. High operating costs in Alaska make it difficult for ranchers and farmers to compete with produce shipped to Alaska from the continental United States. Except in isolated cases, present agricultural practices do not conflict with caribou.

What are the potentials for the future? At the present time, approximately 47 million acres of land have been set aside for parks, wildlife refuges and national forests. However, only a relatively small portion of this land includes caribou habitat. An additional 80 million acres is scheduled for similar classification in the near future, and hopefully these lands will include large portions of caribou habitat.

Land management and planning in Alaska became more complicated when Congress passed the Alaska Native Claims Settlement Act in December 1971. It granted 40 million acres of land to Alaska Natives. The result will be an infusion of tracts of private land into existing undeveloped public domain. This will complicate land planning efforts and may significantly alter caribou habitat in the future. Biologists will also find it increasingly difficult to implement functional management plans on lands under multiple ownership. Fortunately, Alaska's caribou population has thus far been largely free from the overexploitation and destruction of habitat that has characterized other parts of the world. We still retain the prerogatives for planning and wise use of the caribou resource, and hopefully the current trend toward environmental awareness will offer some assurance for

the future.

A SPECIFIC PROBLEM: THE REACTION OF REINDEER AND CARIBOU TO PIPELINES

Kenneth Child
Alaska Cooperative Wildlife Research Unit
Fairbanks, Alaska

In the summer of 1971, Alyeska Pipeline Service Company, BP Alaska Inc., and the U. S. Bureau of Sport Fisheries and Wildlife co-sponsored studies of the behavioral responses of barren ground caribou to pipeline structures and man's activities on the North Slope of Alaska. Also, the three sponsors jointly planned and directed the construction of two pipeline simulations on the oilfield at Prudhoe Bay. Alyeska Company created a 10,200 foot (3,109 m) optical barrier with 4 foot (1.2 m) snowfencing and burlap sacking as a mock-up of the proposed 48-inch (1.2 m) TransAlaska pipeline. At six locations along the length of the pipeline experimental passage provisions, two gravel ramps and four underpasses were constructed to act as access points for caribou to reach the other side (Fig. 1). The fencing

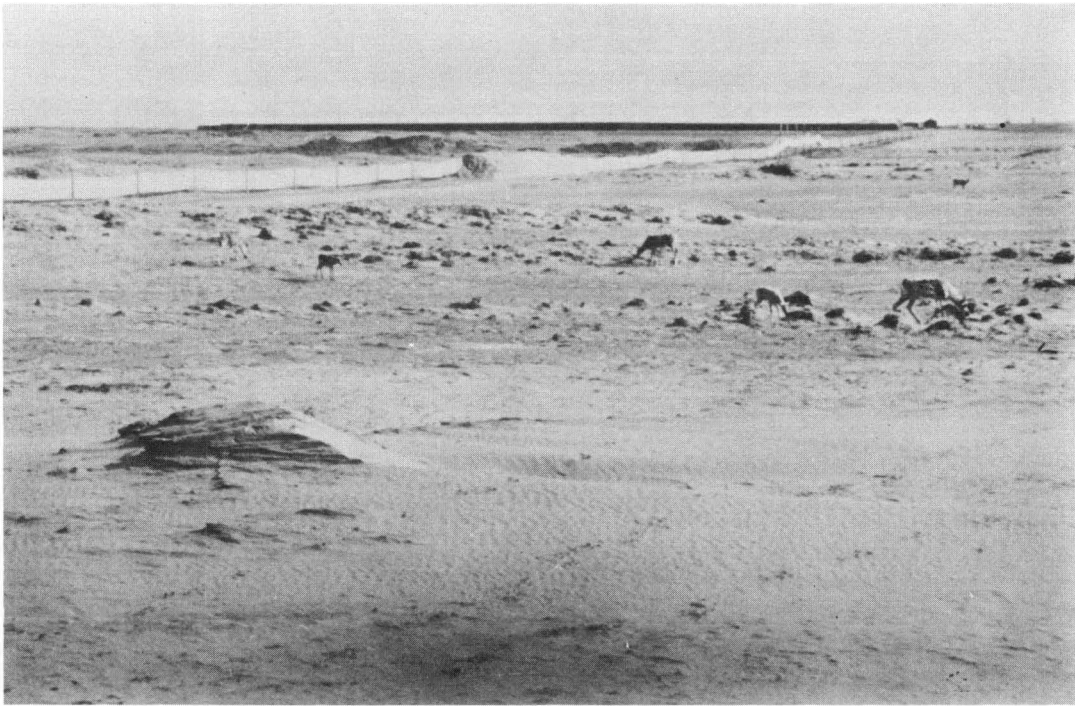


Fig. 1.—A small group of caribou feed on *Artemisia borealis* adjacent to Alyeska's simulated 48 inch pipeline. A ramp and underpass structure constructed to facilitate caribou movements across the 'pipeline' are shown.

was raised two feet (0.6 m) above ground for its total length which is the expected minimum ground clearance of the TransAlaska pipeline when elevated above ground. The

two ramps were 75 (21 m) and 100 feet (31 m) in width, 8 feet (2.4 m) in height at the verticals, and both were similarly constructed with 2:1 side slopes. Three of the four underpasses, on the other hand, were 100 feet (31 m) wide and elevated approximately 8 feet (2.4 m) above ground. The fourth underpass was 150 feet (46 m) in width but elevated only 4 feet (1.2 m) above ground. At each underpass, two parallel spans of snowfencing and burlap sacking were raised and anchored to piling supports in order to construct as best as possible a three dimensional pipeline-like structure (Fig. 1).

In 1972, the design of the mock-up was altered considerably as an attempt to increase the use of the crossing facilities by caribou. Both gravel ramps were remodelled. Vertical heights were increased to 11 feet (3.4 m), side slopes extended radially (360°) from the axis of the ramps and slope ratios were increased to 5:1. Two of the underpasses were completely redesigned as well because the wind-induced movements of the burlap were suspected to have had a deterrent effect on those animals that approached the structure in 1971 but did not cross. Therefore instead of using the original materials to construct these underpasses 10 joints of 34-inch (0.9 m) galvanized culverting were spot-welded together, raised and anchored 8 feet (2.4 m) above ground on pilings for a total length of 200 feet (61 m) (Fig. 2).

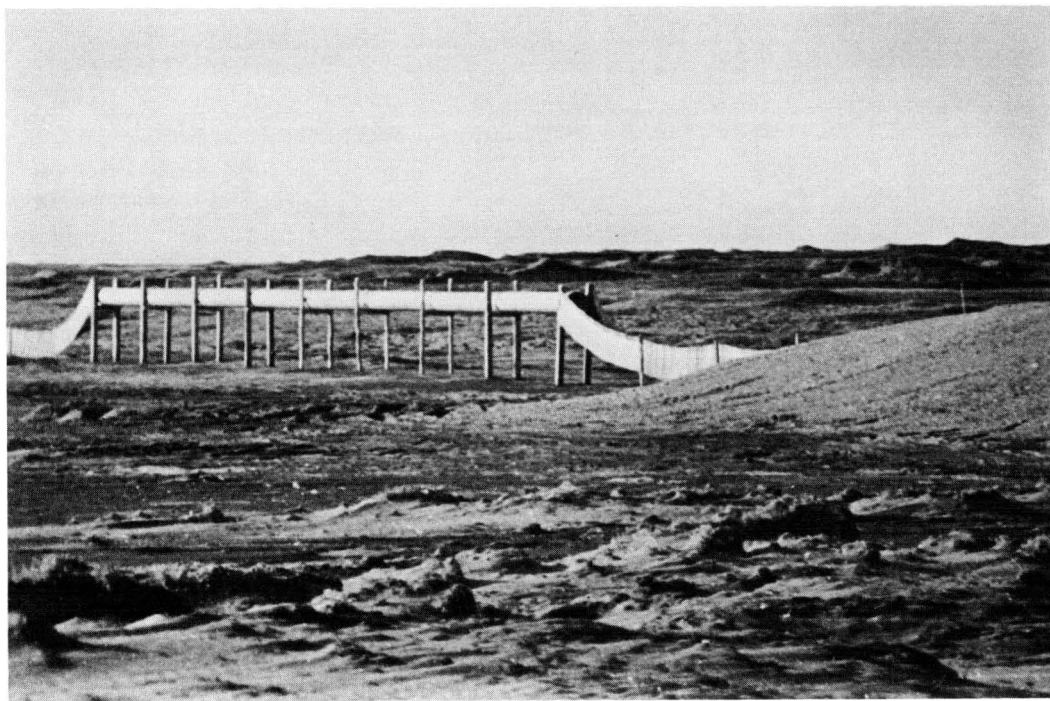


Fig. 2.—Oblique view of modified ramp and underpass crossing structures at Alyeska's simulated pipeline. These designs were expected to increase the efficiency of the structures as crossings for caribou.

The field objectives were similar for the two summer seasons and primarily questioned

how individual animals (by age and sex) and groups of caribou (by size and composition) reacted on initial and subsequent encounters with these terrain features. With both ramps and two underpasses redesigned in 1972, crossing success of caribou over the pipeline was expected to increase substantially over the observed success in 1971.

As Mr. Hemming has previously mentioned, the intricate and dichotomous network of feeder pipelines, expected to total 375 miles (604 km) at full production of the oilfield, will pose a serious problem to the free movement of caribou on their summer range. Because of this potential problem, BP Alaska Inc., constructed a simulated feeder pipeline in 1971 to permit an on-site evaluation of the design criteria necessary in these systems to facilitate the passage of migratory wildlife. The experimental feeder pipeline was approximately 7,800 feet (1.25 km) in length. Except for a 600 foot (183 m) section of pipe that was raised from 3 (0.9 m) to 8 feet (2.4 m) above ground on various types of piling supports, the simulation was elevated 30 inches (0.7 m) above ground for its total length on water-filled oil drums (Fig. 3). Within the shorter section of the pipeline, an expansion loop was constructed that

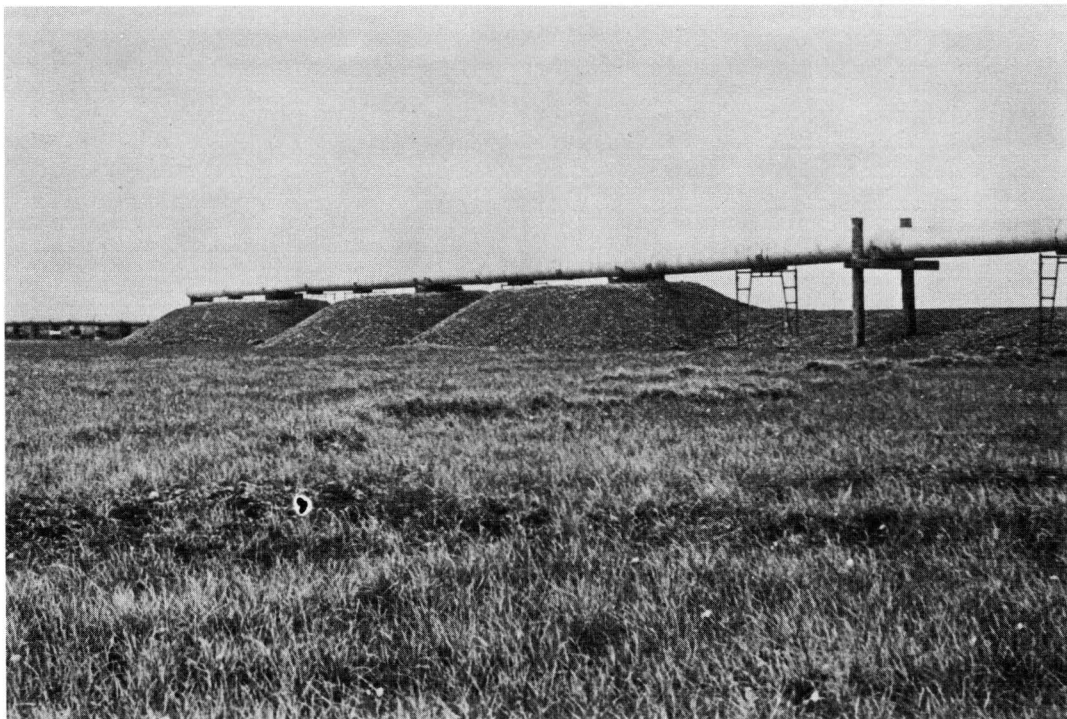


Fig. 3.—Looking southwards along BP Alaska's feeder pipeline mock-up. Galvanized culverting was suspended on various types of piling supports to provide variation in ground clearances believed adequate to permit easy passage of caribou beneath the overhead obstacle.

provided a maximum clearance of 8 feet (2.4 m) beneath the obstacle which was believed adequate to permit easy passage of caribou from either direction (Fig. 4). At the northern end of the simulation, a cable-drum barrier was erected in order to intercept caribou

movements and channel their direction towards the simulation (Fig. 5).

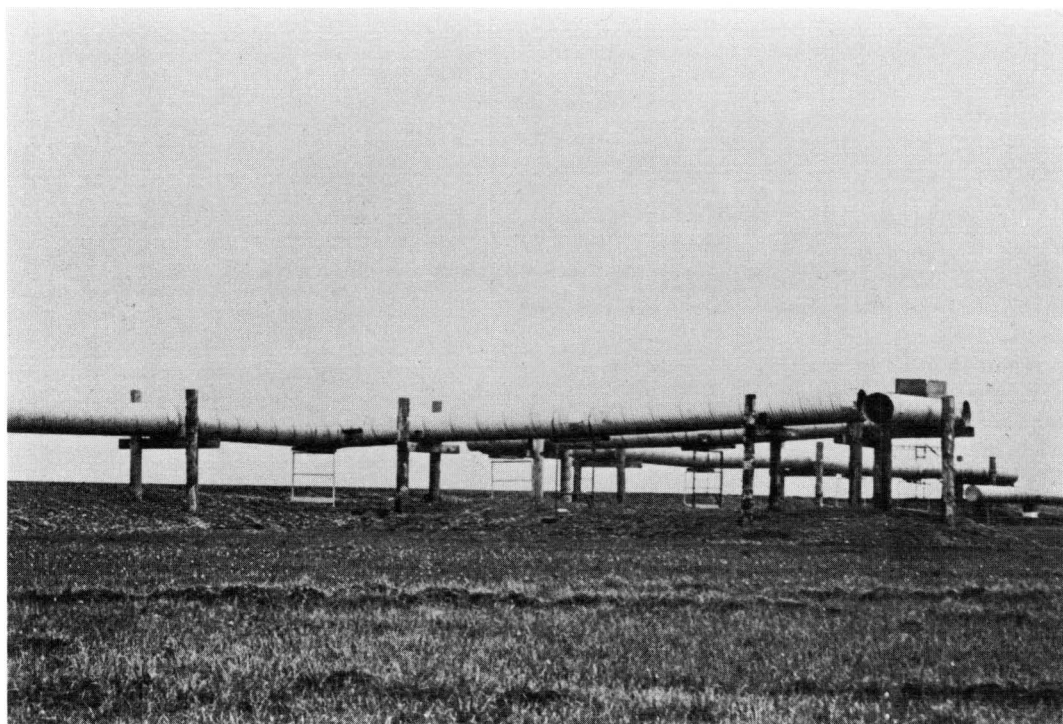


Fig. 4.—The expansion loop constructed within the simulation provided a maximum clearance of 8 feet above the tundra. The observation tower can be seen above the loop on the service road.

In 1972, this feeder pipeline mock-up was also modified. In anticipation that it will be necessary to operate multiple feeder lines to transport the large volumes of oil from the well sites to the gathering centers, a design which might in fact increase the possible barrier effect of pipelines on caribou movements, BP Alaska constructed a 200 foot (61 m) section of similar design in the original feeder-line simulation. The simulation was also lengthened and two low profile ramps with 10:1 slopes were constructed over the pipeline about 2,000 feet (610 m) from each other. As another attempt to better the efficiency of these ramps to facilitate caribou movements, four cable leads were positioned at each ramp, one pair on each side of the ramps, with each lead being set at 45° to the axis of the roadbed (Fig. 6). With this experimental set-up at each ramp, it was hoped that caribou coursing the simulation could be easily intercepted and led by the offsets over the ramps to either side of the pipeline.

One of the main interests in this study was to determine whether or not caribou would adapt to the presence of these pipeline structures and become increasingly successful in their use of the crossing facilities. To gain an insight into the relationship of crossing success of caribou over pipelines and their previous learning experiences with the pipelines, an aerial dyeing operation was conducted on the oilfield in the spring of 1972. A Supercub aircraft



Fig. 5.—Three caribou run from the vicinity of BP Alaska's feeder pipeline. The cable-drum barrier constructed to channel caribou against the simulation can be seen on the horizon.

equipped with a modified Sorensen tank, similar to that used by biologists of the Canadian Wildlife Service for Dall sheep studies in the Yukon Territory of Canada, was used to spray caribou. Three non-toxic colored fabric dyes (red, green and yellow) were applied to nursery bands of caribou within a 35 mile (56 km) radius of Prudhoe Bay. During the course of the summer, it was possible by sighting the marked animals to (a) determine the direction and origin of herd movements, (b) follow individual animals and groups of caribou as they traversed the oilfield and encountered various topographic features and, more importantly, (c) study changes, if any, in the crossing success of animals across pipelines as they repeatedly encountered the simulations.

Currently, a second study is being conducted to supplement the Prudhoe Bay caribou investigations. This study concerns the reaction of semi-domesticated reindeer to an experimental large-diameter elevated pipeline on the Seward Peninsula of Alaska. A 32-inch (0.8 m) pipeline was constructed by a team of workers from the Alaska Department of Fish and Game, the U. S. Bureau of Sport Fisheries and Wildlife and the U. S. Bureau of Land Management across the Penny River valley. Only one gravel ramp (4:1 side slope) and a 200 foot (61 m) elevated section serve as the experimental crossing facilities for the reindeer (Fig. 7). At both ends of the pipeline, wing fences have been constructed to reduce any likelihood of escape of reindeer once the deer have been moved against the simulation.

Whereas the Prudhoe study concerned the behavioral responses of caribou to pipeline structures at post-calving time, the Seward study, by lending itself to some field control, permits some ease of gaining a better insight into the seasonal response differences of *Rangifer* to man-made obstructions.

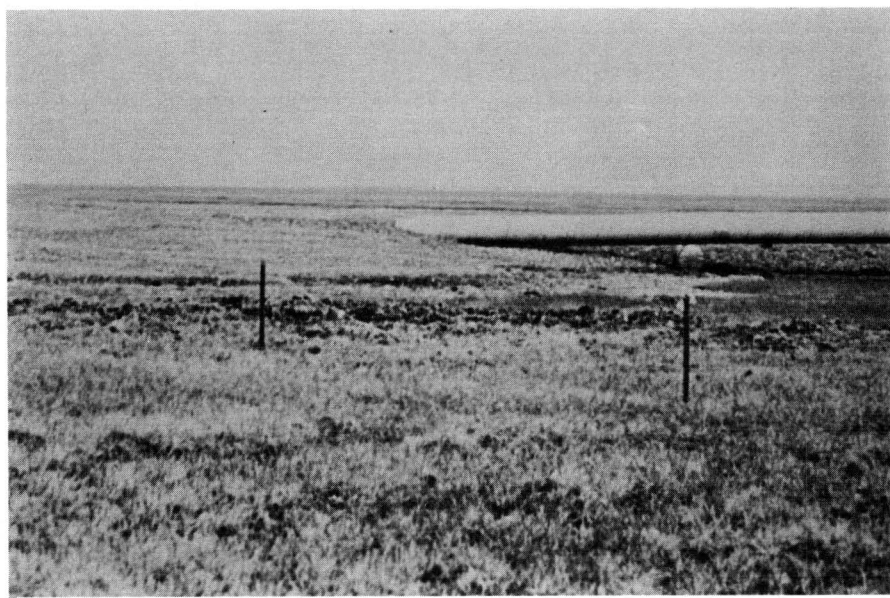


Fig. 6.—A low profile ramp constructed within BP Alaska's pipeline. An experimental cable offset is shown (Photo by C. A. Smith).



Fig. 7.—A herd of reindeer mill in close proximity to a simulated pipeline in the Penny River valley, Seward Peninsula, Alaska. The elevated section and gravel ramp constructed as experimental crossings can be seen behind the herd (Photo by D. R. Klein).

RESPONSE FROM THE DISCUSSANTS

Eldar Gaare, Norwegian State Game Research Institute, Trondheim, Norway:

I thought perhaps I could mention two different things which have not been drawn attention to yet. One is a positive factor which in Norway results from changing patterns of use of agricultural areas in our mountains. We have traditionally had the so-called seter system of mountain farms to which the farmers take their cattle to feed during the summer months. Furthermore, in the past they harvested large amounts of lichens from the surrounding areas as supplementary feed for the cattle during the winter period. Most of that has stopped now, with the greatest decrease taking place after the second World War. We must conclude that possibilities for reindeer to feed in the same areas have increased. This example will perhaps help to clarify the picture that there are not only negative aspects with modern development.

The second thing I would like to mention is the pollution of our rivers in the southern part of Norway derived from sulphur dioxide in atmospheric pollution. This has caused a very extensive death of our fish through increases in the acidity of the waters. In several rivers we do not find any of the fishes we had earlier. There is also concern that the sulfur dioxide fallout may influence the growth of lichens. Lichens are perhaps the most sensitive to pollution of the different types of terrestrial plants and we have a complete lichen death in the center of most industrial cities. Whether this really means anything at the present level of atmospheric pollution in Norway we do not know, and unfortunately no effort is being made to find out. The work which has been done in Canada by Roe and LeBlanc some few years ago indicates that the chlorophyll is decomposed in lichens which are subjected to an atmosphere of 0.25 ppm. Now that is a fairly high level, but before the death of lichens takes place we might expect that their possibilities for growth are reduced. The significance of such an effect would be great because lichens are a very important food for reindeer in Norway.

Bengt Westerling, College of Veterinary Medicine, Helsinki, Finland:

We have heard the Scandinavian point of view on reindeer herding and the effect of developments on reindeer. We all know that there is a very big difference between caribou and domestic reindeer but I notice here when I listen carefully that there are also differences between the ways of reindeer herding within Scandinavia, into which I now count Finland. We have heard very much about the effect of obstructions in the terrain of reindeer, and as a matter of fact, northern Finland is full of obstructions. They have been built there by the reindeer herders to keep the reindeer from migrating too much. Reindeer herding has developed in Finland as a family based economical system in which every family had its own land on which its reindeer were herded. They were not supposed to allow the reindeer to pass over the boundaries of the family units in the past even if there were no fences. Now that the people do not herd the animals closely they have to build fences instead. We have perhaps 50 different reindeer herders associations and each has its own grazing lands. In order to keep the reindeer separate it is necessary to build fences where natural terrain features to act as barriers are lacking. In this respect, Finnish Lapland is not the same as Norway and northern Sweden, where the terrain is more broken up. Our reindeer do not have a well developed habit of migrating, perhaps because they do not have to do it. Finnish Lapland is not an arctic area. It is a forest zone, a taiga zone with mostly lichen, heaths and some alpine sites on the higher levels in between. The reindeer do not have to move far from winter to summer pastures, and vice versa. In this respect the fences to restrict movements

of reindeer are not a bad thing. In fact they are urgently needed in many parts of our reindeer breeding area.

Probably the most important factor of northern development affecting reindeer is tourism. In the best grazing areas of central Lapland we have a rather large alpine vegetational zone which is also a very good skiing area and now there are plans for building a winter resort center there for about 10,000 people. That project will take away the winter grazing lands from about the same numbers of reindeer, which would be about 5 per cent of the country's reindeer. And not even the reindeer herders have yet made up their minds whether they would like to have this center there or not. Some of them want to keep things as they are; some think that they will obtain work in conjunction with the new facilities which would lead to a higher standard of living. Because northern Finland is not an industrialized area and will not be for a very long time yet, the problem of unemployment is severe. Quite a lot of people have moved out of the area, most of them into Sweden, but not very many of the reindeer owners or reindeer herders have left.

Amos Lane, Point Hope, Alaska:

Ladies and Gentleman, it is a pleasure to be here. As a matter of fact it is the first time I have been in a big meeting in my life and I have met a lot of good people here. Through tonight's meeting, as I looked through the slides that were shown, I was very concerned about what this pipeline can do to our caribou. A surface pipeline will present many problems, and as you can see through all the pictures not any caribou were crossing these passages. There should be a better method of putting up the pipeline if it has to be built.

I was born in the native village of Point Hope and have made a living by hunting and depending on caribou. All of these disturbances that are coming to northern Alaska will be problems to our wildlife. Finally, through all these meetings I could not understand all the big words that are used by these doctors; I have not been to school like these people. I did not go past seventh grade. I only know a few of those words, but if I have to start using long words it will be in Eskimo, which has longer words than yours.

(Editor's note: The discussion was here opened to participation from the audience. Due to a malfunction in the recording system the questions and comments from the audience were poorly recorded. It has therefore been necessary in some cases to paraphrase contributions from the audience to best fit the interpretations that could be made from the tapes.)

George Scotter, Canada: Mr. Child did a fine job of describing the experimental design of the simulated pipeline studies, but what we are all interested in is the results. Can you give us some of the results?

David Klein: I am not sure whether I should offer the opportunity to Ken Child to respond to that question or not. I see by his head nod, however, that he would leave me in the awkward position of responding to you.

In our agreement with the oil and pipeline companies there is an understanding that no parties will release to the public information of an inconclusive nature; that is, release of information before the field data have been analyzed. Results of last summer's study (1971) were presented by Mr. Child at the Ungulate Behavior Congress in Calgary in November, 1971; however, this summer's observations have not as yet been completely analyzed and they undoubtedly will alter the tentative conclusions from last summer's work. In general, I think Mr. Lane's observation was a rather perceptive one, we wondered whether anyone would notice the absence of caribou actually crossing the pipeline in the slides that were

shown. That was perhaps deliberate because we did not want people to be drawing false conclusions. Actually, there have been crossings of the simulated pipeline by caribou and in other cases animals have been turned back or refused to cross. In 1971, as Mr. Child can verify, the majority of the caribou encountering the pipeline did not cross. One of the objectives in the modifications of the crossing facilities this year was to try to allow for a greater proportion of the animals to move across the pipeline.

Paul Frelief, California: Are there any results from the study of reindeer at Nome, or is that part of the Alyeska sponsored project?

Kenneth Child: Now I can speak. At the Nome site we have been successful in having a few reindeer use the pipeline crossing facilities. In late April we had one run of 221 animals and another group of 58. These were unsuccessful in getting over the facility. We left these animals in the presence of the pipeline for three days. Each morning we would move them from where they had wandered (usually about 500 meters from the pipeline) back to the pipe. We then watched their activity throughout the day. The closest they would approach to the pipe was about 10 meters. On the final day, after they were sufficiently habituated to the site, we attempted to force, or drive, them over or under the pipeline. We were unsuccessful, as the reindeer apparently had other plans. We did have some crossings of the pipeline, however, in our absence. The interesting thing was that they crossed the pipe where it was almost completely buried by the snow and there was the formation of a small snow ramp. Only about 10 cm of the pipe was exposed above the snow.

In May, Mr. Hemming, Dr. Lent and I went again to Nome where we were able to observe the reactions of a herd of 165 reindeer, including cows, calves and yearlings. These were herded close to the pipe as in the previous trials and they would approach only to about 100 meters and then move parallel to the pipe. When they moved past the ramp and elevated section and attempted to go into the dense willows and waterlogged snow drifts along the Penney River, which are characteristically avoided at this time of year, we tried to herd them back and over the gravel ramp. The animals refused to cross the pipe and finally reversed their direction and crossed the Penney River to the southwest. Our own observations then, are that the reindeer will move parallel to the pipeline rather than crossing it and will choose difficult terrain conditions rather than use the facilities designed to give them access across the pipe. In our absence, however, apparently a few reindeer did cross the pipe. Mr. Johnson Stalker, the herder who was assisting us, reported seeing from a distance reindeer cross over and under the pipe under conditions of extreme insect harassment. I later examined the ground both over the ramp and under the underpass and I found the tracks of 15 reindeer and one wolf that had used the ramp to cross the pipe from north to south and only one track through the underpass.

Richard Bishop, Alaska: One would expect considerable difference in the reaction of caribou to obstructions depending upon whether they were in migration, feeding and so forth. What was the situation with the caribou at Prudhoe Bay?

Kenneth Child: At Prudhoe Bay there appeared to be two types of movements through the area. One is unidirectional and included a concentrated movement of 2,000 caribou from east to west. Superimposed on this was an oscillation of animals from the southwest to the northeast and return as the general movement to the west occurred. This oscillation is due to changes in wind intensity and direction. When the winds die down insect harassment becomes severe and the animals move to the coast for relief; with increasing winds and few insects they again drift to the southwest. So animals in the Prudhoe Bay area, because of

this oscillatory movement, are going to have a lot of encounters with pipelines. While it is not a migratory movement in the conventional sense, I want to emphasize that it is also not a random movement. It is predictable in relation to weather conditions and insects.

Unidentified member of audience: If this research project at Prudhoe Bay fails to provide the answers to how to get caribou across an elevated pipeline, do you have plans to continue the studies?

David Klein: We have a contract to undertake the current study. Whether or not we continue the studies beyond the term of this contract is dependent upon the supporting agencies. Therefore I think that your question should be directed to a spokesman for the oil industry to determine the interest in funding further studies in the event the present study does not provide the desired results.

Dale Branden, Alaska: I am not a spokesman for Alyeska Pipeline Service Company but I think that what we hope to gain in funding your study is information which will enable us to design the pipeline in such a way that caribou can readily cross it. If the study were to fail to provide information I am sure that we would try additional work.

Unidentified member of audience: I do not know very much about reindeer or caribou but perhaps putting dummies of caribou on top of the gravel ramps over the pipeline would help to attract the animals and get them to use the ramps.

David Klein: You may not know very much about reindeer and caribou but it is an interesting idea that might be worth trying. It would, however, present some practical problems if there are large numbers of crossing facilities along the pipeline.

Sven Skjenneberg, Norway: In Norway, we have experienced in some special cases where a very limited impact of man's activities can have a very great influence on reindeer. Due to reductions in total area available for grazing, reindeer may be forced into high concentrations, for example during calving or when migrating on narrow peninsulas, and damage to the range from trampling or overgrazing may occur. We should also be aware that reindeer and caribou and other arctic animals are often living at the very limits of vegetative growth so that recovery of damaged range lands, from whatever causes, may be very long.

In Norway, there has been a gradual attrition of reindeer grazing areas through mining, hydroelectric development, agriculture, forestry and other activities of man so that reindeer are now being supported on less favorable ranges than in the past. Any further impact therefore will have a very great effect. We are now developing, in Norway, regulations which require that whenever any project is undertaken, such as water impoundment, mining, etc., the reindeer herders and administrative agencies must be contacted and consideration given to what the effect will be on reindeer. A plan can then be drawn up so that the effect on reindeer and their range lands can be minimized.

Robert LeResche, Alaska: I would like to ask Jim Hemming to comment on the impact of the pipeline on caribou other than at Prudhoe Bay, as the pipeline will also pass through much more caribou habitat further south.

James Hemming: As I mentioned earlier, the proposed TransAlaska pipeline would cross the ranges of three caribou herds. It would dissect the existing range of the Nelchina caribou herd and our greatest potential conflicts exist there. This is a group of caribou that occur

from the Alaska Range, through the Paxson, Sourdough and Glennallen areas, east to the Talkeetna Mountains and west to the Wrangell Mountains. Currently these animals move each year across the proposed pipeline corridor to winter on ranges near the Wrangell Mountains and we would have potential problems there. I should point out that our greatest potential problems are on areas where we have permafrost and particularly on this relatively warm permafrost of interior Alaska which is easily thawed. These areas are much more susceptible to damage. Ideally, the oil companies would like to bury as much of the pipeline as possible, and of course if we talk about buried modes of construction we are talking about very minimal problems with large animal movements. However, in the Copper River Basin, the area we are concerned about with regard to the seasonal movements of the Nelchina caribou herd, we have a warm permafrost zone and extremely unstable conditions. This means that the pipeline will probably have to be above ground here with the attendant problems to animal movement.

Perhaps I can add here a little more about the Arctic and Porcupine herds. The existing oil development at Prudhoe Bay and the proposed pipeline would go just about on a direct line down the boundaries between these two caribou populations. I am not implying that the populations have a fixed fence-like boundary. These two caribou herds do overlap one another. Some years a great deal, some years very little; and of course over long periods of time they may be increasing and decreasing and therefore during some periods they may be absent from parts of that area. In general, however, movements in the Brooks Range area are north in the summer and south in the winter or late fall and would generally parallel the pipeline structure on the North Slope and into the southern foothills of the Brooks Range. So our greatest potential problems with caribou movements from the proposed TransAlaska pipeline would be in southcentral Alaska. However, an expanding oil industry on the North Slope with feeder line complexes such as would have to be designed and built from each wellhead to the main transit line will cause impact on caribou both by removing habitat and decreasing production and also through limiting movements of caribou.

Götz Schürholz, West Germany: Basically, are the oil companies sincere in their support of your research? If the studies are kept secret will you be able to have any effect on the pipeline construction if the results of the study are unfavorable to the oil companies?

Kenneth Child: There are mixed feelings, of course, about the studies, and the pipeline is involved in a political hassle. Personally I feel somewhat frustrated in not being able to speak freely about our work. I think, however, that if our results are conclusive the public will become aware of them, but one should also take into account the viewpoint of the oil industry. If our results are unfavorable to their interests they quite likely would not like to see them released. Hopefully, we will be able to provide the oil companies with information that will enable them to allow for the free crossing of a very large proportion of the caribou encountering the pipeline. Until our results are available I am really not free to speculate.

David Klein: I think that I might add a point or two. One is that most scientists that are doing studies are not under this type of pressure because the focus of public attention is not on them. If they are halfway through their research and someone asks them to release information to a wide audience, they are understandably reluctant to do so. Well, there is a great amount of pressure on us in this case, and of course a lot of people would like to know how things are going even though we can not give conclusive results at this time. So it is quite a unique situation and I do not think all of the blame should be put on the oil companies, nor do I think that our position is unreasonable. The oil companies do have a public image to protect. If a sufficient number of people know that the study is going on

and if the oil industry were to try to sit on the results, and I don't think that they can, but if they were to try, it would be to their disadvantage because the public would immediately apply pressure of various sorts on them. It is a political game as Ken mentioned, and as scientists we do not particularly like this kind of involvement but we are trying to play it straight and we hope the oil industry is also. We can only proceed on such an assumption.

Gordon Haber, Alaska: What will be the effect of oil activities on predators? There has been mention of the impact of man from hunting on changing sex and age structures among wolves, bears and other species. Perhaps a more specific response could be made in evaluating the impact of oil development to include, but not be restricted to, habitat destruction, the increased hunting on caribou, particularly when hunting takes place along a road *en masse*, for example as has been the case along the Denali Highway.

James Hemming: You have raised a point that has been raised before, Gordon, with regard to the problems of caribou harvest. Caribou, of course, are gregarious and because they move in large bands there are times when large numbers of animals do come in contact with roads and particularly in the southcentral region of Alaska where we have the Denali Highway, the Richardson Highway, the Glenn Highway and the new Anchorage-Fairbanks Highway. So we do have times when caribou are readily accessible and high hunter harvests occur. I still maintain, however, that with suitable regulations and bag limits and armed with the knowledge that there is a potential for fairly high harvest in a short time we can effectively protect the population from over-utilization.

Gordon Haber: I am not so much concerned about the amount of animals taken as with the effect on the migratory pattern of a line of hunters along the highway; what is the long range effect.

James Hemming: Well, as Skoog reported in 1968, some of the early shifts in various caribou herds in the state were undoubtedly affected by high level of hunting activity, during the whaling days, during the mining days, when trappers were abundant and so on, and certainly when you reach a certain activity level whether it is by hunters or vehicles on the road, you will affect movements. It has been interesting to note that the Nelchina herd increased its movement across the Richardson Highway in the last five to six years when earlier the animals did not extend beyond this area. This has happened in spite of many predictions to the contrary because of the sharp increase in hunter activity, the sharp increase in the use of snowmachines and a normal increase in road traffic. The animals have continued to move across the highway at defined areas where food was available in these winters. In some of the first instances, places like the upper Chistochina and Gakona River valleys happened to have relatively light snow in those years and animals moved in to utilize forage that was normally not available. And this was in spite of a very high level of activity on the road system. So it is not a simple matter.

Gordon Haber: What will happen to prey populations if predator populations are altered?

James Hemming: I think there are others in the audience better qualified to discuss predators than I am. I do not believe, however, that in Alaska we have a situation of predators controlling caribou. Certainly they are a very important modifying influence and at times of high wolf abundance and excessive hunting pressure problems are bound to occur. Man's influence from hunting can be comparable to predation under some circumstances, however, the impact of vehicular traffic, disturbance of grizzly bears in open

tundra situations and other aspects of the high level of intrusion into wildlife areas, undoubtedly will have far reaching effects on wildlife. Regulations controlling these influences will have to be developed but the problem is not a simple one. Have I got to the point you were concerned about?

Gordon Haber: Again I want to emphasize that I am not so much concerned with the direct killing of predators as with the disruptive effects of human activity and disturbance by altering traditional patterns of animal activity.

James Hemming: I am sorry if we have appeared to be treating those factors lightly. I feel that most of us tonight have emphasized that we are talking about a battle of attrition, and we are going to be constantly losing habitat. We will be faced with increased barriers to animal movements which will have many effects but I think the habitat considerations are perhaps the most important. These would affect all the other organisms that are associated with caribou. We are trying to develop wise planning for the future in areas in which some of the countries represented here have had very much experience while others have not. We still have a lot of prerogatives available to us. I think it is very important that we plan properly.

John Henshaw, Alaska: I have a technical question which requires drawing on the blackboard. This is directed to Mr. Child and Dr. Klein. My comments are related to the winter rather than the summer and I am assuming a pipeline on level ground such as occurs on the North Slope. Three alternatives appear to exist from the information that has been presented for an above ground pipeline 4 feet in diameter. It can be raised slightly above the ground with no other modifications, it can be elevated 7 or 8 feet to provide an underpass or it can be covered with a mound of gravel. If the wind direction is at right angles to the pipeline the snow accumulation pattern would look something like this. A fairly steep area of hard packed snow here (just to windward of the pipe or ramp), followed by a long drawn out tail of softer snow (leeward of the pipe). The sudden loss of velocity of the wind as it strikes the pipeline will cause a piling up of snow on the windward side. I visualize that caribou may have trouble in trying to cross the pipe when they encounter the deep snow, particularly if it is as much as 4 feet deep and soft. I do not know what has been done in the way of winter snow studies in relation to the pipeline but I do have an idea for overcoming the problem I have outlined. The engineers may not like it, however. It is simply to dig a large hole or trench into which the pipeline is laid but left exposed to prevent thawing of the underlying permafrost. A bridge at ground level is then constructed to provide passage for the caribou over the pipeline. Since none of the construction would project above ground level the problem of drifting snow would be eliminated.

David Klein: Before either Ken Child or I respond to your proposal perhaps someone from Alyeska or one of the oil companies has information from snow studies that would shed more light on the question.

Dale Branden: First of all I am an oceanographer. I know of no cases where the pipeline would be constructed as shown in the third example. Also, I do not think, from what I have heard today, that caribou winter in areas that the pipeline will transect and therefore it is difficult to see that such a problem with snow drifting will occur.

James Hemming: Yes, caribou do winter along the pipeline route and particularly the Nelchina herd.

Unidentified member of audience: In the Nelchina area, although there are extensive areas of permafrost where the pipe will have to be above ground, there are also areas without permafrost where the soil would remain stable after thawing where the pipeline can be buried.

John Sweet, Alaska: I can only speak to a couple of points raised about snow and the pipeline from my own observations at Prudhoe Bay. The roads which are perpendicular to the wind seem to have an equal amount of snow on either side. This is not a measured depth but just that they look level with the top of the roads. So far as the pipeline itself is concerned, or the pipeline covered with a berm of gravel, there is no reason for me to believe that they would act any different than the raised roadbeds. Also the drifted snow along the roads gets as hard as concrete. I can not speak to the middle condition [the pipe elevated 7 or 8 feet, but the proposal to lay the pipe in an open trench is a 'no no' because that would involve digging into the tundra and the permafrost, and for a variety of reasons that is avoided unless absolutely necessary.

David Klein: I would like to emphasize a couple of qualifications with regard to Ken Child's study. First, Ken pointed out that the study was done in summer when caribou are present in the area. In winter there are only a handful of caribou remaining there so it is not practical to continue the study then. Also the snow fencing is not constructed to withstand the winter winds so it is taken down at the end of summer. This question of snow and how its drifting around the pipe might influence movements of caribou is certainly a separate issue, and our study is not going to provide answers to it. The question is going to remain and it needs to be answered, therefore I think Mr. Henshaw has raised some good points. We know that even though the snow is hard packed in open tundra areas and perhaps would normally support the movement of caribou, in the springtime when caribou may be in the area during melting, such drifts at the crossing facilities could actually obstruct the movements of the caribou or entrap newborn calves. We know that this happens occasionally under natural conditions where drifts occur along river banks. I think you could see from some of the slides Ken showed from Nome and also one of the BP facility in wintertime that the situation is altogether different in winter. Animals encountering an elevated pipeline with considerable snow accumulated under it are not going to be able to pass under it. But in many cases the fact that the pipeline will be elevated will allow for free movement of wind underneath it and this will cause any drifting to occur at some distance from the pipe rather than directly under it. Another point is that in the situation where there is no ramp of any kind and the pipeline is elevated over the tundra, there probably would be no snow accumulating around the pipe under most situations because of the fact that it is elevated. But under some storm conditions, such as occurred at the Nome site, I imagine it could occur that the pipe would be at least temporarily buried. Remember it is going to be carrying heated oil. While the snow would melt fairly rapidly where it was in contact with the pipe, the resulting space between pipe and snow could create a hazardous condition for animals attempting to cross over on the drifted snow.

Oliver Burris, Alaska: There is an underlying fact that both caribou and reindeer are both in a generally critical adjustment to this range which is reflected in North America by observation that these animals may vary in numbers by a factor greater than 10. Is it not possible that if development does occur, such as pipelines, roads and other things which will eventually cause fracturing of the various herds, that the total carrying capacity might be increased and some of the wide fluctuations we have seen in the past might be stabilized because of more manageable populations?

David Klein: Would one of our Scandinavian friends who is familiar with the situation with reindeer there like to comment on Mr. Burris' statement?

Bengt Westerling: Well it is easy to speak when it is not one's own problem, but I do not think this last suggestion sounds so unreasonable. I spoke earlier about the fences used in Finland to separate reindeer herds and what we have as a result are small, more manageable herds. If the oil must be transported I would think that breaking up the caribou herds might be less dangerous than an oil disaster in the Gulf of Alaska on the order of 200,000 tons.

David Klein: The statement by Bud Burris perhaps could stand a little more comment. This is a reindeer/caribou symposium and there is no effort to have all the experts here on the panel, so perhaps someone in the audience would like to speak.

Frank Banfield, Canada: I only wanted to make the observation that in the eastern part of Canada heavy hunting pressures and other disturbances have broken up long migrations in some caribou herds.

George Calef, Canada: We tend to overdo the use of this term 'management' and I wonder if perhaps we should give more thought to what we mean by the term. If the problem is just to raise the maximum amount of meat perhaps we should not be talking about caribou, but rather reindeer. If so, then our talk should be of feeding methods, fencing procedures and so forth. I think, however, that there is an underlying atmosphere in this room, particularly when we are talking about conservation of animals that are now wild, that we want something more from them than meat or economics. This point, I think, has been very much neglected in all the technical details. We must not lose sight of why we want to conserve caribou, why we want to preserve their migratory patterns and what is important about an animal and its habitat. Obviously, I do not have the answers to these questions but I would like to hear more comments on them.

David Klein: Thank you Mr. Calef, you have made a very good point. Certainly there is a tremendous distance to travel between management of a wilderness species such as caribou and intensive management of semi-domesticated reindeer where the land is broken up into relatively small components and problems of transportation, economics and sociology have all been fairly successfully resolved. It was pointed out earlier this evening that domestic reindeer husbandry in Scandinavia has had at least 1,200 years to evolve.

George Calef: Perhaps we could have a comment from Mr. Lane as to whether he herds reindeer or hunts caribou and which he prefers.

Amos Lane: I will try to answer that question as best I can. To start with, I have only seen reindeer when I was about 15 years old and that was when the caribou herds came through our area and took the reindeer herds with them. That was about 25 years ago. I would rather hunt caribou than herd reindeer in our area because there is no way of controlling the reindeer when caribou are around.

Gordon Haber: I would like to support Mr. Calef but also to point out that one of the greatest atrocities that man has done in the past has been to adjust his environment to suit his social and economic institutions and I think that the day that he learns to adjust his social and economic institutions to suit his environment he will have accomplished one hell of a feat.

John Krog, Norway: (Dr. Krog's comments could not be clearly discerned from the tapes but they related to the adaptability of reindeer in Scandinavia to man's developments, including roads, railroads, etc. Additionally, he commented on the venturi effect of increased wind velocity under an elevated pipeline which would tend to keep it free of snow. This was in reference to John Henshaw's proposal for the design of the pipeline.)

Eigil Reimers, Norway: Experience in Norway with wild reindeer and a road and railroad near Snohetta raise the question of whether reindeer will return to their normal behavior of crossing these barriers or will the range and its use be permanently affected? Reindeer discontinued their use of a major portion of their range some years after a road and railroad were constructed there and the result was an abnormally heavy grazing pressure by the reindeer in the area they were confined to. The area from which they were excluded was unused by reindeer for many years although a small herd now exists there after some animals did cross the road and railroad. Also I would like to comment on the effect of increased tourism which was mentioned earlier by Dr. Westerling. We have reindeer areas in Norway where up to 50 to 60 per cent of the grazing areas are avoided by reindeer during the tourist season because of activity of the tourists.

Unidentified member of audience: I would like to suggest an alternative method of transporting oil from Prudhoe Bay. Perhaps the most feasible method would be to use a railroad, and the pipe itself, now in storage at Valdez, Fairbanks and Prudhoe Bay, could be modified as containers for the oil.

David Klein: Would someone from the oil companies like to respond to that?

John Sweet: Dr. Klein, our trip from Anchorage to Fairbanks this morning was on a plane with the cabin full of gasoline fumes and I feel like it is two o'clock in the morning rather than 10 o'clock at night. I am not going to answer anymore questions like that one. Let's adjourn the meeting and go home.

David Klein: Your suggestion, John, is well taken, however I think we should have some additional expression from the audience as to whether we should adjourn immediately or go on for an additional period of time. I am sympathetic with you and we do appreciate the fact that you joined us this evening and that you have stayed here this long, especially under the circumstances of the oil pollution in the airplane. If you would like to leave, of course you may but we would appreciate any comments that you might have to make relative to questions that have to do with oil and the pipeline.

Unidentified member of audience: Can someone on the panel tell us how the Alaska Native Claims Settlement Act will affect oil development in Alaska.

James Hemming: On this we will get a bit off the subject of caribou. The Natives are to receive 40 million acres of land as a result of the settlement. This land will be parceled out over a period of time depending upon the areas selected by the individual Native groups. The effect on development will be that of the problem of breaking up the public domain with various sized tracts of private lands. The scheme for the selection of these lands has already been established with most selections occurring in the contiguous townships surrounding Native villages. These selections and the use of the lands are beyond the prerogatives of the resource manager and planning for the future. There is, however, a planning commission established by the Settlement Act which functions as an advisory group to aid

in the planning and development of the Native lands as well as state and federal lands. The impact of this action on caribou, as I see it, is not clear because it will be largely up to the owners of these private lands how they are managed.

Jack Luick, Alaska: I would like elaboration on the point made by Mr. Jakimchuk earlier about fire and reindeer and caribou range. Perhaps George Scotter also has something to say on this.

R. D. Jakimchuk: I am not sure just what I said earlier but fire certainly does have a devastating effect on lichen range. There are, however, conflicting viewpoints in the literature as to the importance of lichens on both Canadian and Alaskan caribou ranges, particularly from the point of view of lichens being a limiting factor for caribou populations. Perhaps fire, under some circumstances, could be limiting but historically even before man came on the scene, fire was an ecological factor. I think other factors are probably more important in limiting caribou populations than is fire. Burned over areas can act as barriers to deflect movements but I do not think that at this time, at least in the Canadian situation, we have to be concerned with this. Dr. Scotter may disagree with what I have said but I certainly do recognize the devastating effect fire does have on lichens.

John Krog: I can comment on the basis of my wife's investigations. There are some advantages in having a wife who is also a specialist on lichens. A very severe forest fire in the north of Norway did considerable damage to reindeer range, effecting many reindeer herds. Fire definitely can be a detrimental factor in Scandinavia. It will take about 50 years before the lichens will grow back.

A young lady representing the Alaska Federation of Natives: It is all very well to be spending so much time worrying about the future of the caribou but please do not forget the Native people who have been, and still are, dependent upon them.

Paul Frelier: On the basis of studies which have been done using Cesium 137 as a marker here at the Institute of Arctic Biology it has been determined that caribou eat 4-5 kg of dry lichen per day during winter. This value must be at least twice as much on a wet basis. In view of this, I do not see how it can be said that lichens are not important in the diet of caribou.

David Klein: I think that what Mr. Jakimchuk referred to are cases where caribou and reindeer have survived and prospered without lichens. On second thought, since I am not sure what prospered means, at least they continued to exist and produce increments. I think, however, that we tend to oversimplify, and if we look at these areas in the Aleutian Islands and perhaps islands in the Bering Sea where this has been true we find either that the wintering conditions are quite different than in typical reindeer and caribou ranges, as is true in the Aleutians, or else the situation was transitory and drastic population declines have followed the elimination of the lichens, as has been characteristic of Bering Sea islands. It is certainly an oversimplification to generalize that caribou do not need lichens. It is only under fairly unique circumstances that they can get by without them. To say that we can have good populations of reindeer and caribou in the areas where they presently exist without depending upon lichens in winter is not very realistic.

Götz Schürholz: We have heard about the impact of northern development on the environment and we have heard from many scientists about their concern and of the lack of

information about northern ecology. It seems like many of us are doing research for the sake of research instead of offering solutions. I think that we should focus more on the problems and go beyond the scientific publications to try to focus the public's attention on these problems.

David Klein: Your observations and comments are quite valid. We certainly need to be looking for solutions to specific problems, and the support to do research that is relevant to today's problems will only be available if the public is aware that the problems exist. Also I agree that scientists frequently do research for their own satisfaction but society may still benefit from it.

Fred Dean, Alaska: I would like to direct my question to Mr. Jakimchuk. Your statements suggested that, at least in northern Canada, we do not have to be concerned about habitat for caribou. The implication to me was that you thought that the habitat there was so extensive that the inroads being made were not significant. On the other hand, it seems like many people feel that the so called minor habitat disturbances do affect caribou. Therefore I ask, if we are not concerned now about this, at what point do we become concerned? It seems to me that the rate of northern development that we have seen since 1957-59 offers a mirror of just how fast things can happen.

R. D. Jakimchuk: There are quite a series of questions involved in your remarks and I will try to remember them. In my remarks I felt that priorities had to be established and I felt that the physical alteration or destruction of habitat, *vis a vis* development, was not one of the priority items at the present time jeopardizing Canadian caribou populations. That does not mean that I feel that habitat is not important. There are certain elements of habitat that I feel are critical, the main one being calving grounds. They constitute the most consistently predictable element of the caribou life cycle, the center of the seasonal behavioral pattern. But in trying to establish priorities, things that we have to consider very closely are these other elements affecting caribou behavior such as their migration pattern, elements that could affect their survival or productivity. And in that sense I feel that we do have very, very extensive habitat in Canada. Summer ranges are very extensive and are unavailable or not utilized for most of the year. Probably the most significant factor in the habitat alteration of winter ranges is fire. I feel that the other items that I have mentioned merit priority at this time with the exception of the calving areas. I think we must safeguard these areas as they are the key to the welfare of caribou. As far as the vast expanses of taiga and tundra that are utilized during the course of the year are concerned, I just do not consider these to be important elements at this time.

Gordon Haber: What is it that we really want from the North? Do we want wilderness or total development?

Edward Murphy, Alaska: We have heard the opinions of a number of participants, for example Mr. Burris, which seem to presuppose that our primary aim in management of caribou and reindeer is to maximize production of meat or to maximize carrying capacity of a given habitat. While this may be a goal in the management of semi-domestic reindeer herds, I do not think this is necessarily a goal for free ranging caribou. Caribou are not solely an economic resource but an aesthetic one as well. Although perhaps fragmentation of caribou range may increase carrying capacity as Mr. Burris suggests, such activity destroys what I believe is an essential element of the caribou resource — the aesthetic appreciation derived from the freedom of movement of the large herds and the vastness of the wilderness

ecosystem of which caribou are a part.

Ian McT. Cowan, Canada: I am quite sure that most of us who are engaged in trying to gather facts about caribou populations have found more than what we were looking for over the years. I think I will be understood if I say that a great many of us here are devoted to positions that are not only practical but sometimes impractical. To me there is a certain majesty in the biological world which we are inescapably related to — the great sweep of hundreds of thousands of geese going over in the spring, the inconceivable noises from a great herd of caribou on the move, the almost equally unbelievable noise of a tremendous herd of, say 300,000 wildebeest, which I happen to have had the good fortune to see recently — these things are, I think, part of the wealth and the breadth of the lives of most of us who are here. We are not interested in a kind of a scheme to provide half tame animals. I think all of us will believe that if we can not keep great areas of wilderness, such as the 14,000 square miles of the Arctic Wildlife Range or even one-half million square miles if necessary to keep some great herds of caribou moving across the tundra and through the mountain barriers in their associated patterns, our lives, all of us, will be impoverished and we will have done a great disservice to our children and our children's children. To me, one of the great issues of this whole question of environmental impact, of course, could not be related here because we are discussing caribou. It is the question of what the kinds of things that are going on do to wilderness. Many of us are involved in this. But damn it all, we are not just looking for peace of mind. We are striving to keep some of the majesty of life, some of the romance, some of the excitement in life that all of us enjoy and we hope that our children can enjoy too.

David Klein: Thank you Dr. Cowan. Your remarks are appropriate ones to end this evening's session. I would like to thank the panel members for their presentations and participation in the discussion and I particularly thank all of you in the audience for your patience and your participation. I hope that we have expanded our realm of knowledge even though we may not have resolved too many problems. I think that if we proceed with that assumption we will be better equipped to solve the problems that face us when we return to our own areas.

NEW RESULTS ON THE HISTORY AND TAXONOMY OF THE MOUNTAIN, FOREST AND DOMESTIC REINDEER IN NORTHERN EUROPE

L. Siivonen
Department of Zoology
University of Oulu
Oulu, Finland

ABSTRACT—An antler of tundra reindeer type which has been found in Tornio in northern Finland and whose age is 34,300 years according to C¹⁴ dating, the latest results on the history of the Scandinavian mammals (the directions of arrival) and on the phases of the Würm glacial period as well as the new measurements of the mountain reindeer (*Rangifer tarandus tarandus* L.) and the forest reindeer (*R. t. fennicus* Lonnberg) and of domestic reindeer indicate that the mountain reindeer had arrived in Scandinavia during the wide interstadial 35,000-45,000 years ago, probably from the south, and had survived the latter cold phase of the glacial period on the Norwegian coast.

The late-glacial 'tundra reindeer' of Denmark and southern Sweden could not spread to Scandinavia because of the sea barrier and therefore died out. The Scandinavian domestic reindeer has been domesticated from the mountain reindeer. Brought to the forest areas of northern Finland it has adapted poorly to that environment. The forest reindeer is a southeastern reindeer which differs sharply from its other north European relatives in taxonomical and ecological respects. It did not arrive in Scandinavia until long after the last glaciation.

As a background for the history and mutual relationships of the north European reindeer types, it is appropriate to recall the two best known interpretations throwing light on the subject. Jacobi (1931) supposed that the prehistoric reindeer in Europe was identical with the American barren ground reindeer, *Rangifer tarandus arcticus*, or at any rate closely related to this form, and not with the recent European (mountain) reindeer. According to Wegener's continental movement theory, North America was in this period still connected with Europe and these areas were inhabited by the same species of reindeer. This reindeer followed the receding inland ice to the north, but was, at the beginning of the Forest Period, stopped at Närke Sound across central Sweden. The climate was then so mild that the advancing forest grew right up to the border of the ice-sheet, and *Rangifer tarandus arcticus* died out in Europe — a situation which Ekman (1948a) also considered possible. Simultaneously the extensive barrier in the form of a belt of lakes going from the Caspian Sea to the White Sea disappeared and the Asiatic reindeer, *R. t. tarandus*, was then able to immigrate into northern Europe.

According to Degerbøl (1959), the ancient Danish (European) reindeer resembled the present Scandinavian *tarandus* in several cranial characteristics, i.e., shape of the nasal bones, short nasals, small rostral length and great orbital breadth. Degerbøl concluded that the differences in antler form are also not greater than could be expected by evolution through the approximately 12,000 years that have elapsed since its immigration to Scandinavia during the late Dryas period. In other words, the recent mountain reindeer is, according to Degerbøl and contrary to Jacobi, the same species as the ancient European reindeer.

R. t. fennicus is, according to Degerbøl (1959) and Banfield (1961), clearly of its own

type, sharply differing from *tarandus* in many respects. Banfield conceived these both as being at an incipient species level today. He has classified the Siberian prehistoric *constantini* as a forerunner of *fennicus*.

In contrast, the origin of the present mountain reindeer continues to be obscure in many respects. For instance, Degerbøl (1959) observed in this connection that "... for a decision on this point, however, we must look forward to future discoveries." Comparable samples and measurements have been too few throughout and they have not always represented pure types. According to Heptner (1966) the origin of the forest reindeer is unclear too. He says that this question will obviously remain unsolved, since the tundra reindeer is actually completely exterminated on the tundras of northeastern Europe, and the forest reindeer almost exterminated in the forest zone of the European part of the Soviet Union.

The Scandinavian domestic reindeer is generally considered to be a descendant of the mountain reindeer, although in northwestern Finland and northern Sweden it is assumed also to be blended with forest reindeer (Lönnberg, 1909; Ekman, 1948b; Forsberg, 1958; Banfield, 1961). Especially in Finland, the opinion is common (e.g., in Finnish encyclopedias and handbooks) that the domestic reindeer in the forests of northern Finland would in fact throughout be descendants of the forest reindeer.

An antler of glacial reindeer, which has just been found in Tornio in northern Finland, and whose age is 34,300 years (+2000 or -1450) according to C¹⁴ dating, the latest results on the phases of the Würm glacial period and the history of the Scandinavian mammals (their directions of immigration, the recent return to eastern Finland of the forest reindeer which was exterminated in Finland 100 years ago, and new taxonomic materials) have permitted a reconsideration of the history and interrelationships of the various types of reindeer in northern Europe. The most important new taxonomic materials consist of 60 male domestic reindeer from the whole region of north Finland, five new, pure-type east Finnish male forest reindeer (all from the Zoological Museum, University of Oulu) and in addition, eight older male forest reindeer and antlers of 20 males from the Zoological Museum, University of Helsinki. The measurements of the mountain reindeer were made by A. Pedersen, of the Zoological Museum University of Oslo. The skull pictures of this reindeer type are also based on specimens received from Oslo. All measurements were made by the same methods employed by Banfield (1961).

The antler of the Tornio reindeer found in 1967 at a depth greater than 3 m in a gravel pit appears to be of the same type as the prehistoric Danish reindeer (Fig. 1). For example, the brow tine (only its point of insertion observable) and the bez tine start from the antler beam at a great distance from each other. The antler beam is flat. According to H. Paarma (personal communication) it is likely that the antler has been transported (as suggested by geological evidence associated with rocks) along the Tornionjoki River Valley from as far as the slopes of the Kölen Mountain Range. The find at any rate demonstrates that reindeer lived in the middle of the last glacial period in northern Scandinavia, possibly on the Norwegian coast and in the Kölen Mountains running east of it.

In order to sketch a background for this find, it is necessary to recapitulate briefly the phases of the last glacial period. In the middle of the glacial period, 45,000 ± 2,000 years ago, the so-called Peräpohjola Interstadial prevailed in north Finland, at which time northern Finland was free of inland ice and covered by tundra vegetation for about 2,000 years (Korpela, 1969). The glacial period is divided into two parts in northern Norway (Dahl, 1968) and according to Armand (1961), the last freezing over the Kola Peninsula fell into two phases. The inland ice of the first phase was more extensive than that during the second phase. It is in fact increasingly believed (e.g., Brinck, 1967) that the Würm glacial period began about 70,000 years ago with great severity, after which the inland ice extended

far out to sea off the Norwegian coast. During the cold period after the extensive interstadial, however, the coast of Norway remained at least partly free of ice. Survival of arctic fell plants and animals on the Norwegian coast and on the nunataks of the Kölen Range over the *entire* last glacial period, which was presumed, for example, by Nordhagen (1936), Ekman (1948a) and Lindroth (1958), would not have been possible (Brinck, 1966; Danielsen, 1971).

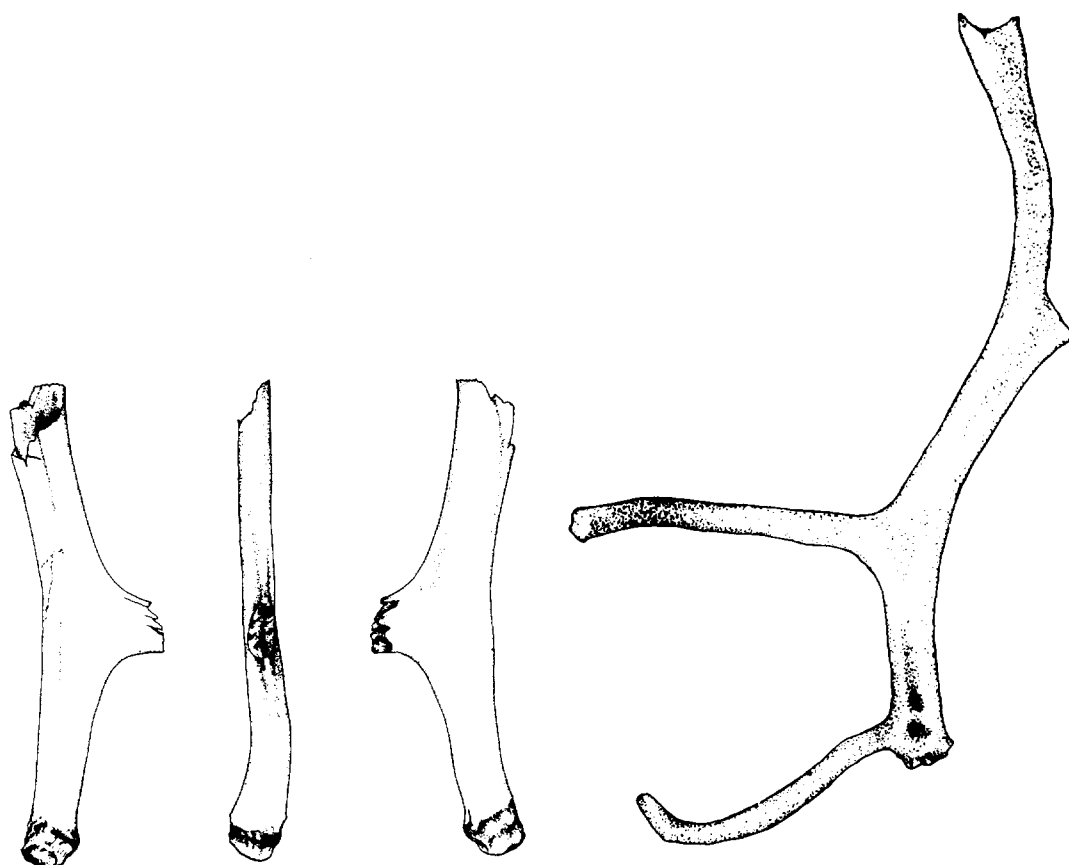


Fig. 1.—Prehistoric Danish reindeer antler is on right side of Figure, i.e., three pictures of Tornio antler, one of Danish.

The present distribution of certain types of mammals on the Norwegian coast as far north as Hammerfest, however, cannot be explained as they could only have arrived there during the late-glacial or post-glacial time. These include most definitely, *Sorex araneus bergensis* and *Microtus ratticeps stimmingi* (Siivonen, 1967, 1972). On the other hand, the bipartite character of the glacial period, as has been described, permits reasonable explanation for the spread of these species; they arrived in Scandinavia most probably from the south (possibly via the North Sea land according to Lundholm) (cf. Lindroth, 1958), during the extensive interstadial and they passed the later stage of the glacial period on the Norwegian coast (Siivonen, 1972). The Tornio reindeer is the newest piece of evidence showing that this is obviously what has happened. The lemming and the arctic fox may have also spread in this manner (cf. Ekman, 1948a).

It is uncertain at what stage of the extensive interstadial the Tornio reindeer arrived on

the Norwegian coast. The fact that its antler very closely resembles that of the Danish reindeer in structure suggests that it could hardly have lived there for many thousands of years, and that it, too, would have come from the south.

If this reindeer survived the latter cold phase of the glacial period on the coast of Norway, as did the other mammals mentioned above, then it had three times as long to develop from the prehistoric European reindeer to the present mountain reindeer as compared with the process assumed by Degerbøl (1959). It should be noted that conceivably the reindeer stocks of that time were adversely affected during different phases and their perpetuation may have depended upon a single population, the hereditary factors of which (e.g., type of antler, as noted below) would have resulted in development of the Scandinavian mountain reindeer type, *R. t. tarandus*.

Several comparative taxonomic studies convincingly support Degerbøl's (1959) and Banfield's (1961) finding that the Scandinavian mountain reindeer and the forest reindeer are quite different from each other. The north Finnish domestic reindeer is entirely indistinguishable with the mountain reindeer — that is, at least, the 'pure' mountain reindeer of today — or rather with its half-tame degenerated form. The characteristics of the forest reindeer, if any have ever been present in our domestic reindeer strains, have been completely eliminated.

In the forest reindeer particularly, the basal skull length, nasal length and diastema are considerably longer than in the mountain and domestic reindeer. Decipitol and canine height are also greater. Since, however, the orbital width is nearly the same, the forest reindeer's skull appears even longer and more slender (Table 1; Fig. 2). The eye socket is

TABLE 1.--Measurements (range and mean, mm) of male skulls of forest, mountain and domestic reindeer.

	n	Basal length	Nasal length	Diastema (maxill.)	Orbital width
<u>Forest reindeer</u> (Eastern Finland and Karelia)	13	359 (332-378)	128 (116-146)	135 (124-148)	166 (153-180)
<u>Mountain reindeer</u> (Norway)	4	329 (320-337)	105 (102-109)	119 (113-125)	165 (159-176)
<u>Domestic reindeer</u> (Northern Finland)	60	307 (283-339)	104 (87-120)	111 (90-126)	156 (143-174)

usually more posteriorly located than in the mountain and domestic reindeer (Fig. 3). The posterior processes of the palatal bones go farther down on the mountain reindeer, etc. The forest reindeer's antlers are characterized, like those of the Tornio reindeer, and in most cases, the prehistoric Danish reindeer, by the fact that the brow tine starts at the burr of the antler and the bez tine considerably higher up (Fig. 4). In the antler of the mountain and domestic reindeer, and in many instances also in the Danish reindeer, both tines start at the burr of the antlers, quite side by side. Furthermore, the forest reindeer's antler crown is regularly narrow, with dichotomously branched antlers; the antler crown of the mountain and domestic reindeer is usually wider, with its antlers usually branching off unilaterally, backward from the beam (Fig. 5).

The domestic reindeer has been imported to the forest regions of north Finland from

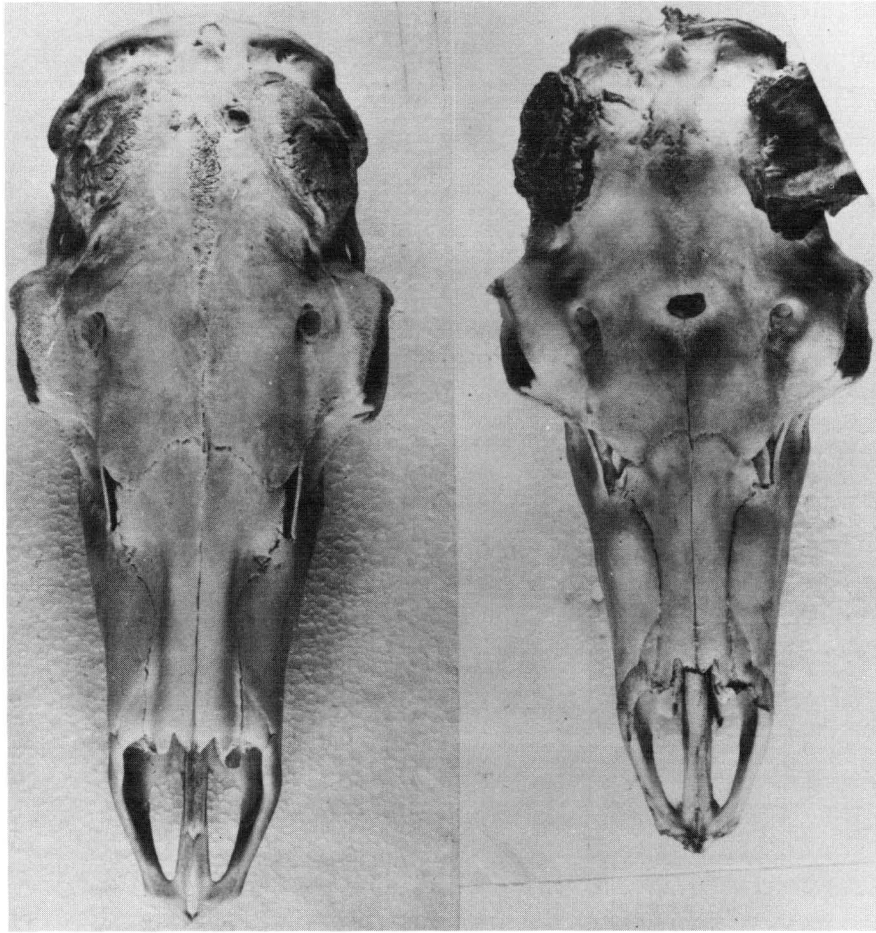


Fig. 2.—Forest reindeer is on left.

the slopes of the Kölen Range as recently as the last two or three centuries. Unaccustomed to wooded terrain, it has encountered numerous difficulties in its adaptation and considerable losses have resulted, especially by the abundant snow. These have been accentuated by the fact, among others, that the domestic reindeer is confined to the area of its appropriate reindeer-owner's association. The free mountain reindeer has the fell as its natural habitat, where some pastures have little snow even in winter (e.g., Ekman, 1948b); under conditions unfavorable for overwintering, the mountain reindeer can find areas where it has easy access to lichens.

Now that the forest reindeer once again displays new vitality in eastern Finland (its increasing stocks already number 100-200 individuals), one question arises; whether one should not tame the forest reindeer for the northern forests, since it is indigenous to coniferous forests. It should be kept in mind that this animal, being bigger and stronger than the mountain reindeer, has already in the course of hundreds of millenia, become particularly adapted to forests and to abundant snow in winter (cf. Nasimovitch, 1955). At any rate, the Fennoscandian forest reindeer is an animal of such great rarity in Europe that a symposium dealing exclusively with it and its future was held at Kuhmo in eastern Finland during August 1972.

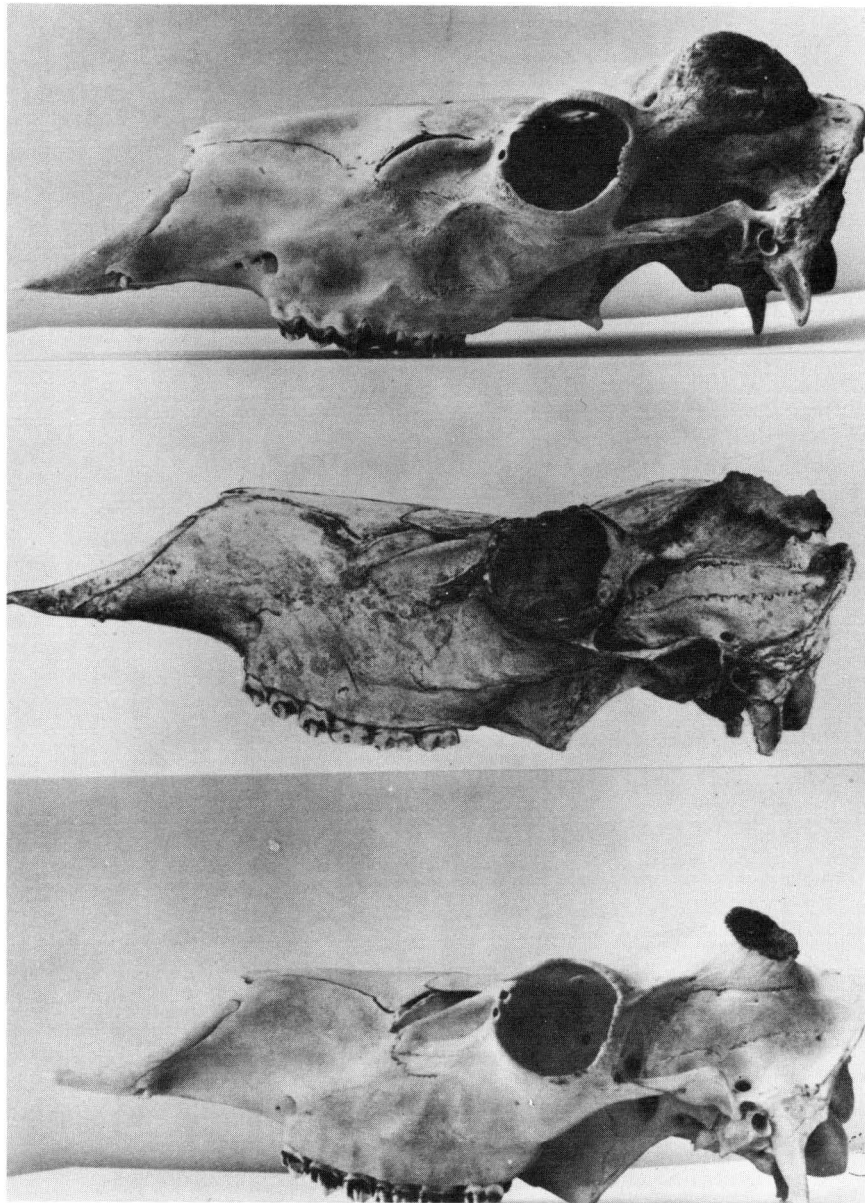


Fig. 3.—Top and center pictures of mountain and domestic reindeer, bottom is forest reindeer.

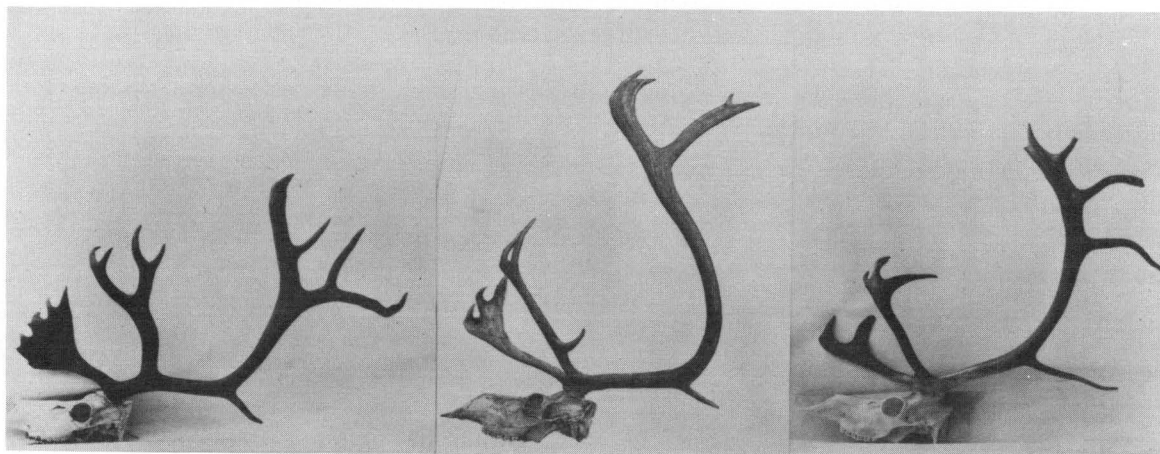


Fig. 4.—Left is forest reindeer, center and right are domestic and mountain reindeer.



Fig. 5.—Left is forest, right is domestic/mountain.

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TAXONOMIC VALUE OF ANTLERS IN GENUS *RANGIFER*, H. SMITH

A. B. Bubenik
Research Branch
Wildlife Section
Ministry of Natural Resources
Maple, Ontario

ABSTRACT—Caribou and reindeer antlers are characterized by the following qualities: an insignificant role of testosterone in the antler cycle, a growing mantle of compact bone in the antler beam, a superficial mode of beam branching into tines and ends which is independent from the successive development plan of the antler construction and a predisposition for immediate regeneration of tines amputated in the velvet period. These lead to the conclusion that antlers in the Genus *Rangifer* represent a very young stage of antlerogenesis. This view is supported by the hypertely of beams and tines and therefore by great variability of the upper zone of the antlers. It reaches a degree not present in recent genera of Cervidae that originated in upper Miocene or Pliocene. The suggestion that woodland subspecies should show some modifications of antler structure or architecture as a result of adapting to the more dense structure of taiga canopy cannot be proved. The available material was too scarce for statistical evaluation in view of the large variability in antler shape of caribou.

Accessory organs like antlers and horns are in their morphogenesis closely connected with behavioral patterns of the species concerned. Because behavioral evolution represents adaptive processes to environmental structures, it can be concluded that antlers or horns are adapted to the physical structure of the habitat.

It is now generally accepted that behavioral elements are important taxonomic characteristics, sometimes more accurate than the morphological and physiological ones. Very often the elements of behavioral patterns use morphological characteristics that function as an unequivocal and easily perceived code, i.e., a simple and most specific signal (Lorenz, 1965).

Unfortunately the close relationship between antlers, behavior and habitat structure has up to now seldom been considered by taxonomists. Neglecting the relationships between behavior and environment, they have either over/or underestimated the taxonomic value of antlers in general and particularly in *Rangifer* (Jacobi, 1931; Banfield, 1954, 1961; Kelsall, 1968; Thenius and Hofer, 1960). Therefore let me show how an ethologist would demonstrate the taxonomic value of reindeer antlers.

SYSTEMATIC POSITION OF THE GENUS *RANGIFER*

The evolutionary history of the reindeer and its subspecies is not clear. It is generally recognized that *Rangifer* originates from Neocervinae Carlette (1922) (Banfield, 1961; Flerov, 1935, 1950). Therefore its early ancestors should be searched for somewhere between the equator and subarctic of this continent (Flerov, 1952; Frick, 1937). Direct evidence about these ancestors is not yet known (Banfield, 1961; Flerov, 1950; Kurtén, 1968; Thenius and Hofer, 1960). It seems probable that some of these ancestors reached

Alaska or Eurasia (Banfield, 1961) during pliocene-pleistocene, where they evolved into a tribe (Rangiferini Simpson, 1945), or subfamily. It is my opinion that characteristics which differentiate *Rangifer* from other Odocoileinae and Cervidae are numerous enough to postulate that the reindeer-like species could build their own subfamily Rangiferinae (Bubenik, 1956, 1959a, 1962, 1966; see also Thenius and Hofer, 1960: 237).

METHODS

Generally antlers are organs whose shape, size and movements are important parts of the ikonographic language of Cervidae (Altmann, 1965). This language is species-specific and could be used as taxonomic characteristics also.

To understand how these signals operate it is necessary to investigate not only their morphological characters but also their functions (Tinbergen, 1968). From this view we have to ask: (1) To what degree does this phenomenon (antler) develop? (2) How does it influence or is it influenced by the behavior of the carrier and its environment? (3) What is the survival value of the specific form of antlers? (4) Which is its taxonomic value?

TAXONOMIC PARAMETERS OF ANTLER OF THE GENUS RANGIFER

The most apparent feature of antlers is their peculiar shape and cycle. What is not apparent is the early history of the species which is hidden in the antlers': pattern of hormonal regulation, histological structures, regenerative capacity and shape. The last is represented by patterns of ramification and bending of beams and tines. Both of these are chiefly behaviorally and environmentally dependent. This means that it remains under the selective pressure of social use and its adaptation to the physical properties of habitat and could vary with them. The first three characteristics are more of evolutionary value and will be discussed first.

Microstructure and Ramification of Antlers in Rangifer

The pattern of histological structure of reindeer antlers fits in the general picture of Odocoileidae which differs from that of Cervinae (Bubenik, 1959b). There is a spongy core and a compact mantle with a narrow, superficial band of tangentially arranged, pink colored lammellae of Haver's system (Fig. 1). These, I assume, are responsible for superficial growth of the diameter of the beam (Bruhin, 1953) and temporary hypertrophy leading to ridges around the vessels (Rhumbler, 1911), pearls, coronets and snags (Taylor-Page, 1957) which make the antler surface rough.

But in *Rangifer*, as generally known, the gutters between the ridges are either very shallow or absent. The coronet is only indicated by a few pearls; the beam is entirely smooth. Transverse sections through different parts of the beam show that the blood-filled lammellae are located only on distinct sites of the beam (Fig. 2).

Here, as I observed, instead of only randomly distributed pearls, true or subsidiary tines and ends could be produced as long as the beam was living (Bubenik, 1956, 1959a; Bubenik and Pavlansky, 1965). In other words the ramification of the beam in reindeer is not limited to the process of dividing at the top of the growing beam as is the rule with other cervids (Řeřábek and Bubenik, 1963). It can occur also by supplementary protrusion from any site on the surface below the top of the beam (Fig. 3). I call such a ramification process *accessory* as opposed to *synchronous*, which is a dividing of the beam end (Bubenik, 1962).

I have found indications of accessory antler growth in other cervid species as well, such

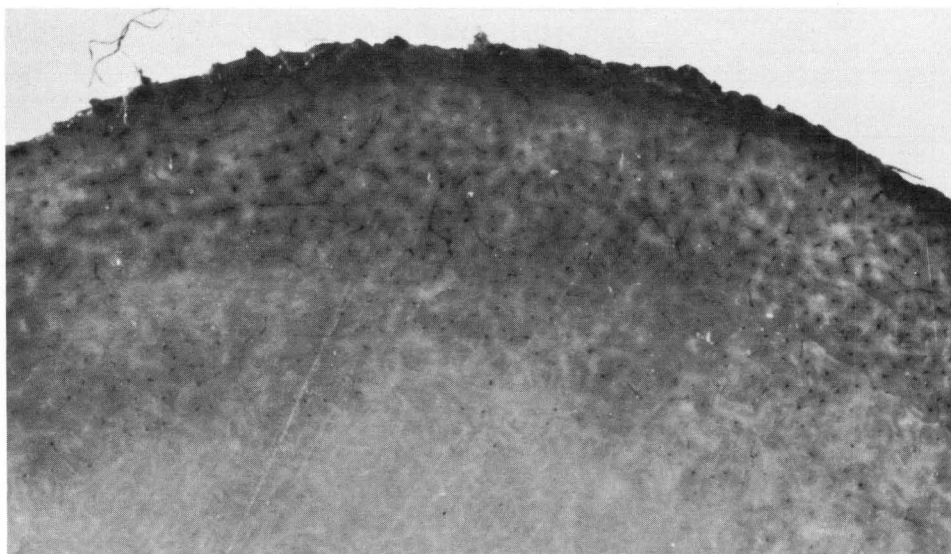


Fig. 1.—Anterior edge of reindeer antler in cross-section. Note the tangentially oriented lamellae filled by blood.

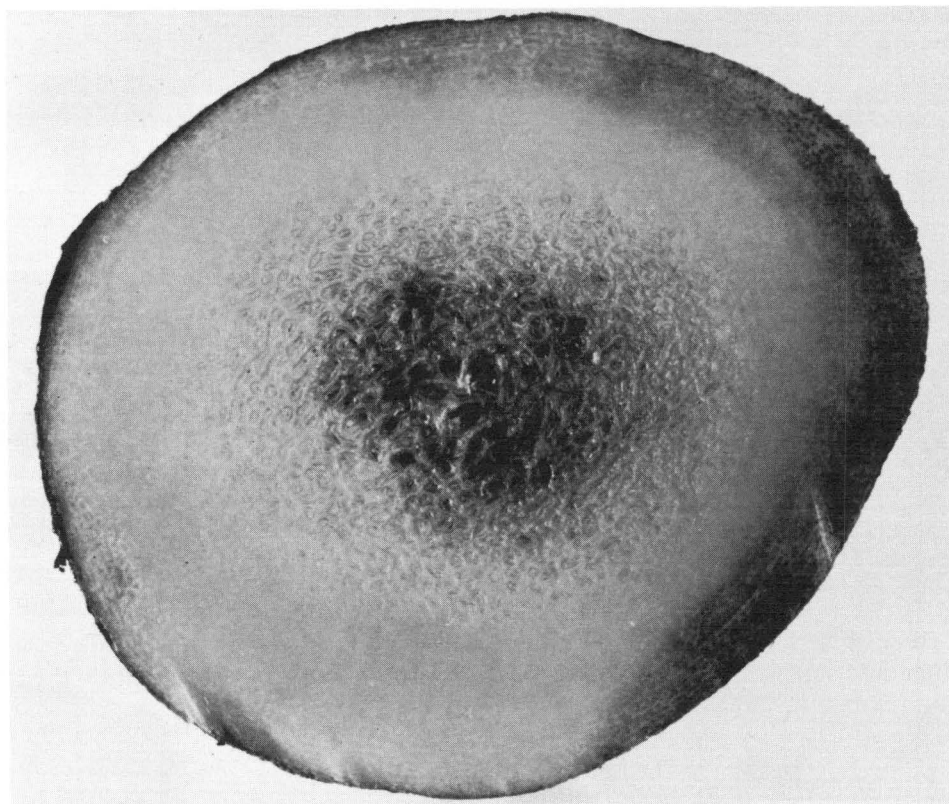


Fig. 2a.—Whole view of the cross-section from Figure 1.

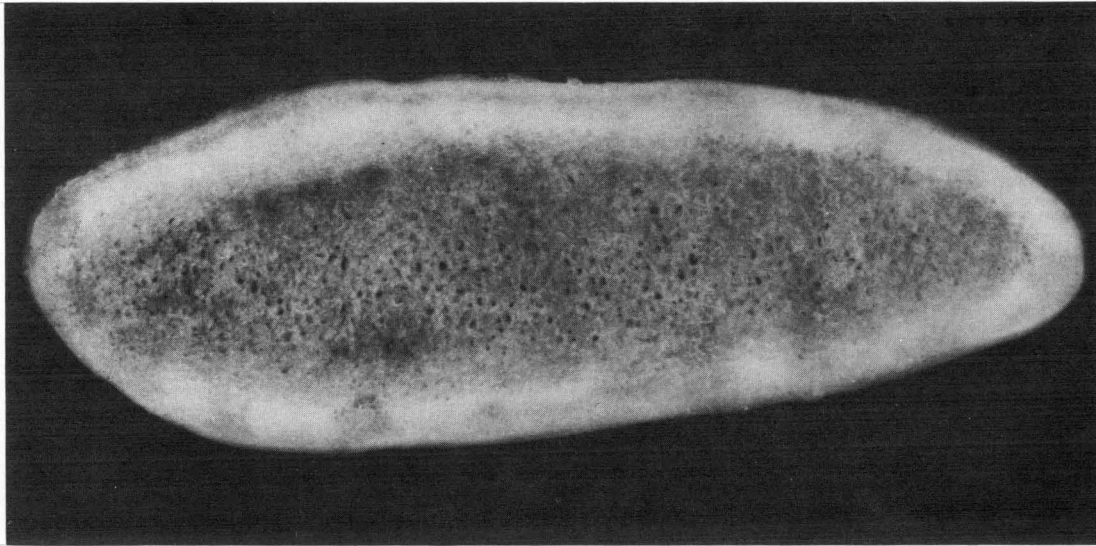


Fig. 2b.—Cross-section of reindeer antler beam above the third tine.

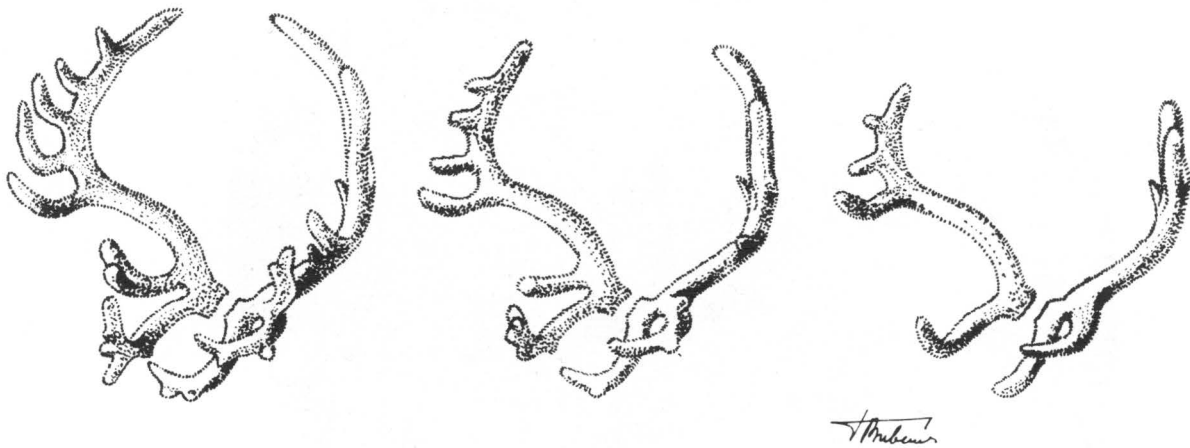


Fig. 3.—Accessory ramification in antlers of three year old reindeer bull. Note the growth of tines and snags from brow tine up to the terminal zone throughout the whole growing period (Bubenik, 1956).

as white-tailed deer (*Odocoileus virginianus*) and roe deer (*Capreolus capreolus*), but the process was always limited to the basal part of the beam and tine-like snags (Bubenik, 1966). In red deer (*C. elaphus*) it can occur only in the first set of antlers (Bubenik and Munkačević, 1967). I have no evidence of any case in the above mentioned species where a broken or amputated tine was regenerated in the same velvet period, as is quite customary in

Rangifer (Bubenik, 1956).

Homologous processes of such a grade are known to me only from the oldest Pecoras of the Miocene period in Eurasia and America, which I have placed in the now extinct family of Procervuloidae (Bubenik, 1962). In species of this family the accessory ramification was either the only one or it was equivalent to the synchronous forking. The Procervulids were vellericorn (Frick, 1937), and the oldest of them did not develop a mantle of ivory bone and their ossicornes were still alive. In America they are represented by the very primitive Miocene Blastomericinae and more advanced Merycodontinae which could not be antilocaprids as suggested by Frick (1937) (Fig. 4). The most common Miocene

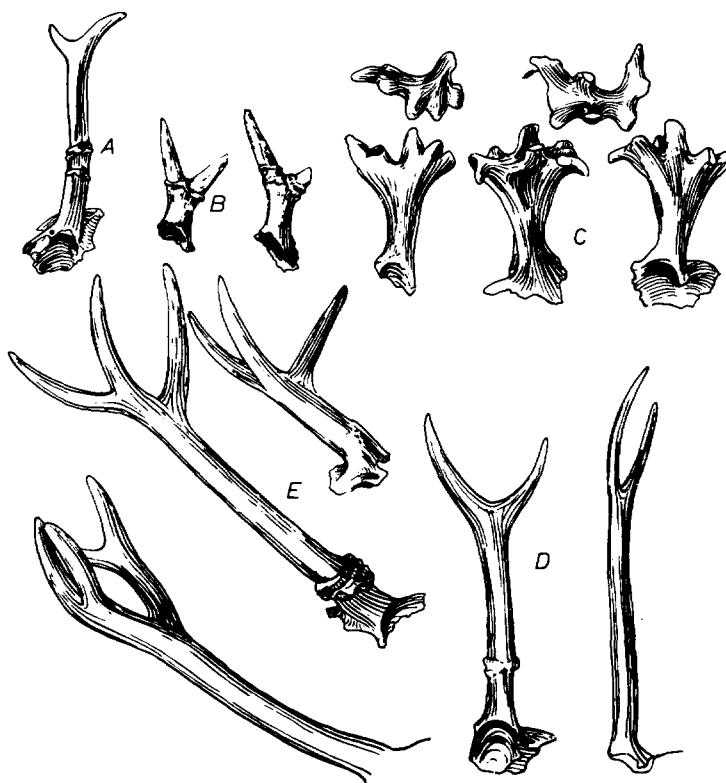


Fig. 4.—Probable procervulids of N. American Miocene which Frick (1937) considered as antilocaprids: A — *Cosoryx* (*Paracosoryx wilsoni*), B — *Meryceros submeryceros*, C — *Ramoceros* (*Merriamoceros*) n. subg., D — *Cosoryx* (*Paracosoryx alticornis*), E — *Ramoceros ramosus quadratus*.

procervulids of Eurasia are *Lagomericidae* and the dicrocerids from Sansan, France (Bubenik, 1962). A search for fossil Neocervines with antler properties similar to *Rangifer* could be, therefore, one of the ways in which we might come closer to understanding the origin of *Rangifer*, the mysterious genus.

Accessory Ramification in Rangifer

There is enough evidence that in reindeer the accessory ramification of antlers is used as often as the synchronous forking. Possibly in the early stages of organogenesis of antlers an accessory ramification was more advantageous. In reindeer antlers we can see that accessory branching could be used to improve the structural pattern when synchronous forking was set off. This is a rather hypothetical assumption, based on two observations which of course could be chance. Despite the high probability of being by chance, they appear to me so important (in searching for other similar materials) that I cannot leave them unmentioned in this report.

The first case is a direct observation, recorded in my paper about antlerogenesis in reindeer (Bubenik, 1959). A tine above the second one, just at the beginning of its growth, was so badly injured that it had to be amputated. In a very short time this tine was regenerated and its shape matched with astonishing accuracy the branching pattern and hypothetical plane of the antler structure (Thompson, 1942) (Fig. 5).

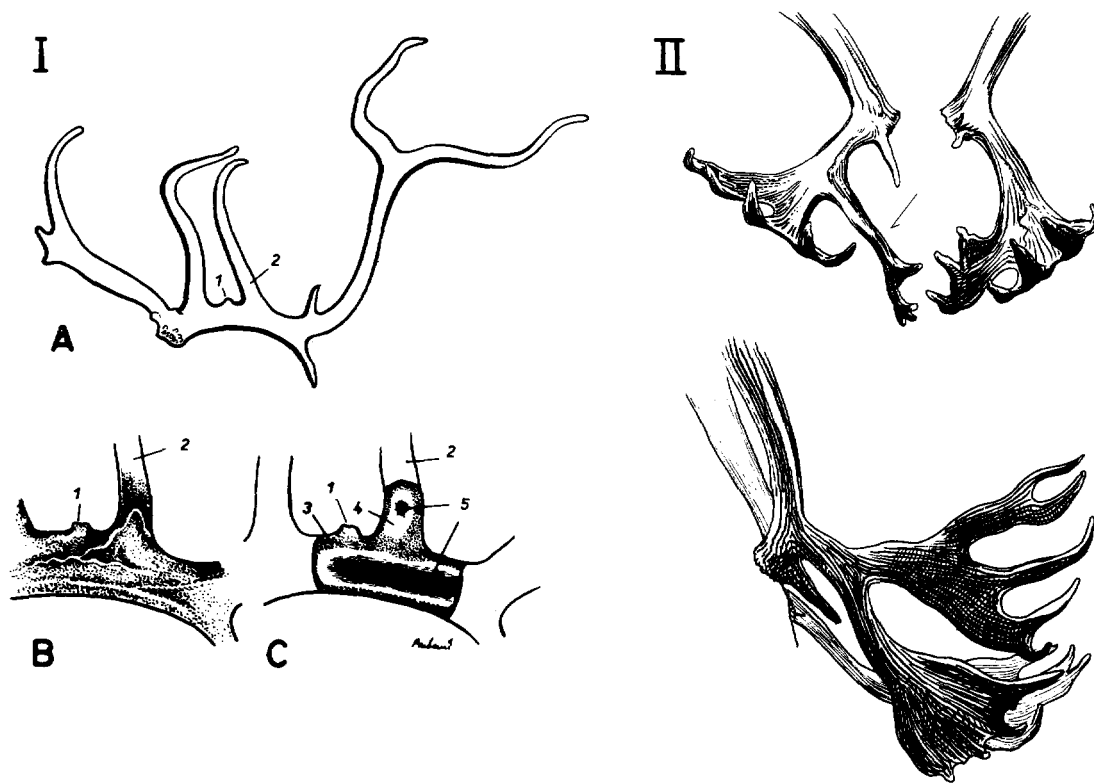


Fig. 5.— (I) Accessory regrowth tine (2) after amputation of the original one in reindeer antler: A — the whole antler with the rest of amputated tine (1), B — partial view on arterial bed to the new tine, C — section through the beam, the amputated and regenerated tine: (3) — the layer of tangential with blood filled lamellae, (4) — compacta, (5) — spongiosa. (II) Reconstruction of brow tine from the lower part of second tine in barren ground caribou (specimen of J. Hemming).

The other peculiar case concerns a set of antlers collected by J. G. Hemming in October 1968 at Anaktuvuk Pass, Alaska. In this very fine specimen the brow tines are only poor spikes (Fig. 5). Surprisingly a new tine, separated from the lower part of the right second tine, separated very early from the shaft and changed shape and direction in a way that it nearly replaced completely the brow tine. I cannot imagine mechanisms that allow such transformations to take place or what kind of control over the gaps in antler structure are present in *Rangifer*. Any speculation in this regard seems to me untimely.

I would only point out that *Rangifer* antlers possess astonishing vigor in growth and regeneration of tines. We can really speak about an inner drive to maintain the antlers' optimum structure. This is one of the most astonishing taxonomic characteristics of antlers in reindeer. It indicates the recent age of this genus and the explosive phase of its antlerogenesis (Goss, 1968, 1969).

The Regulation of Antler Cycle in Rangifer

It is hard to believe that there is no knowledge of the pattern of hormonal control in the antler cycle of *Rangifer*. From what we know we can only assume that this pattern of hormonal regulation must be quite different from all other genera of Cervidae (Fig. 6).

Reindeer fetuses of both sexes have pedicle bases and the calves are born with growing pedicles (Banfield, 1954; Frankenberger and Bubenik, unpubl.). Castration of males does not stop pedicle or antler development and periodicity. Since both sexes carry antlers, it is necessary to assume that testosterone is not greatly involved in these processes and that its action is substituted by another hormone.

I suggest that this hormone should be searched for among the corticoids because some of them could be transformed into substances with androgenic character (Forsham, 1965) or at least with growth inhibiting and/or calcifying effect. Certainly the lack of testosterone does not induce the uncontrolled proliferation of velvet and antler tissue that leads to perruque-like organs in castrated males of evolutionally older genera (*Muntiacus*, *Capreolus*). In such antler cycles testosterone has a dominant position in calcification and the casting processes (Bubenik, A., 1966; Bubenik, G., 1972; Tachezy, 1956).

This does not mean that perruque-like proliferation is unknown in *Rangifer*. It appears in the best conditioned bulls of both subspecies. Two kinds of perruques are known: those in which only the velvet proliferates, and those in which the antler tissue also proliferate. In both of these cases the perruques are probably localized only on one beam and one site (Fig. 7). Proliferated velvet will be shed and there is no subsequent evidence of this process on the hard antlers. In the case of proliferated antler tissue, this becomes calcified and remains on the antler (Fig. 7).

In general we can conclude that the role of testosterone in the antler cycle of reindeer is minor. It is neither necessary as the inductor of the pedicle nor as the inhibitor of antler growth (Blauel, 1935, 1936; Bubenik, G., 1966; Frankenberger, 1953, 1954; Goss, 1968; Tachezy, 1956; Tandler and Grosz, 1913; Wislocki, 1956). The absence of testosterone causes in reindeer only a delay in casting of antlers and inhibition of shedding of velvet (Banfield, pers. comm.; Jacobi, 1931; Herre, 1955; Tandler and Grosz, 1913).

Under such conditions we may suggest that there are no physiological objections to females having antlers and antlers can develop as species specific releasers in both sexes even in prepubertal age (Banfield, 1954; Jacobi, 1931; Murie, 1935). When the testosterone role in the antler cycle is of such low importance it becomes possible that under deep stress, as during an exhausting rut, some older bulls can drop their antlers before the rut comes to the end (Murie, 1935). Because of this, bulls without antlers immediately lose their social rank and cease their sexual activity (Espmark, 1964a, b). They start to feed and recover better

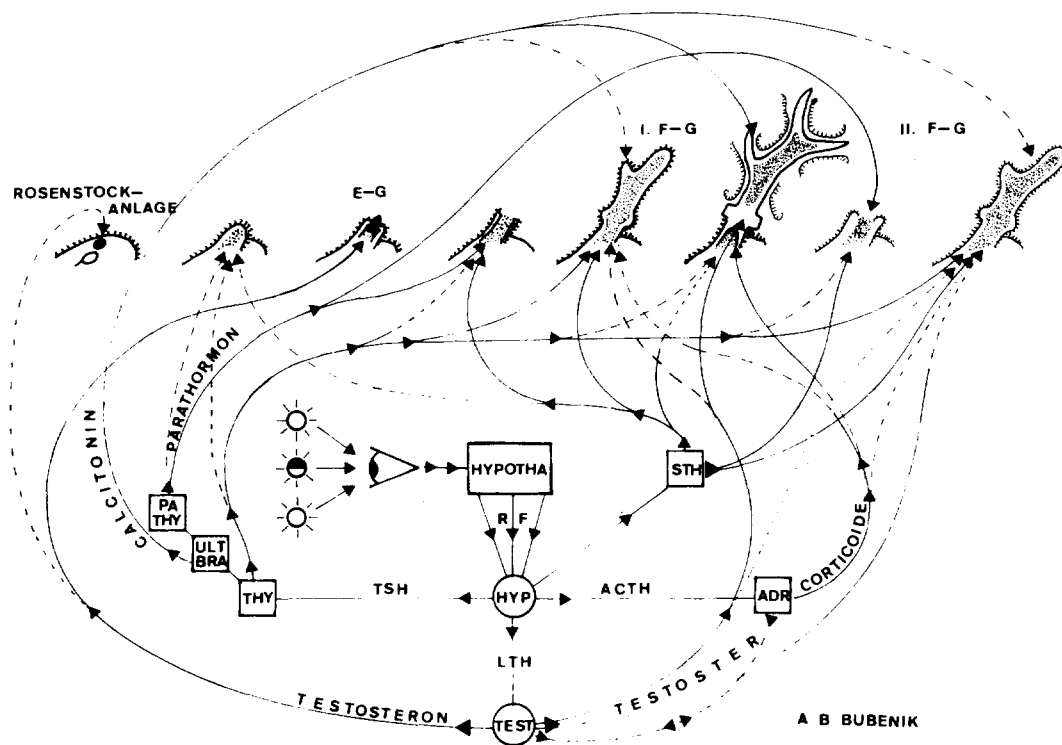


Fig. 6.—General scheme of neurohormonal regulation of pedicle and antler growth: Rosenstock-Anlage = pedicle basis, E-G = primary (first) antler, I. F-G = first set of following antlers, II. F-G = second set of following antlers, HYPOTHA = hypothalamus, RF = releasing factors, HYP = pituitary glands, THY = thyroid, ULT-BRA = ultimobranchial bodies, PA-THY = parathyroid, ADR = adrenals, TEST = testes.

than many prime bulls which were active through the whole rut. In the severe conditions of the Subarctic and Arctic such a self-sustaining mechanism could be of great survival value.

We know that in the evolutionally oldest genera with primitive antler characteristics (*Capreolus*, *Muntiacus*) testosterone is the only agent responsible for control of antler growth and antler cycle. In more recent genera (*Odocoileus*, *Cervus*) the influence of testosterone in the antler cycle is less. Lack of this hormone, as caused by castration for example, stimulates antler growth but does not induce uncontrolled proliferation and perruque-like organs. The calcification of antler tissue continues at a lower rate. Following the evolutionary trend of how testosterone interferes in antlerogenesis we could assume that in the most recent cervids its influence should be the lowest of all, i.e., it will neither inhibit the growth nor the antler cycle. This is the situation which we have in *Rangifer* and what I have suggested in the more primitive Procervulids (Bubenik, 1962).

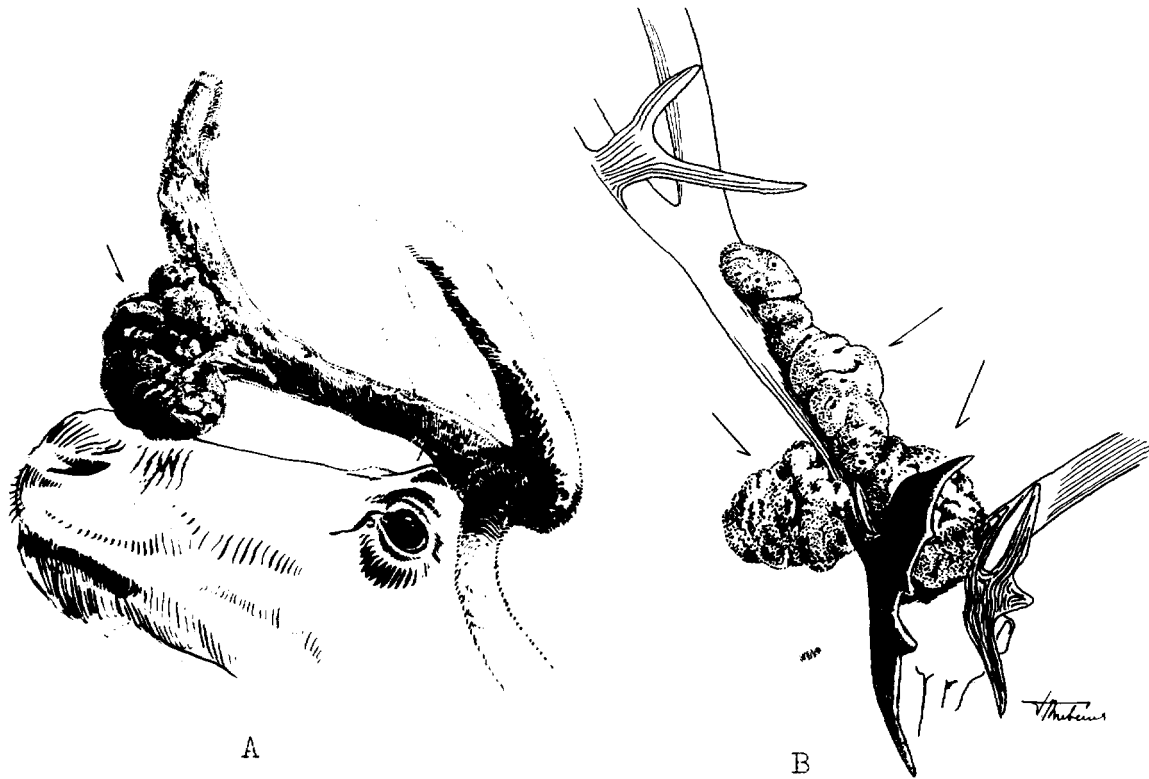


Fig. 7.—A: Proliferation of velvet in reindeer. B: Proliferation of antler tissue in woodland caribou (Dugmore, 1913).

Structure and Architecture of Antlers in Rangifer

The structural patterns of antlers in reindeer are among the most complicated of all. The pattern is stabilized only in the lower part. This terminates with a short third tine, which is not oriented posteriorly (Banfield, 1961; Kelsall, 1968; Murie, 1935), but medial-posteriorly, similar to that in fallow deer (*C. dama*), chital (*Axis axis*) and others. The bending and shape of the first two tines of reindeer antlers are genus specific. The medial-posterior third tine seems to be in regression and, therefore, without taxonomic value.

Up to the third tine the beams in lateral view are usually very uniformly bowed. However, from the front they vary considerably in males, less in females.

The structure and architecture of antlers above the third tine vary widely. It is this part of the antler structure which frustrates the taxonomists. The 'bow' and 'sharp' bend of the beam above the third tine cannot be accepted as taxonomic characters as long as we do not know their origin, or function. They are not specific for American or European subspecies as postulated by Gripp (1943) and Jacobi (1931).

Probably the only useful taxonomic characteristic is the shape of the beam in cross-section. Tundra and taiga reindeer are presently divided by the description 'cylindricornis' and 'compressicornis' (Jacobi, 1931).

Evolutionary Differences Between Male and Female Antlers

It is regrettable that taxonomic studies have not paid enough attention to the taxonomic significance of female antlers in reindeer. All my experience suggests that female antlers represent the earliest stages of structural pattern in the antlerogenesis of *Rangifer*. Therefore they could be of greater taxonomic value than male antlers (Fig. 8).

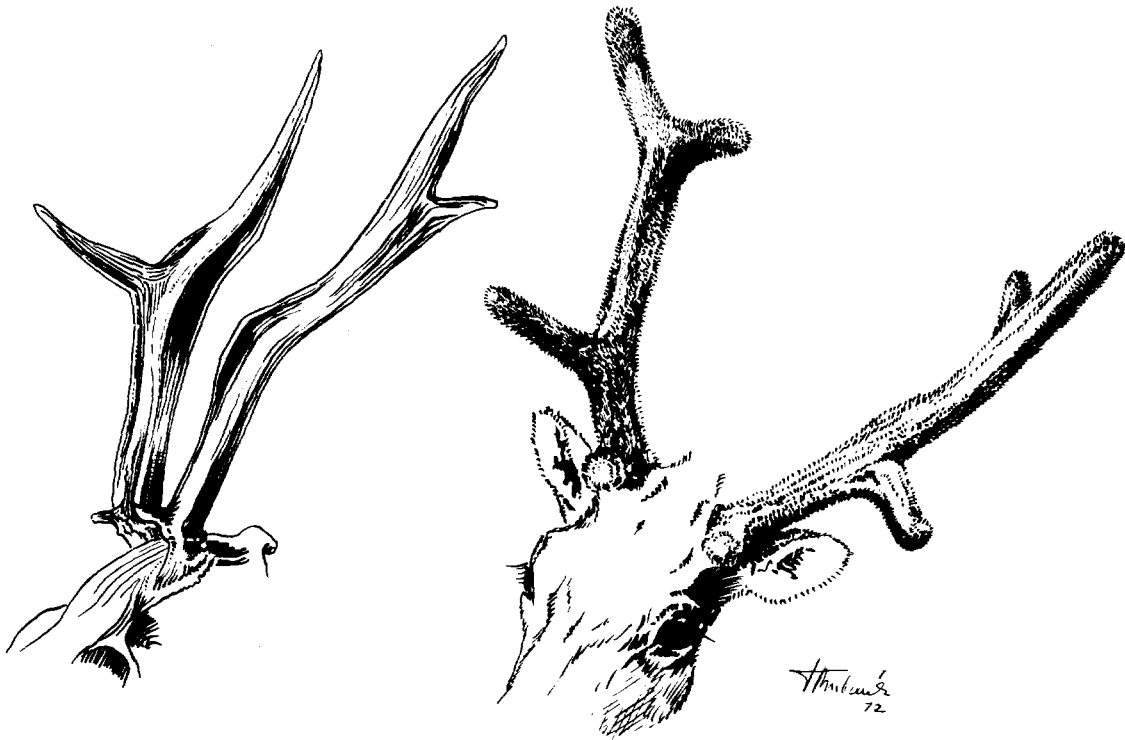


Fig. 8.—Antlers of females in *Rangifer*.

The whole pattern in female antlers indicates that they are created more for offensive threat than those of males. The observations of Espmark (1964a), Henshaw (1968), Lent (1965a, b, 1966) and Pruitt (1960, 1966) about significance and use of antlers in barren ground caribou support my conclusion about the offensive character of antlers in females.

I cannot agree with Henshaw (1968) that antlers in reindeer females developed independently from male antlers to give social advantage to gravid females. I suggest that the explanation of this phenomenon is much more simple. Due to the special pattern of hormonal regulation of antler cycle there are no reasons why females cannot have antlers. I recognize many of the arguments of Henshaw and will say that because of these advantages the females have retained their antlers even though they do not develop them to the same extent as in males. The explanation I think lies in pregnancy, the nutrients needed for the fawn, and in the social circumstances existing during the winter. As a result of the fact that the majority of prime-age males 'teenagers,' i.e., males that have not accomplished physical,

physiological and behavioral maturation, are without antlers during the winter, therefore the small antlers of the female are large enough to maintain the necessary higher rank in the population. The early shedding of antlers in barren females may fit the theory of social selection, but it can also be explained by earlier changes in hormonal levels.

Morphometric, physiologic and ethologic studies of female antlers in reindeer should be pursued further. More attention should also be paid to the shape of antlers in castrated males. They may represent intermediate stages of antlerogenesis between the more primitive structures in females and the more advanced in males. After this general consideration of antler shape in reindeer let me now pay more attention to its details.

First tine: (Fig. 9) The first tine in *Rangifer* antlers is homologous with the brow tine

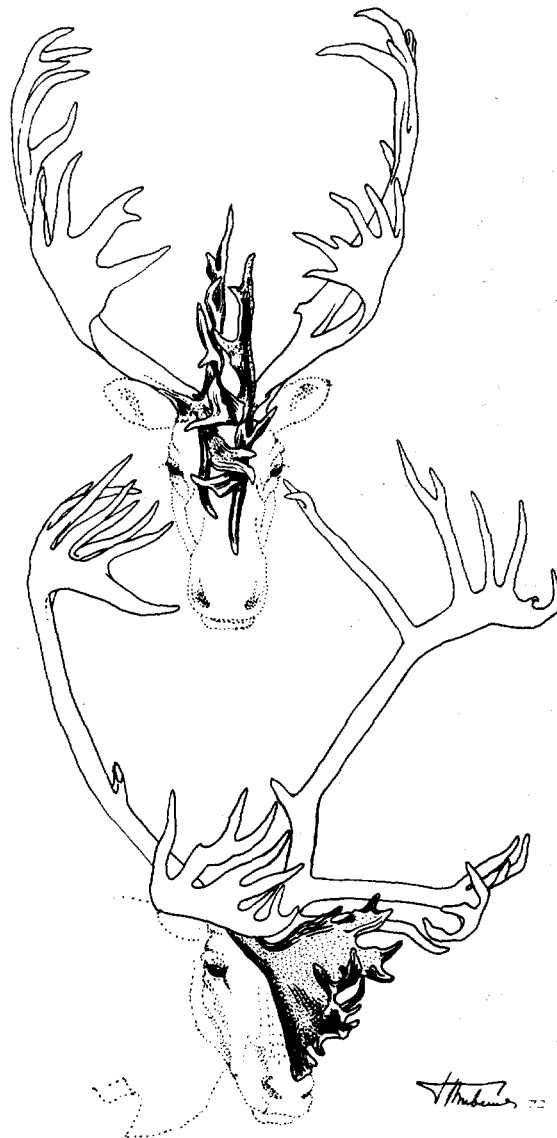


Fig. 9.—The alternate bending of points in the brow tine of reindeer antlers.

in *Cervus*. In mature, well-fed bulls it is generally palmated. Usually only one brow tine is dominant and extended vertically over the profile of the animal. Banfield (1961) found in 35 sets of barren ground caribou antlers that the left brow tine dominated in 69 per cent of this sample, the right in 23 per cent and in 3 per cent they were equally developed. The sample size is of course too low to allow generalizations about the dominance of the left brow tine. The largest palms I have seen were always on sets of antlers where the brow tine was absent or developed like a spike or fork. The position and shape of this tine is specific to the genus. As I have pointed out in another paper (Bubenik, 1972) the palmated brow tine is of great social significance. The regression of one brow tine and the dominance of the other one may be influenced by selective pressure. I came to the conclusion that from the ethological viewpoint one well-palmated brow tine is more advantageous than two if the antlers are used as offensive weapons. The injuries of face skin and even those of the frontal bones (Fig. 10) demonstrate well that the brow tines of reindeer can be dangerous weapons.

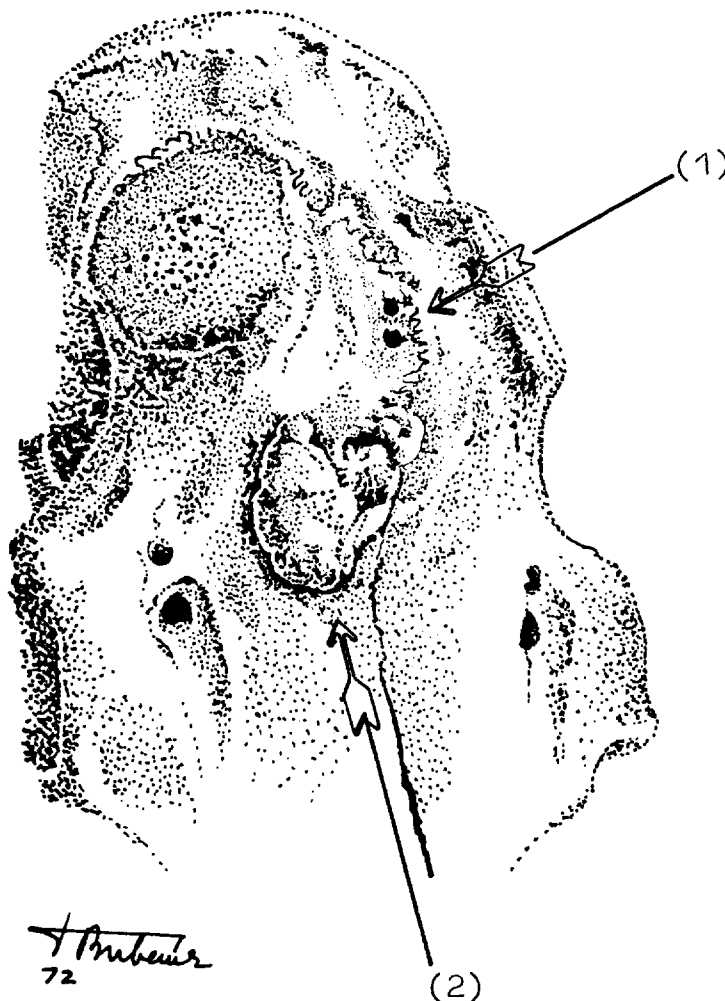


Fig. 10.—Two holes (1) in the forehead bone probably effected by brow tine and exostosis in response to this injury (2).

The fact that in large and long brow palms the points are alternately bent to the left and right could be interpreted as the attempt of selective pressure to minimize the dangerous effect of a direct hit by the brow palm ends.

Second tine: The second tine in reindeer antlers is generally called the bez tine (Murie, 1935; Pocock, 1933) or the bezel (Banfield, 1954). It is necessary to point out that the terms brow, bez and trez tine were originally used only for tines in antlers of cervine species. When they are used in other genera or families it should mean that they are homologous. This is not always true especially in such distant genera as *Cervus* and *Rangifer*. In such cases only in vivo tests on growing antlers (Bubenik, 1966) or very careful ontogenetic comparison can show which, if any, of the tines are homologous or convergent.

The bez tines, i.e., tines homologous with bez tines in wapitoid deer (*Cervus canadensis* with its Eurasiatic subspecies) and red deer (*C. elaphus*) are not true tines like brow tine, trez tine and others. Their history is not clear enough. In *Cervus* species in general the bez tine does not fit into the hypothetical plane of antler structures (Beninde, 1937a, b; Bubenik, 1966). I would suggest that it developed originally as an accessory tine, similar to the more rudimentary medial snag, described by Lehmann (1959). In *Cervus canadensis* and *C. elaphus* it has the important role of providing an effective shield for the eyes (Benzel, 1967; Bubenik, 1966) (Fig. 11).

But the second tine in reindeer fits well into the hypothetical plane of antler structure.

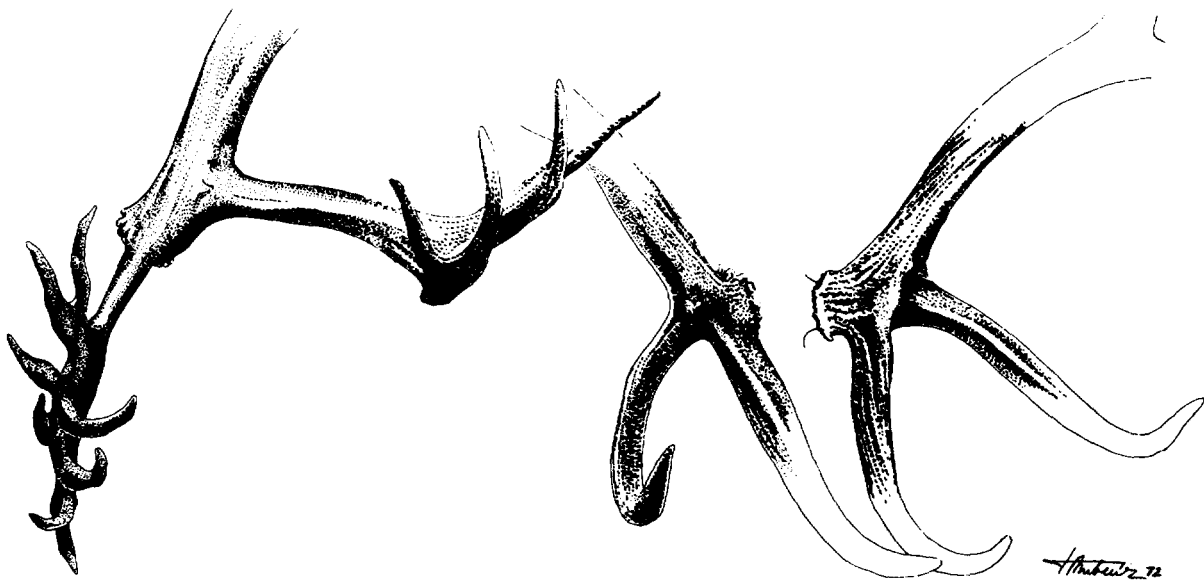


Fig. 11.—Comparison between second tine in *Rangifer* and the bez tine in wapiti (*C. canadensis*): bez tine ramifies underneath the hypothetical plane formed by brow and trez tine.

It is well formed and adapted as a protective shield not only for the eyes but for the whole facial region.

From the ethological viewpoint this shield should be better developed in herds with higher 'social temperatures,' that is, "the social and physical kinetics of the individual" (Calhoun, 1965) and readiness for fighting. One should check morphometrically for any statistical differences in different subspecies or herds between the distance from the first to the second tine, their angles to the beam, palmation grades and outward-inward bending, as suggested by Jacobi (1931) and denied by Fries (1941). The best evidence that the second tine is homologous with the trez tine in *Cervus* is provided by the first and second sets, or poorly developed male antlers, in antlers of castrates and especially in female antlers (Fig. 12). Antlers of females and castrates show clearly that the second tine is the trez tine. Its high location on the beam, its bending and lack of palmation show that it is functionally a

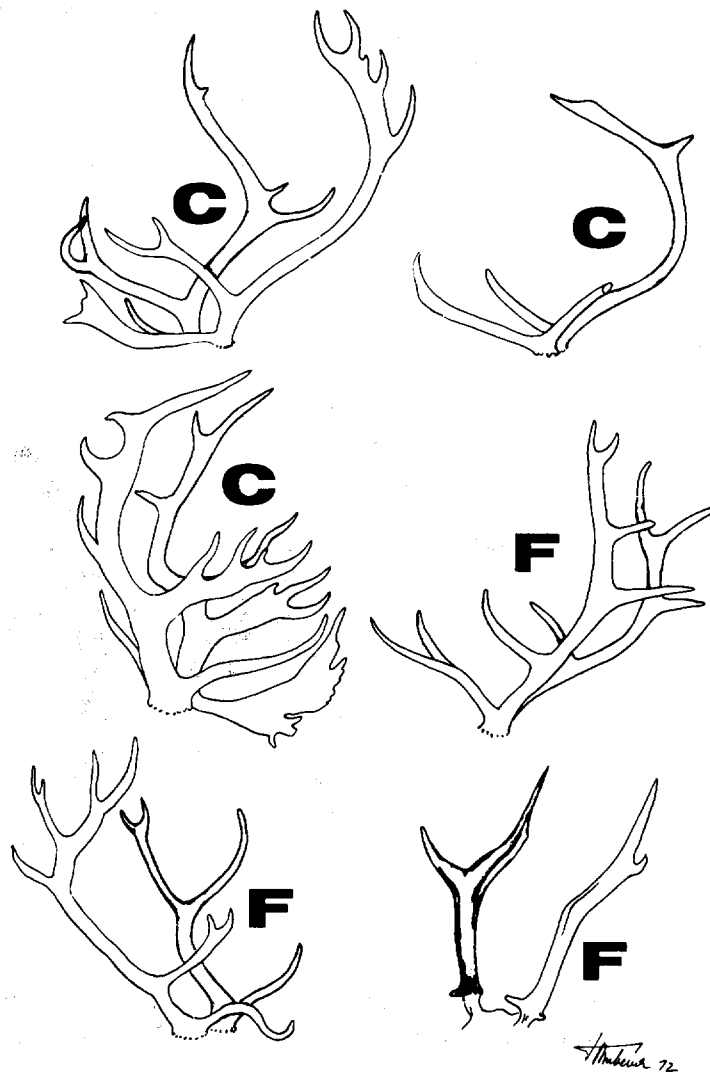


Fig. 12.—The position of second tine in male castrates (C) and females (F).

trez tine, which parries the rival's antlers and holds them away from the face.

Third tine: As I have mentioned above, it is oriented not posteriorly but medial-posteriorly (Fig. 13). In recent reindeer it is usually small or absent. In a few

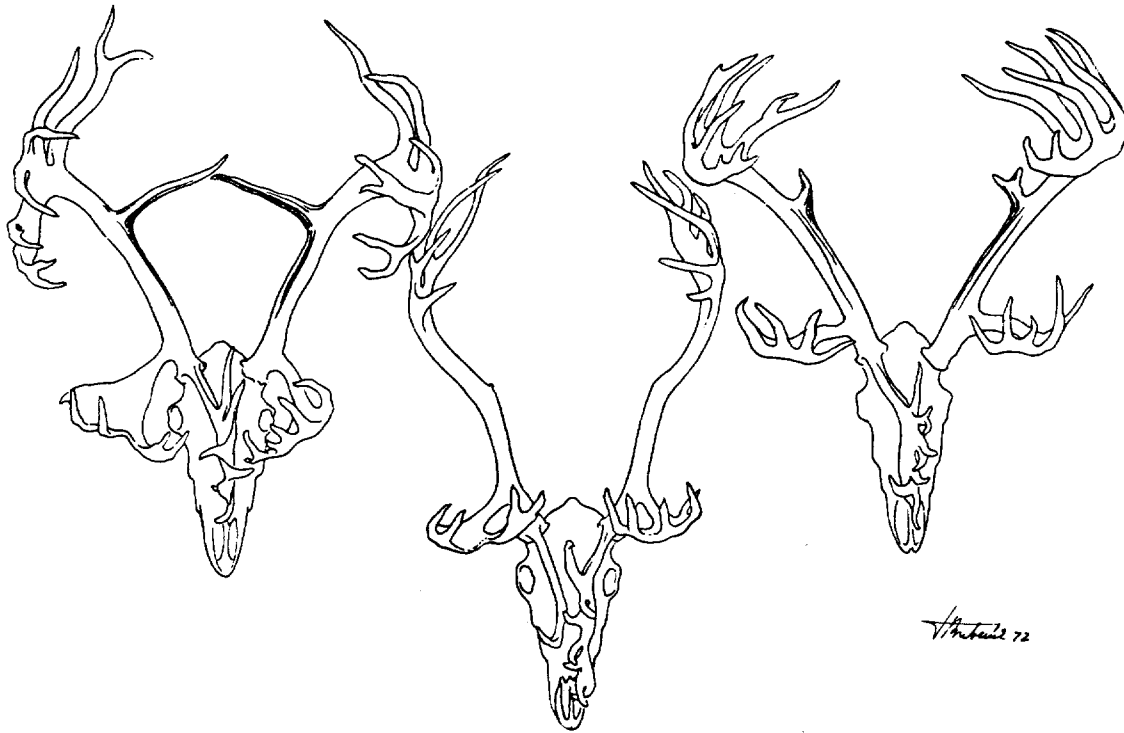


Fig. 13.—Well developed, poorly developed and regressed third tines.

specimens it is large and sometimes bifurcated. Its regression to a rudiment suggests that it is losing its importance. This does not mean that it should not be considered as a taxonomic character. In the ancestors of Rangiferinae this tine was probably as large or larger, as it is known in castrates, females and some males of recent reindeer and caribou.

In recent Cervids the medial-posterior tine (not always the third one) is found in antlers of fallow deer (*C. dama*), where it disappears sometimes in the palm, in axis deer (*Axis axis*) and Eld's deer (*Rucervus eldi*).

All of these species have antlers of poor catching-ability. Some of them like fallow deer and Eld's deer have the upper zones of their antler structures like those of *Rangifer*. It is interesting that the fighting techniques and behavior in combat in fallow deer have elements very similar to those in reindeer. In both species the lateral blow towards the body, which will be caught by the antlers, is used before the antlers crash together. In fallow deer, as in reindeer, three or more stags can fight simultaneously. These facts indicate very primitive, i.e., very poorly ritualized fighting techniques opposite to the view of Müller-Using (1966).

Frequent damage to the third tines of male caribou indicates that these tines are often used. They may serve as hooks or at least as foils which can parry or diminish the blows in the neck region of the distal ends of the rival's antlers.

The Structure of the Upper Zone of Reindeer Antlers

This is a relatively 'unstable' part of reindeer antlers. Regardless of the variability in beam bending (noted above) the most apparent differences are among the types of ramification (Fig. 14). We may see in any population at least two kinds of ramification: the

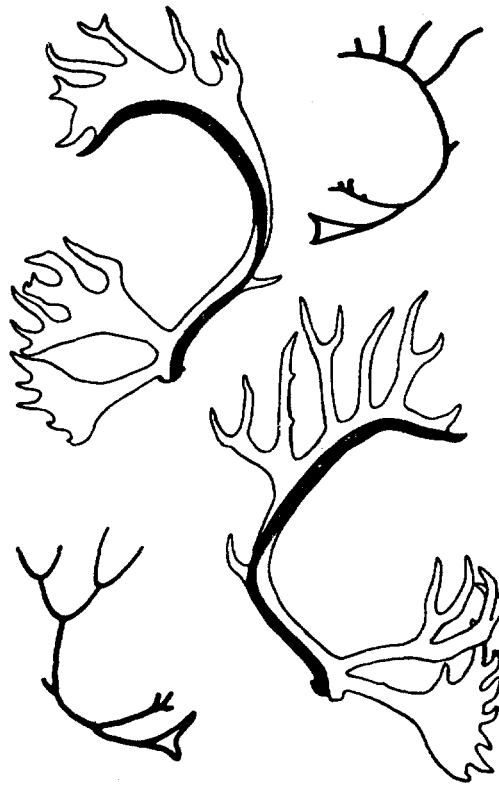


Fig. 14.—Monopodial and dichotomous ramification in terminal zones of reindeer antlers.

single beam (monopodium) with tines on anterior and then posterior edge of beam and the forked (dichotomous) beam. Beams and tines can be hypertelic, i.e., to grow in palms or to fork to the third grade of branching. This produces spaciouly directed ends, called in red deer 'royals' (Fig. 15).

Rarely are tines produced only from the anterior edges of the beam (Fig. 16). This branching leads to structure very similar to that of *Euclados tetraceros*, an extinct, large cervine deer from Villafranchian Europe. It would be most interesting to know if this 'eucladocerine' or simply 'cervicorne' construction is known also in caribou and reindeer of Northern America.

With regard to these three types of ramifications in *Rangifer* antlers, especially in the terminal zone, we must admit that we do not know if each of the types represents a special genetic pattern or if single beams, which are anterior-posteriorly branched, are only the result of poor nutrition similar to red deer in which hypertelic ramification, i.e., 'royals,' can be

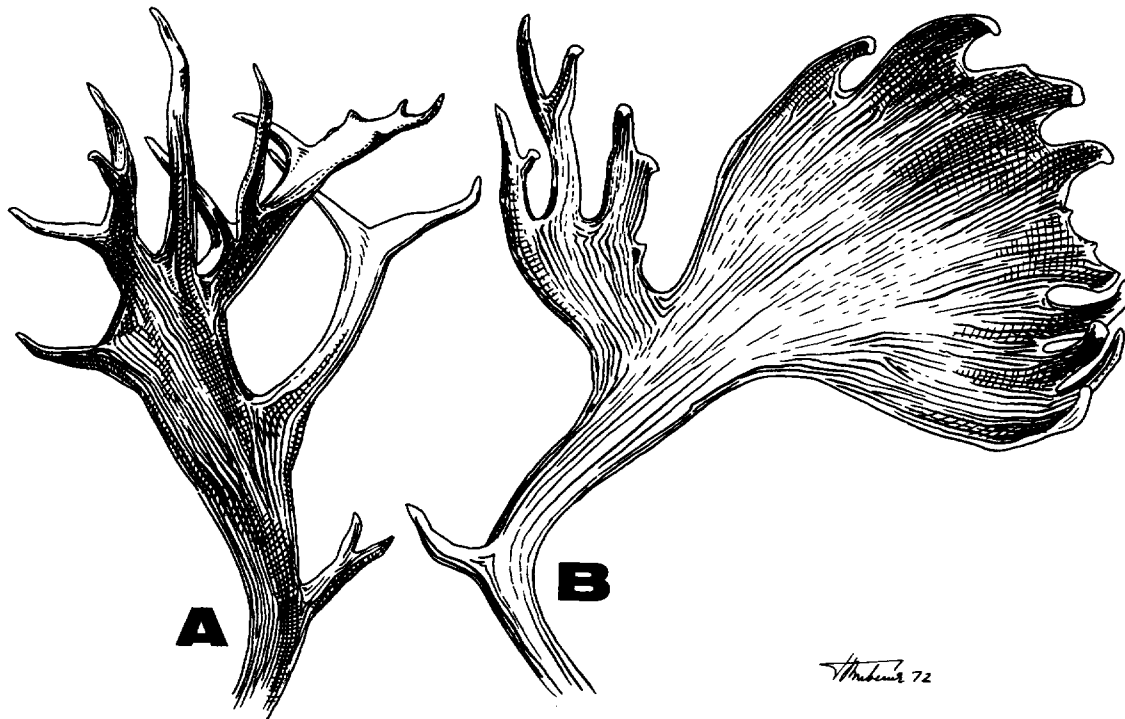


Fig. 15.—Hypertely of terminal zone in reindeer antlers: A — third grade of branching with 'royals,' B — palmation of beam.

formed only under a surplus of nutrients. Hypertelic antlers of zoo reindeer indicate that this assumption may be true. Of course it will not be easy to estimate which of the three types of ramification pattern is of greatest taxonomic value or which is their evolutionary history since we should not take into account such factors as: behavioral patterns of the subspecies, individual rank and environmental conditions. A third possibility should also be considered that one of these types of ramification can be more or less a 'dormant,' i.e., preadaptive pattern, waiting for future circumstances (Portmann, 1960).

In general the large variance of structures in the terminal zone of reindeer antlers shows that it is probably a genus in an evolutionally explosive phase which has not yet reached a culmination as have other recent cervids.

Architecture of Antlers in Reindeer

As I mentioned in the general description, the lateral and frontal bends of beams and tines are broad. From the lateral view the beam could be curved more anteriorly or more sharply bent, but antlers with nearly stretched beams like in *Cervus* species (the cervicorne types) are not unknown. Also the frontal bending of beams shows a very rich pattern of forms and spread. From very wide 'U' forms over 'V' and 'heart'-shaped beams, up to a very narrow 'U', all patterns will be found, but such variability occurs in all species of cervids and



Fig. 16.—'Eucladocerine' type of branching in *R. t. tarandus*.

should be considered only individual-specific. It would be most interesting to test morphometrically if and how 'social temperature,' sociability and environmental structure influence the parameters of antler architecture in *Rangifer*.

The use of antlers in reindeer behavior gives the impression that beam and tine bending of antlers serve chiefly for defensive purposes in combat. It is my assumption that the frontal bending provides a better shield when the hypothetical plane created by tines and ends of antlers is very closed (Fig. 17). If morphometric differences between different subspecies should be found, then I predict that in highly sociable herds with low social temperature and exposed to strong wind will have more open antlers than semigregarious populations living in woodlands.

The Lateral Profile

As I have pointed out in another paper in this volume, reindeer antlers have special aerodynamic properties, i.e., movement in a crosswind is awkward when they are large, appropriately bent and well branched. The relatively simple branched upper zones in barren ground populations and the well branched antlers of woodland caribou could be in relation to the influence of wind (Murie, 1935). My own experiences are related only to barren

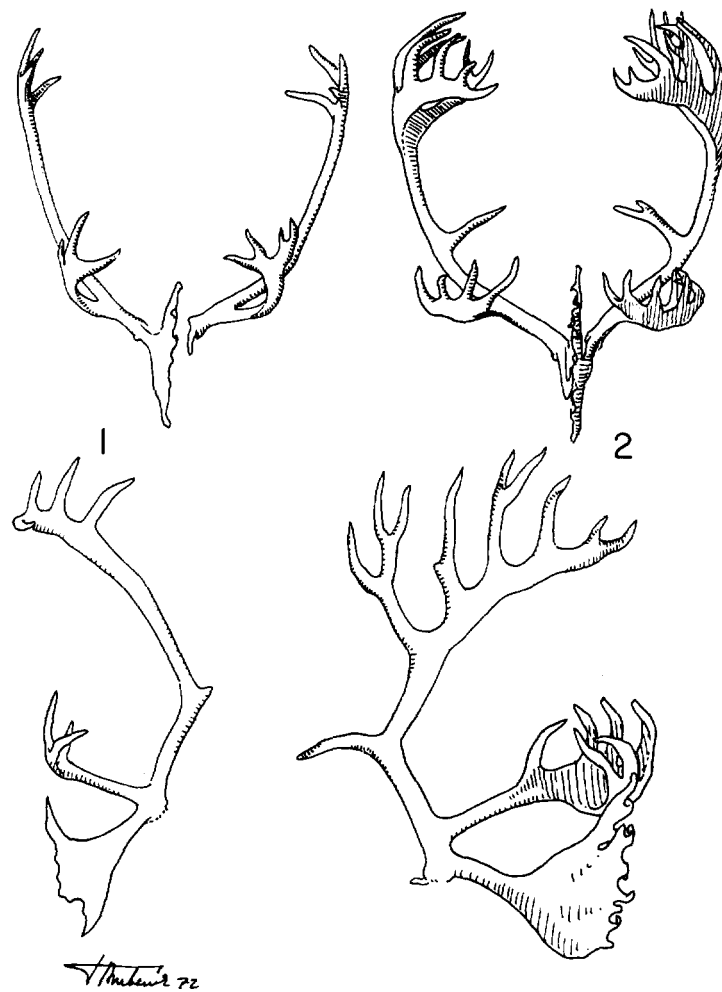


Fig. 17.—(1) Open and (2) closed types of reindeer antlers.

ground caribou of the Arctic and Nelchina herds (Hemming, 1972). Both of these are presently socially disorganized and the Arctic one (at least those seen by me southeast of Selawik) was apparently undernourished. When we compare the size of animals and antlers harvested 20 and more years ago it is difficult to say if the present status of their antlers is representative.

It is also difficult to decide if the length of beam and its lateral bending are different in tundra and woodland reindeer as suggested by Gripp (1943) and Jacobi (1931). Theoretically, and in accordance with the rule of Müller-Using and Schloeth (1967) that environmental conditions influence movement, sociability pattern and antler shape as well—one could expect that: (1) woodland reindeer antlers should be (a) more bent, i.e., their 'C' shape should be more closed, (b) more ramified in all parts of their structure, and that (c) the beam should be flattened to have greater strength because of the higher aggressiveness of bulls holding harems and not accustomed to behavior in rutting communities; (2) in tundra reindeer the reverse characteristics should be prevalent: (a) the beams should be

more widely bent, (b) the ramification should be more simple, and (c) the beam more cylindrical as a result of the more altruistic behavior necessary in large herds with communal rut.

Of all these characteristics only one is presently accepted: the beam profile which should allow us to distinguish the cylindricorn tundra reindeer from the compressicorn woodland races. But, Murie (1935) referred to and I have seen many antlers of tundra reindeer which were flattened too. In this regard Banfield (pers. comm.) states the following: "I believe that the caribou of eastern Alaska have woodland blood in them."

From reports of authors studying the migratory behavior of reindeer herds it is evident that woodland reindeer are less sociable, of higher social temperature and higher 'social velocity' (as the measure of social interaction, Calhoun, 1965) and less migratory than tundra reindeer (Banfield, 1954; Bergerud, 1974; Jacobi, 1931; Murie, 1935). These behavioral patterns may be reversed completely as soon as these herds leave the taiga. Then of course one should investigate if the antler shape will respond to other environmental conditions and how many generations of antlers, or reindeer generations, this requires. If such a capability is not found then we may conclude that the incapacity to change antler shape could be a factor which holds woodland reindeer in the taiga.

CONCLUSIONS

Returning to the four points postulated in the section on methods in this paper, I can suggest that:

- (1) There is enough evidence that among living cervids antlers in reindeer represent the most primitive step of antlerogenesis from the viewpoint of physiology, histology and growth.
- (2) Our knowledge about relationships between antler shape and behavior is presently insufficient to decide which of these two is the cause and which is the effect.
- (3) Knowledge about the relationships among antler shape, behavior and environmental factors is incomplete but it may be concluded that structure, architecture and cycle of antlers in *Rangifer* are well adapted to life in arctic conditions and the social behavior of the animals.
- (4) Without an intensive morphometric and behavioral investigation which will take in account environmental influences, the current taxonomic value of antlers in reindeer is limited to two possibilities.
 - (a) In prime, well-fed males it is only a genus-specific taxonomic character as far as it can be related to the basic structure of the ramification pattern. The other parameters of antler shape which I have grouped under architectural details could be subspecific or individual characteristics or could represent the pressure of particular environmental conditions. Up to now data are not available to draw valid conclusions.
 - (b) The character of antler tissue, antler shape and use of antlers in females and castrates are taxonomic characters which could provide clues to the ancestors of *Rangifer*. The data concerning these characteristics are so few that up to now we can only speculate about them. It is my expectation that when investigations of these matters are completed the taxonomic value of reindeer antlers will attain great significance.

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RADIOCESIUM CYCLING IN REINDEER/CARIBOU

Dan F. Holleman and Jack R. Luick
Institute of Arctic Biology
University of Alaska
Fairbanks 99701

ABSTRACT—There are several factors which determine the radiocesium body burden of a terrestrial animal. Factors of primary importance include: (1) the intake of radiocesium, (2) the absorption of radiocesium from ingested foodstuffs and (3) the kinetics of cesium in the animal. By evaluating each of these factors, an operational model was developed which described the annual cycle for the radiocesium body burden in reindeer/caribou. Both analog and digital computer simulations of the annual cycle have been attempted and the results of these simulations are presented.

Several factors influence and ultimately determine the body burden of an environmental contaminator for terrestrial animals. These include the intake of the contaminator, absorption of the ingested contaminator and the kinetics of the contaminator in the animal. Although these factors are qualitatively obvious, often they are difficult to evaluate quantitatively. The objective of the present study was to evaluate the factors which influence the radiocesium body burden of reindeer/caribou of interior Alaska. Once the factors were established quantitatively an operational model could be developed to describe the annual cycle for the radiocesium body burden in this arctic herbivore.

These studies were conducted at the Cantwell Reindeer Research Station, Cantwell, Alaska and the Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska.

MATERIALS AND METHODS

Experimental reindeer were injected intravenously with radioactive cesium (^{134}Cs) to determine the *in vivo* kinetics of cesium in reindeer/caribou. Following the single cesium injection, the body burdens of the reindeer were monitored periodically for approximately 30 days. Whole body counting techniques were used. Details of the counting procedures and equipment have been discussed previously (Holleman *et al.*, 1971). The cesium retention data for each experimental reindeer was plotted as the logarithm of the cesium body burden versus the time after the single injection of ^{134}Cs and the resulting curve was resolved into two exponential components. Retention studies were performed at various times of the year to obtain the seasonal influence on the cesium kinetics in reindeer/caribou.

Lichen feeding trials were conducted using 10 reindeer to determine the extent to which ^{137}Cs was absorbed from fallout contaminated lichen. All reindeer, except for the two controls, were kept in individual pens and offered only lichen. Groups 1, 2 and 3 were fed lichen *ad libitum*, 1.3 per cent and 1.0 per cent of body weight per day, respectively. The control reindeer were given essentially cesium-free, commercial livestock pellets only. Prior to the experiment all reindeer were maintained on the low cesium commercial diet. At the completion of the feeding experiment the reindeer were killed and the ^{137}Cs concentrations in skeletal muscle, viscera, bone and hide were determined by gamma-ray spectroscopy. An absorption factor was calculated for each reindeer from the measured

cesium body burden and the cesium intake of each animal. Previously determined cesium kinetics for reindeer were used in the calculation.

Forage intakes for freely grazing caribou (or reindeer) were estimated from measured ^{137}Cs body burdens of field collected caribou and from ^{137}Cs concentrations of plant material consumed by these animals. ^{137}Cs body burdens of caribou were taken from published data (U. S. Publ. Hlth. Service, 1968) as well as collections made during this study. All animals were collected from the Nelchina caribou herd which ranges south of the Alaska Range in the interior of Alaska (Hemming, 1971). Concentrations of ^{137}Cs were determined in plant species taken from the same locale. Radiocesium intakes were then calculated from this data and the kinetic model developed previously (Holleman *et al.*, *ibid*).

The kinetic model was patched on an analog computer (EAI, TR-20) and the annual cycle for the cesium body burden of reindeer/caribou was simulated. Kinetic parameters as well as the radiocesium intakes were altered during the cycle. These alterations corresponded to measured changes in kinetics and intakes. Simulations of the cesium kinetic model were obtained from digital computation using the computer program SAAM (Berman and Weiss, 1966).

RESULTS

In vivo kinetics of cesium — The retention of ^{134}Cs following single intravenous injection could be described as the sum of two exponential terms for all reindeer tested. A two component, exponential retention for a single injection suggests a two compartment model, such as the model shown in Figure 1. In Figure 1, Q_1 and Q_2 represent the quantity

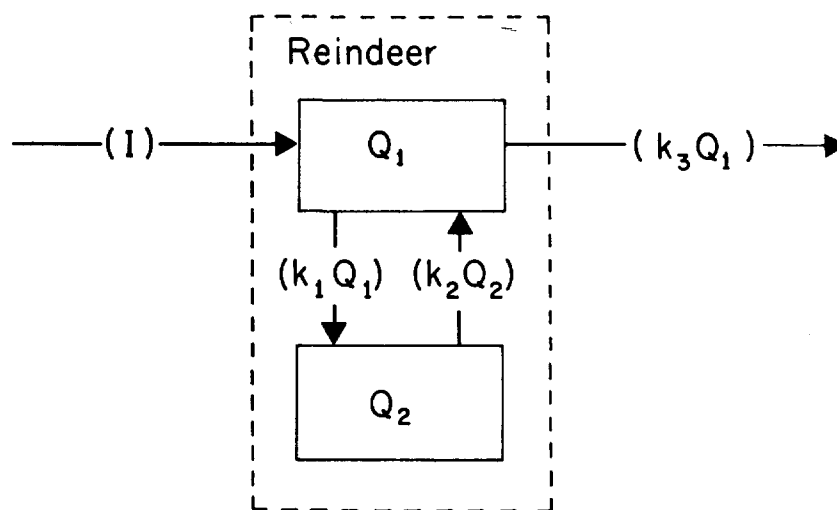


Fig. 1.—A schematic representation of the proposed model for the radiocesium kinetics in reindeer/caribou.

of radiocesium in its respective compartment, thus Q_1 plus Q_2 equal the total body radiocesium in the animal. The kinetic factors k_1 , k_2 and k_3 are fractional rate constants, representing the fraction of the pool eliminated (transferred) per unit time. The product of

the pool size and a corresponding fractional rate constant is equal to the transfer rate for that particular elimination component. If the radiocesium intake (I) is constant (as contrasted to a single injection) the resulting radiocesium body burden (Q) becomes:

$$Q = I (C_o + C_3 e^{-m_1 t} + C_4 e^{-m_2 t}) \quad \text{eqn. 1}$$

under the conditions that Q is equal to zero at time zero. The kinetic term in parenthesis is only a function of time (t) and the fractional rate constants. This equation has been presented in detail elsewhere (Holleman *et al.*, *ibid*).

Values for the fractional rate constants are influenced by the diet of reindeer/caribou, therefore they are dependent upon the season of the year. Figure 2 shows the relationship

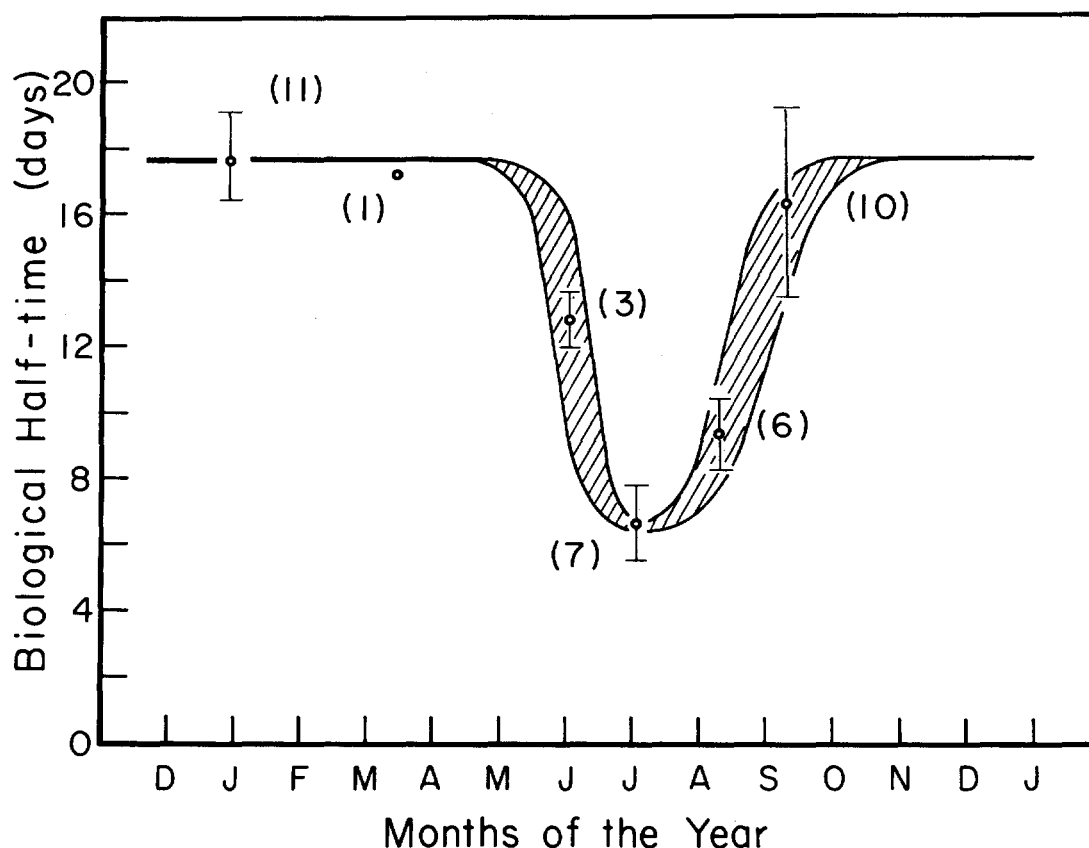


Fig. 2.—The biological half-time of radiocesium in reindeer as related to the annual season. Values in parenthesis refer to the number of experimental reindeer contributing to the mean (circles). The bar through each mean represents the standard deviation. Transition periods for the diet of reindeer/caribou are indicated by the lined areas.

between the biological half-time of the slow elimination component for cesium and the month of the year. The cross-hatched areas indicate transition periods from a winter to summer diet during June and from a summer to winter diet during August and September.

Absorption factor — The results of the lichen feeding trials are presented in Table 1. The average lichen consumption rates and the radiocesium body burdens at the time of slaughter are given for each reindeer. The length of the feeding trials were 38 and 52 days

TABLE 1.--Summary of the data contributing to the calculation of an absorption factor and the absorption factor for ^{137}Cs in reindeer.

Reindeer	Average lichen consumption rate (g/d)*	Radiocesium body burden (nCi)	Radiocesium in skeletal muscle (%)**	Absorption factor
Group 1 (<i>ad libitum</i>)				
C-12 (control)	0	<3.0	--	--
C-18	1440	131.5	77.5	0.25
C-22	1490	120.2	79.4	0.22
C-23	1381	124.3	76.5	0.24
C-8	1317	154.8	82.0	0.31
Group 2 (1.3% body weight per day)				
#21	1110	71.4	81.7	0.20
#42	780	48.7	83.2	0.22
Group 3 (1.0% body weight per day)				
#20	1040	69.0	83.5	0.19
#46	500	35.7	82.7	0.25
#47 (control)	0	<2.0	--	--
			80.8 (2.7)***	0.24 (0.031)***

*Measured as dry weight.

**Per cent of ^{137}Cs body burden present in skeletal muscle.

***Mean (S.D.).

for group 1 and groups 2-3, respectively. The percentages of the cesium body burdens in skeletal muscle are also listed on the table.

The intake of radiocesium (I) can be resolved into the rate of food consumption (R), the mean concentration of ^{137}Cs in the food (c), and the absorption factor (a). The relationship is $I = Rca$. Substituting into equation (1) and rearranging to solve for the absorption factor yields,

$$a = Q/[Rc(\text{kinetic term})] \quad \text{eqn. 2}$$

An absorption factor was calculated for each reindeer and this data appears in Table 1.

Radiocesium intake — At present the only significant quantities of fallout radiocesium contaminating plant material which contribute to the diet of reindeer/caribou are associated with lichen. Therefore, the radiocesium intake is directly proportional to the intake of these plants. The average ^{137}Cs concentration for four caribou sampled in late spring, 1968, was 9.9 pCi/g of wet muscle (U. S. Publ. Hlth. Service, 1968). The reported radiocesium concentration in lichen was 36 pCi/g (dry weight). Under these conditions the present model would predict that these caribou were consuming 3 kg (dry weight) of lichen per day. Lichen consumption rates calculated from muscle and lichen samples collected during this study yielded similar values for the period of late autumn through the middle of spring. Samples collected in late summer yielded lichen consumption rates of approximately 20 per cent of the winter consumption rates. Estimation of lichen consumption for the transitional periods, namely May-June and August-September-October, are unreliable since the radiocesium intake and *in vivo* cesium kinetics are changing. During these periods an equilibrium radiocesium body burden is not attained.

A radiocesium intake rate was calculated for a theoretical 100 kg reindeer/caribou using the above lichen consumption rates (R) and a radiocesium concentration (c) of 30 pCi/g in dry lichen. The radiocesium intake rate equals the product of R and c. The radiocesium concentration in lichen of 30 pCi/g represents a mean value for lichen during 1971 in the Cantwell, Alaska area. The radiocesium intake rate for the theoretical reindeer/caribou is indicated in Figure 3 as a function of the month of the year. The effective half-time of radiocesium in lichen is approximately 10 years, as measured in the Cantwell area (Luick, 1972), and the appropriate correction has been made in preparing the radiocesium intake rate curve in Figure 3.

Simulation of the annual cycle — An analog computer simulation of the radiocesium body burden of a reindeer/caribou is presented in Figure 3. Assumptions for the simulation are as follows: (1) a 100 kg reindeer/caribou consuming 3 kg of dry lichen per day during the period of November-May and 0.6 kg of dry lichen per day during July and August, with intermediate rates during the transitional periods; (2) the ^{137}Cs concentration of lichen is equal to 30 pCi/g of dry lichen initially, then declining with effective half-time of 10 years; (3) an absorption factor of 0.25; and (4) kinetic parameters changing as determined experimentally (Fig. 2).

DISCUSSION

The two compartment model appears to be the simplest model which adequately describes the *in vivo* cesium kinetics in reindeer. Its complexity, however, is sufficient to yield reliable information, as indicated from continuous intake studies using ^{134}Cs (Holleman *et al.*, *ibid*). The practice of applying a kinetic model, as determined for reindeer, to caribou can only be justified on the basis of species similarity, at least for the present time.

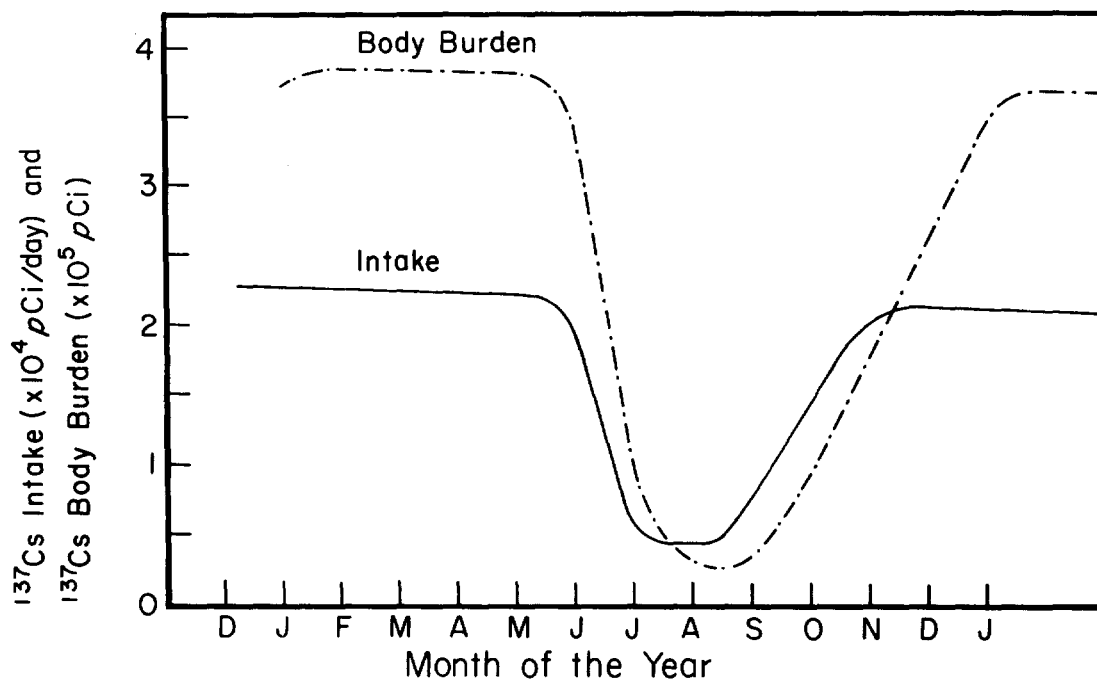


Fig. 3.—A simulation of the radiocesium intake rate and the radiocesium body burden of a theoretical reindeer/caribou as related to the month of the year.

The *in vivo* kinetics in reindeer would depend upon the annual season. During summer, the kinetics of cesium were accelerated, being 2-3 times more rapid than during winter. The most plausible explanation is based on the diet of the reindeer/caribou. Summer forage consists chiefly of deciduous shrubs, grasses and sedges and is relatively high in potassium; in contrast, winter diets being a large percentage lichen, are of very low potassium content. Due to physical/chemical and biological similarities of cesium and potassium, an increase in potassium intake results in an increase in cesium turnover (Wasserman and Comar, 1961). During the transition periods the kinetics of cesium were variable and dependent upon the vegetation available to the grazing animals.

The mean absorption factor for eight reindeer was 0.24 ± 0.031 , where the statistic is the standard deviation. This implies that approximately 20 to 30 per cent of the ingested radiocesium from naturally contaminated lichen was absorbed into the cesium body pool of the reindeer. The absorption factors, as determined for three levels of lichen consumption, were not statistically different. This finding suggests the possibility of determining lichen consumption rates from the measurement of the cesium body burden of a free-grazing reindeer/caribou and the radiocesium concentration in the lichen consumed. This assumes that the only significant radiocesium intake is via lichen and that *in vivo* cesium kinetics are relatively constant. Preliminary calculations of lichen consumption rates for caribou using the present model have been made for interior Alaska (Holleman *et al.*, *ibid*) and for northern Alaska (Hanson *et al.*, 1975).

The radiocesium intake for a free-grazing reindeer/caribou depends directly upon the diet of the animal and indirectly upon the annual season. Summer forage, namely deciduous shrubs, grasses and sedges, contain little radiocesium; therefore, the radiocesium intake during this season is minimal. Lichen contains relatively large quantities of fallout radiocesium, thus during autumn, winter and spring the radiocesium intake is significant

since the diet consists of a large percentage of lichen. The maximum radiocesium intake rate during 1971 for the theoretical reindeer/caribou equals 2.25×10^4 pCi/day during January. The minimum intake rate, 0.45×10^4 pCi/day, occurs during mid-summer, July and August.

During the period from November through May, the radiocesium intake rate approximates a constant. Under the conditions of constant intake and constant *in vivo* kinetics, the cesium body burden increases and asymptotically approaches an equilibrium value. For the present simulation, an equilibrium radiocesium body burden is reached in early winter and persists through the month of May. With the appearance of green vegetation in early June, the radiocesium intake rate decreases rapidly. The radiocesium body burden also decreases since the animal's elimination rate for radiocesium exceeds its intake rate. The decrease in the radiocesium body burden is primarily due to a decrease in radiocesium intake; however, the more rapid kinetics associated with the summer diet also contribute to a lower radiocesium body burden. Changes in cesium kinetics with diet is the reason that the radiocesium body burden of the theoretical reindeer/caribou is not proportional to cesium intake (Fig. 3).

During September and October the cesium body burden increases, again due to the higher radiocesium intake rate on the autumn diet as well as the slower cesium kinetics associated with this diet. The annual cycle is completed when an equilibrium radiocesium body burden is reached in early winter.

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LICHEN FORAGE INGESTION RATES OF FREE-ROAMING CARIBOU ESTIMATED WITH FALLOUT CESIUM-137

Wayne C. Hanson, F. Ward Whicker and James F. Lipscomb
Department of Radiology and Radiation Biology
Colorado State University
Fort Collins 80521

ABSTRACT—Lichen forage ingestion rates of free-roaming caribou herds in northern Alaska during 1963-1970 were estimated by applying a two-compartment, eight parameter cesium-137 kinetics model to measured fallout ^{137}Cs concentrations in lichen and caribou. Estimates for winter equilibrium periods (January-April) for each year ranged from 3.7 to 6.9 kg dry weight lichens per day for adult female caribou. Further refinement of these estimations were obtained by calculating probabilistic distributions of intake rates by stochastic processes based upon the mean and standard error intervals of the eight parameters during 1965 and 1968. A computer program generated 1,000 randomly sampled values within each of the eight parameter distributions. Results substantiate the contention that lichen forage ingestion rates by free-roaming caribou are significantly greater than previously held.

Forage consumption rates of caribou/reindeer have mainly been estimated with penned animals or by visual approximation. Emphasis has been placed on lichen forage because of its importance as a winter food of caribou/reindeer, its slow recovery from damage and its importance in limiting carrying capacity of northern ranges (Scotter, 1965a; Scotter, 1965b).

Radiation ecology studies have also centered on the lichen-deer relationship, because it has been recognized as the main route by which appreciable amounts of stratospheric fallout radionuclides are transported through food webs to northern peoples, especially subsistence hunting groups or reindeer breeders (Hanson, Watson and Perkins, 1967; Lidén and Gustafsson, 1967; Miettinen and Häsänen, 1967; Nevstrueva *et al.*, 1967). Cesium-137 is the single most important radionuclide from that standpoint, and serves as an excellent tracer for measuring transfer rates in biological systems (Comar, 1965; Patten and Witkamp, 1967). The lichen-caribou food web is especially amenable to investigation by this technique because the low concentration of potassium in lichens (Scotter, 1965b) enhances the accumulation in muscle tissue of ^{137}Cs , its chemical analog, and modern technology permits measurement of environmental quantities of gamma-emitting radionuclides such as ^{137}Cs with excellent precision. Furthermore, the short potassium-cesium half-time in caribou (of the order of 30 days or less) permits establishment of an equilibrium condition (intake rate = loss rate) on winter ranges. These conditions afford an opportunity to apply results of several investigations of reindeer/caribou on lichen diets during a critical season for the purpose of estimating ingestion rates of lichens which have been contaminated with fallout ^{137}Cs .

METHODS

Long-term studies of the lichen-caribou-man food web transfer of fallout radionuclides

(especially ^{137}Cs) were conducted in northern Alaska during the period 1962-1970, centering on the ecosystem around Anaktuvuk Pass which is located at $68^{\circ} 10' \text{N}/151^{\circ} 46' \text{W}$ (Hanson, Watson and Perkins, 1967 *op cit.*; Hanson, 1971). The seasonal cycle of ^{137}Cs in caribou was defined in 1964-1970 by frequent sampling of caribou taken during October-June by Eskimos and by repeated sampling of *Cladonia* lichen mats at selected sites. A rather well-defined equilibrium level of ^{137}Cs in caribou muscle was noted during late winter months (January-April) of each year (Fig. 1). Emphasis was placed upon results from those periods of 1965 and 1968, during which the caribou wintered near the village site and provided a greater number of samples close to the lichen sampling sites.

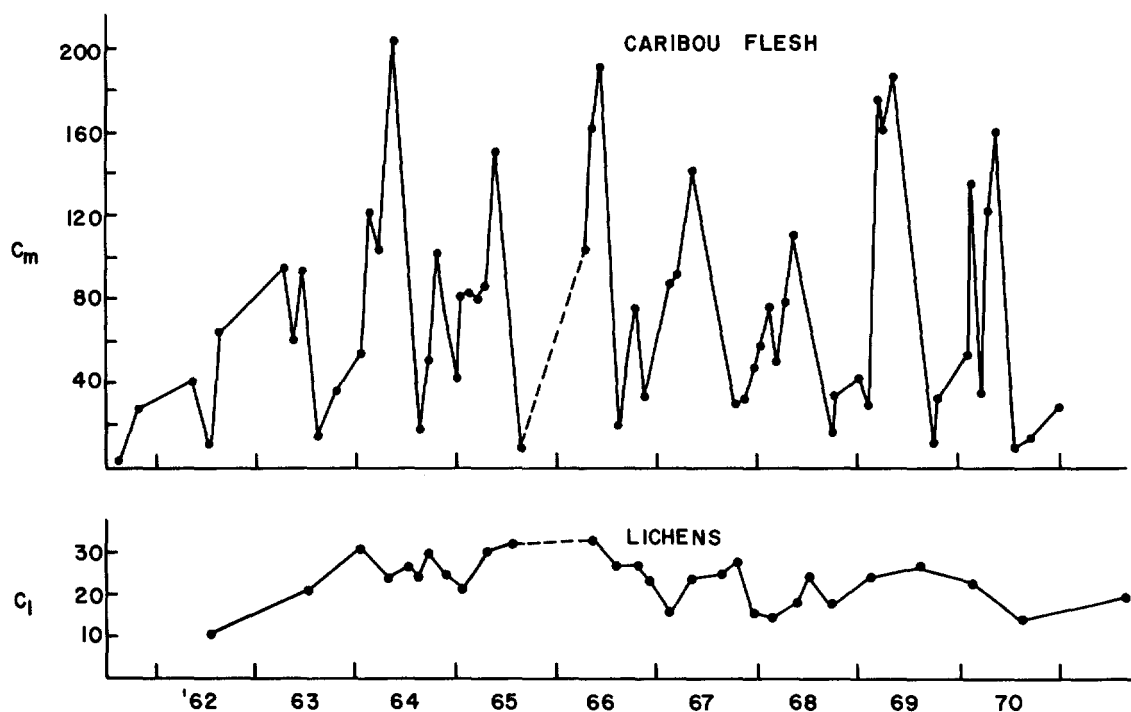


Fig. 1.—Fallout ^{137}Cs concentrations in lichens (C_l) and caribou flesh (C_m) at Anaktuvuk Pass, Alaska during the period 1962-1970. Units of C_l and C_m , in pCi $^{137}\text{Cs}/\text{g}$ standard dry weight.

Several biological parameters needed to establish a model for calculation of feeding rates of free-roaming caribou were provided in studies of reindeer maintained on natural mountain tundra pastures near Cantwell, Alaska (Holleman, Luick and Whicker, 1971). In addition, several hundred stable element analyses of lichens were obtained during 1964-1967 and used in combination with metabolic rate constants to provide more accurate estimates of kinetic parameters on the low potassium intake that characterized caribou diets consisting principally of lichens.

Our general model was

$$Q = RC1a(C_0 + C_3e^{-m_1t} + C_4e^{-m_2t}) \quad (1)$$

from Holleman, Luick and Whicker (*op. cit.*). The whole body burden, Q , was partitioned into several terms such that Equation(1) could be expressed in terms of C_m , the measured

^{137}Cs concentration in caribou muscle (pCi/g standard dry weight):

$$C_m = \frac{f_t R C_l a}{d W f_m} \left[C_0 + C_3 e^{-m_1 t} + C_4 e^{-m_2 t} \right] \quad (2)$$

where

- f_t = fraction of total body ^{137}Cs in muscle
- R = forage intake rate in dry g/day
- C_l = ^{137}Cs concentration in lichens in pCi/g standard dry weight
- a = fraction of ingested ^{137}Cs that enters the body pool (Holleman, Luick and Whicker *op. cit.*)
- d = standard dry to wet weight conversion factor for caribou muscle
- W = mean adult caribou weight in g
- f_m = fraction of body weight that is muscle
- C_0 = a kinetic factor, having the units of days, that is related to the rate constants describing loss of Cs from caribou. Given by $(k_1 + k_2)/(m_1 m_2)$ in (*ibid.*)
- C_3 and C_4 = kinetic parameters, having the units of days, which are related to the rate constants describing loss of Cs from caribou (*ibid.*). C_3 is given by $(m_1 - k_1 - k_2)/(m_1(m_2 - m_1))$ and C_4 by $(k_1 + k_2 - m_2)/(m_2(m_2 - m_1))$.
- m_1 and m_2 = constants describing the two exponential component whole body Cs loss from a caribou following acute intravenous injection of tracer Cs (*ibid.*) in units of days $^{-1}$.
- k_1 , k_2 and k_3 = inter-compartmental, first-order rate constants which describe the kinetics of Cs transfer and loss in caribou and which are functions of m_1 and m_2 (*ibid.*) in units of days $^{-1}$.
- t = time in days for a given chronic intake value for $R C_l a$.

If reasonable estimates of m_1 and m_2 are available, as well as the fractional time zero intercept value for either m_1 or m_2 , one can calculate values of k_1 , k_2 , and k_3 ; and then, values for C_0 , C_3 and C_4 (Holleman, Luick and Whicker, *op. cit.*). It is generally accepted that rate of cesium loss is dependent upon the potassium intake rate (Wasserman and Comar, 1961). In experiments with reindeer, Holleman, Luick and Whicker (*op. cit.*) found that the slow component biological half-time was about 17 days with a dietary K concentration of about 1 mg/g dry and about 6.7 days with a dietary K concentration of about 5 mg/g dry. Extrapolation on a log-log plot gives a corresponding half-time value of about 30 days for a K concentration of 0.37 mg/g, which is the mean measured value for 17 lichen samples collected at Anaktuvuk Pass (Table 1). Using this approach, it was estimated that $m_1 = 0.252 \text{ day}^{-1}$, $m_2 = 0.0231 \text{ day}^{-1}$, and A , the fractional intercept for m_1 , = 0.39 for adult female (75 kg) caribou feeding on lichens near Anaktuvuk Pass. Using these values and estimates of their standard errors based upon seven or more separate animal trials, it was calculated that $k_1 = 0.111 \pm 0.018 \text{ day}^{-1}$, $k_2 = 0.052 \pm 0.013 \text{ day}^{-1}$, $k_3 = 0.112 \pm 0.006 \text{ day}^{-1}$ and that $C_0 = 27.9 \pm 4.3 \text{ days}$, $C_3 = -1.54 \pm 0.23 \text{ days}$, and $C_4 = -26.5 \pm 4.0 \text{ days}$.

Using these values for C_0 , C_3 and C_4 in equation (2), a build-up curve can be generated for caribou coming onto ^{137}Cs contaminated forage (Fig. 2). The animals can be expected to reach 50 per cent of equilibrium in about 28 days, 75 per cent at 60 days, and 90 per cent at 96 days if the model and parameter estimates are accurate. Caribou that were sampled at

TABLE 1.--Potassium concentrations in *Cladonia* lichens at Anaktuvuk Pass during the period 1964-1967.

Date of collection	N	Potassium concentration (mg/g standard dry wt.)		
		Mean	\pm	S.E.
April 1964	3	0.41		0.12
January 1965	4	0.47		0.08
April 1965	1	0.34		
May 1966	4	0.35		0.01
February 1967	3	0.27		0.02
May 1967	2	0.34		0.003
Overall Mean		0.374		0.016

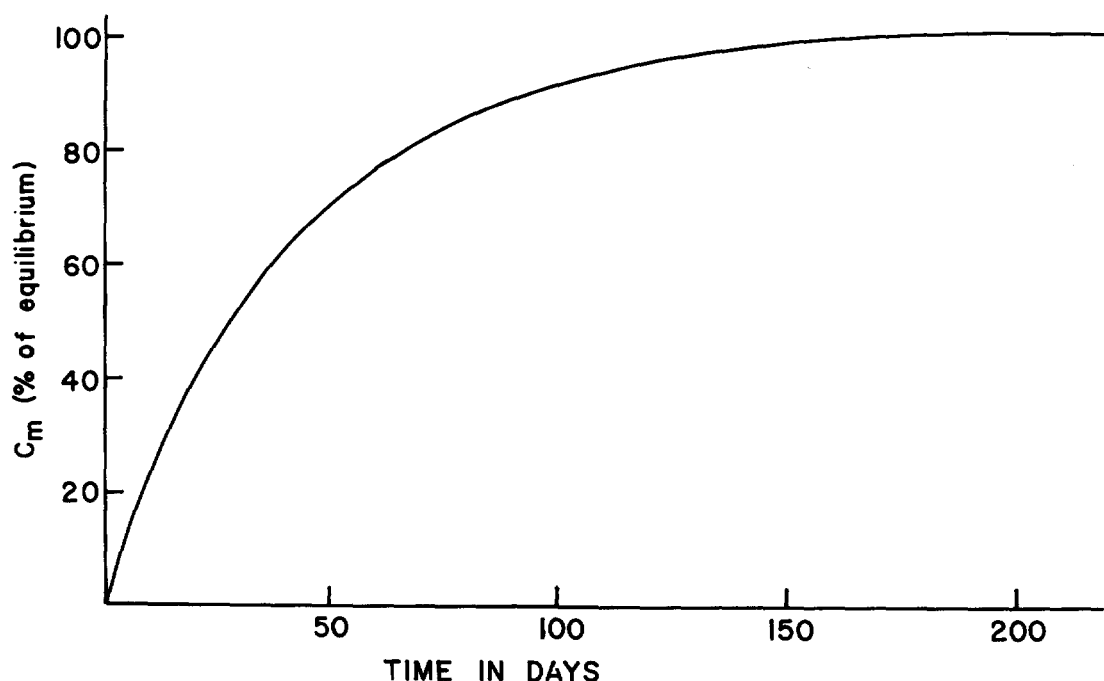


Fig. 2.—Concentration of ^{137}Cs in caribou flesh, C_m , as a percentage of the equilibrium value, versus time in days the animal has fed upon ^{137}Cs contaminated lichens. Curve is described by Equation (2) and parameters given in the text.

Anaktuvuk Pass in late winter months (January-April) were considered to be at >90 per cent of equilibrium since they usually start feeding heavily on lichens in the fall months. By rearranging terms in Equation 2, it was possible to calculate the mean daily intake rate of dry lichen forage (\bar{R}) at equilibrium conditions between ^{137}Cs intake and excretion based on samples and reported values ($\bar{x} \pm \text{S.E.}$) indicated below for the equation

$$\bar{R} = \frac{C_m d W f_m}{C_1 f_t a C_0} \quad (3)$$

where

d = dry to wet weight conversion factor for caribou muscle, 0.235 ± 0.0027 , n = 111

W = average adult female caribou weight, Arctic Herd, during spring, 75 ± 0.636 kg, n = 102 (from Skoog, 1968)

f_m = fraction of body weight that is muscle, 0.41 ± 0.0081 , n = 5 (Holleman, Luick and Whicker, *op. cit.*)

f_t = fraction of total body ¹³⁷Cs in muscle, 0.789 ± 0.0121 , n = 4 (*ibid.*)

a = fraction of ingested ¹³⁷Cs entering body pool, 0.26 ± 0.02 , n = 4 (*ibid.*)

C₀ = kinetic parameter 27.9 ± 4.3 days, n = 10 (*ibid.*)

These parameters defined a normal frequency distribution for each of the random variables. A value for \bar{R} in each year was calculated by inserting mean values for the variables in Equation 3 (Table 2). The values obtained in this way represent the medial values for daily

TABLE 2.--Calculated average lichen intake rate (\bar{R}) for each winter equilibrium (January-April) period during the years 1963-1970.

Year	Mean ¹³⁷ Cs concentration (pCi/g dry)		K ¹ (kg/day)	\bar{R} ² (kg/day)
	Caribou flesh (C _m)	Lichens (C ₁)		
1963	77.2	24.2	1.26	4.02
1964	116.7	32.7	1.26	4.50
1965	82.6	28.3	1.26	3.68
1966	103.0	33.0	1.26	3.93
1967	87.8	19.2	1.26	5.76
1968	75.6	16.5	1.26	5.77
1969	131.0	23.9	1.26	6.90
1970	98.9	23.6	1.26	5.28
means			1.26	4.98
S.E. (among years)				0.40

$$^1K = \frac{d W f_m}{f_t a C_0}$$

$$^2\bar{R} = \frac{K C_m}{C_1}$$

intake rate. Dispersion about any calculated \bar{R} value is a composite of the variance in each of the parameters in Equation 3 and in turn, the parameter variances result from true population variations as well as variations associated with sampling and measurement. In order to obtain an estimate of this dispersion, it was necessary to assume some distribution function for the variables entering into the calculation of \bar{R} . For each variable, the normal

distribution was judged to be the most reasonable approximation. The distribution function of each variable was described by the mean and standard error. Use of the standard error implies that the resulting distribution of \bar{R} is characteristic of the mean of that portion of the population which was sampled.

An analytical determination of the probability distribution for \bar{R} would be quite difficult; therefore, a Monte Carlo approach was used in which the frequency distributions for 1965 and 1968 (years in which the best sampling data were available) were assumed to approximate the probability distribution for \bar{R} in all years. For 1965 and again for 1968, 1000 \bar{R} values were calculated using Equation 3. The eight factors entering the calculation of \bar{R} were chosen independently and at random from the appropriate distributions for each of the \bar{R} calculations.

The computer procedure for generating numbers at random from normal distributions was that described by Naylor *et al.* (1966). The procedure is based on the Central Limit Theorem and truncates the distribution at $\mu \pm 6\sigma$. This limitation is of no practical importance in this case and the histograms (Fig. 3) compiled from the computer output provide an accurate approximation of the true distribution of \bar{R} . An assumption of independence is implicit in the above procedure. If non-zero correlations exist between factors in Equation 3, the spread of the distribution would be reduced; however, the skewed shape of the curves and the values of \bar{R} would be essentially unaffected.

RESULTS

Values of \bar{R} during the January-April period of the years 1963-1970 (Table 2) varied from 3.7 to 6.9 kg dry weight lichens per day, with an overall mean of 5.0 kg/day. The values for 1965 and 1968 were examined in detail by stochastic methods because they represent values near the extremes of the full range of \bar{R} during the time period and because the wintering caribou herds were located near the village and lichen sampling sites during those years. The frequency histograms in Figure 3 are similar although there was a difference in the calculated modal values of \bar{R} . This difference may be the result of changes in the ^{137}Cs content of lichens during the 90 days immediately preceeding sampling in both years. The frequency data for 1965 and 1968, as well as the deterministic data for all years suggest that the true value for \bar{R} lies in or near the interval 4.5-5.0 kg dry weight lichens per day.

DISCUSSION

Previous estimates of lichen forage intake rates of about 3 dry kg/day have been based upon extrapolation of domestic ruminant studies or upon direct consumption measurements for penned caribou/reindeer. A rule of thumb for dry matter intake for ruminants is $I(\text{kg per day}) = 0.11 W^{0.75}$, where W is the live body weight (kg) of the animal. This is based upon Kleiber's standard equation for basal metabolism rate for ruminants of 70 kcal/day $W^{0.75}$ (Brody, 1945). For a 75 kg caribou, this yields 2.8 kg dry matter intake per day for basal metabolism; this intake rate hardly seems adequate for an animal as mobile and as cold and wind stressed as the northern caribou during winter months. Nor would it seem applicable to forage of such low nutrient value as lichens, which have one-half to one-third the nourishment of poor hay (Scotter, 1965b, 1972). Kelsall (1968) reported that 3.5-4.5 kg dry weight lichens were required daily to nourish the average caribou, and that animals on feeding trials of 8-20 days duration on feeding regimens of 2.1 to 2.5 kg lichens per day lost weight. It seems apparent, therefore, that the commonly used estimate of 3 kg/day is much lower than would be expected for the free-roaming reindeer/caribou herds of the Holarctic

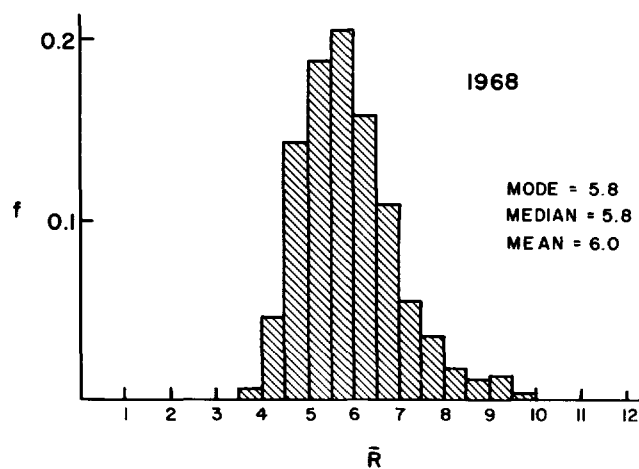
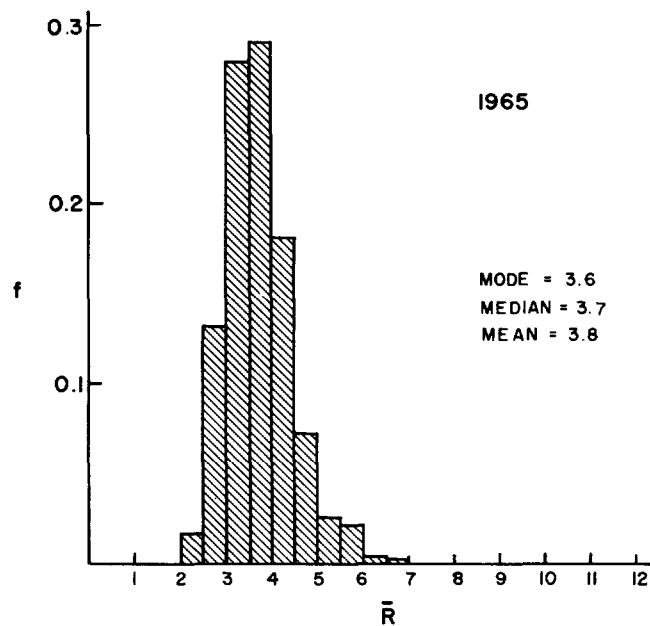


Fig. 3.—Frequency distribution of \bar{R} , the daily lichen intake in dry kg for the adult female caribou population mean for the years 1965 and 1968 at Anaktuvuk Pass. Distributions for \bar{R} are based upon 1000 stochastic applications of Equation (3) with parameter values chosen at random from the specified parameter distributions.

regions, where the stresses of cold, food hunting in snow cover, subsistence hunters, and predators would require greater energy expenditures than normal penned conditions impose. Lidén and Gustafsson (*op. cit.*) have previously reported an estimate of about 7.0 kg/day wet weight (about 3.5 to 4.0 kg/day dry weight) lichen consumption by reindeer in

northern Sweden, based on 0.65 uptake of ^{137}Cs from lichens. Assuming that 0.26 assimilation of ^{137}Cs more nearly approximates the true situation, this yields an intake of about 7 kg/day dry weight for reindeer in northern Sweden. Furthermore, Herre (1955) summarized several Alaskan and Russian studies that estimated caribou/reindeer lichen intake rates of 4.5 to 7 kg/day dry weight.

Extensive measurements of lichen biomass in *Cladonia* mats at Anaktuvuk Pass yielded values of 1.4 to 1.6 kg standard dry weight per m^2 . Assuming that grazing caribou crop the top 6 cm, they would remove about half the standing crop from 6.35 m^2 per animal per day. Various allowances must also be made for selectivity of lichen species, trampling and other factors that would increase the areal use of lichen stands (Pegau, 1968). It seems more realistic to estimate the average daily winter grazing requirement of Arctic Herd caribou to be at least 10 m^2 per animal for a vigorous lichen stand.

CONCLUSIONS

The combination of results from controlled studies of reindeer and field observations of free-roaming caribou over eight winter seasons has allowed the first realistic estimates of daily lichen forage intakes under natural conditions. The high probability that consumption rate lies in the interval 4.5 to 5.0 kg dry weight lichens per day has been shown by a stochastic model that generated 1,000 random values from each of eight measured parameter distributions. These results agree with an overall mean of 5.0 kg/day for the annual values for the period 1963-1970. It was concluded that the daily lichen forage intake during winter months in northern Alaska during the period of observation was near 5 kg per day, which corresponds approximately to 10 m^2 lichen biomass.

ACKNOWLEDGMENTS

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Present address: W. C. Hanson, Los Alamos Scientific Laboratory, Los Alamos, NM 87544; J.F. Lipscomb, Colorado Division of Wildlife Research Laboratory, Ft. Collins, CO 80521.

ACCUMULATION, DISTRIBUTION AND DECREASE RATE OF IRON-55 IN REINDEER IN FINNISH LAPLAND

Timo Jaakkola
Department of Radiochemistry
University of Helsinki
Finland

ABSTRACT—The concentration of ^{55}Fe in reindeer was investigated during 1961-1971. The ^{55}Fe level in reindeer meat reached a maximum (7.5 nCi/kg) in 1965. At that time the body burden of ^{55}Fe in reindeer was 2 μCi . The total amount of stable iron was 6.4 g. Seventy-four per cent of the total ^{55}Fe was in blood, 10 per cent in meat and 7 per cent in liver. In winter 1964-65 the specific activity of ^{55}Fe (pCi/mg Fe) in meat was 40 per cent lower than in other tissues and organs. Since March 1967, no significant difference of ^{55}Fe content in the diverse tissues and organs was found. In 1971, the ^{55}Fe content in reindeer meat was 1.4 nCi/kg fresh wt. The effective residence half-time of ^{55}Fe in reindeer meat was 1.5 years, which is slightly higher than that in lichen (1.3 y). The maximum ^{55}Fe level (330 pCi/mg Fe) of blood gave the total dose rate of 30 mrad per year to the erythrocytes of reindeer.

The ^{55}Fe level of wild animals feeding on reindeer tissues and organs was determined in 1966. The ^{55}Fe level of a wolverine was 70 per cent and that of a wolf about 20 per cent of the ^{55}Fe level in reindeer. The ^{55}Fe content of muscle of wolverine was 46 per cent of that of other tissues. In the wolf the ^{55}Fe concentration was the same in all tissues and organs.

As a result of large scale nuclear detonations in 1961 and 1962, ^{55}Fe became one of the most abundant radionuclides in the biosphere. ^{55}Fe was produced by neutron activation of iron present in the structural materials of nuclear weapons and in the soil. Although the half-time of ^{55}Fe is comparatively short (2.7 y) and the energy of the radiation emitted low (5.9 keV K X-rays; 5 keV Auger electron emission) the investigations of ^{55}Fe are of interest because of the slow turnover rate of iron in man and because the radiation is absorbed mainly by cells containing iron, especially by red blood cells.

By the mid-1960s, relatively high concentrations of ^{55}Fe were discovered in Alaskan Eskimos as well as in Swedish and Finnish Lapps (Palmer and Beasley, 1965; Palmer *et al.*, 1966; Persson, 1967; Jaakkola, 1967). The high values were due to the accumulation of ^{55}Fe along the food chains lichen-reindeer(caribou)- man and sea-plankton-fish-man.

According to the results published earlier the ^{55}Fe content of reindeer and caribou reached peak values in 1965. At that time the estimated average body burden of ^{55}Fe in caribou in Alaska was 0.95 μCi (Palmer *et al.*, 1968) and in reindeer in Swedish Lapland 1.5 μCi (Persson, 1967). The maximum concentration of ^{55}Fe in reindeer meat was 8 nCi per kg fresh weight both in Finnish and Swedish Lapland (Jaakkola, 1969; Persson, 1969).

The aim of the present study was to investigate, in particular, the distribution of ^{55}Fe in reindeer, the changes of ^{55}Fe level, the decrease rate of ^{55}Fe in reindeer and the introduction of ^{55}Fe into some wild animals feeding on reindeer. Therefore, samples from about 130 reindeer were collected in Finnish Lapland (68°-70° N and 21°-30° E) during 1961-1971. In some cases blood, liver, kidney, lung, spleen and bone samples were collected

in addition to the muscle samples. In 1966, when the ^{55}Fe content in reindeer was close to the maximum level, samples of various tissues and organs of a wolverine and a wolf were analyzed.

METHODS

The method for determining ^{55}Fe content has been previously described in detail (Jaakkola, 1969). The samples were dried at 110°C and dissolved by means of wet ashing with nitric acid and perchloric acid. Iron was separated from samples using isopropyl ether extraction and ion exchange. Iron was electroplated onto copper plates and radioassayed by means of a sealed argon-filled, proportional tube and a 512-channel multichannel analyzer. The concentrations of inactive iron were determined by atomic absorption spectrophotometry.

RESULTS AND DISCUSSION

The specific activities of ^{55}Fe in reindeer meat as pCi ^{55}Fe per mg Fe are given in

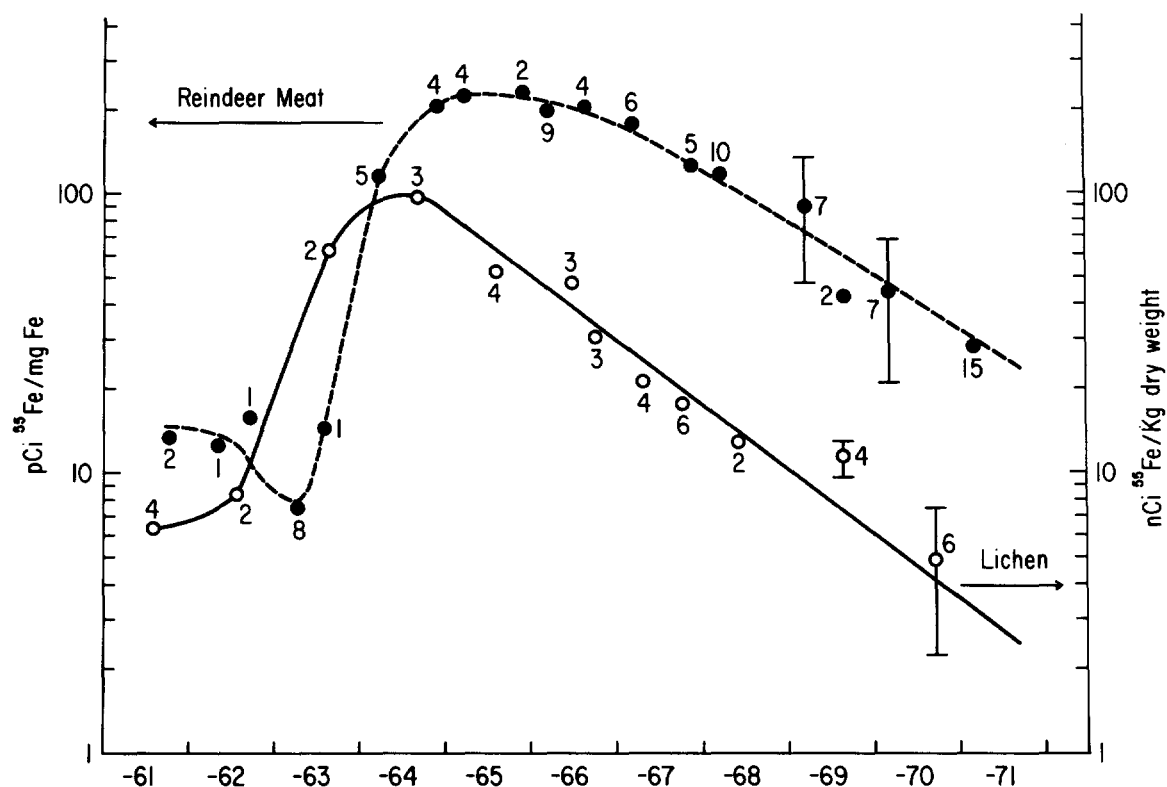


Fig. 1.— ^{55}Fe in reindeer meat and lichen (*Cladonia alpestris*) in Finland in 1961-1971. The figures at the dots indicate the number of samples pooled for each analysis. In four cases the ^{55}Fe values are averages of separate determinations, and in these cases the standard deviation of the mean (\pm one δ) is marked.

Figure 1 for the period of 1961-1971. The ^{55}Fe level was 20 to 25 times higher in 1965 than during 1961-1963. The ^{55}Fe content of about 10 pCi/mg Fe found in samples before

1963 is due to the nuclear tests carried out in the 1950's. Figure 1 also shows the ^{55}Fe content of lichen (*Cladonia alpestris*), which is the most important fodder for reindeer in Finnish Lapland during the winter. The ^{55}Fe content of lichen reached its maximum level in 1964. Table 1 lists the ^{55}Fe content (pCi/mg Fe and nCi/kg fresh wt.) as well as the stable iron content of reindeer meat during 1965-1971. The meat samples probably contained a varying quantity of hemoglobin iron, since great variations were found in the stable Fe content of the samples. The samples were collected during various seasons because the ^{55}Fe content of reindeer's feed after 1963 (the year of a maximum ^{55}Fe content in fallout) was many times higher during the winter time (lichen-rich diet) than in the summer time, i.e., when the diet of reindeer consists mainly of grass, leaves of trees and bushes, etc. No significant seasonal fluctuations in the ^{55}Fe content of meat were found. Primarily, this is due to the relatively slow turnover rate of iron in reindeer meat. In addition, the individual variation in the ^{55}Fe content is considerable. The values of November 1968 and September 1969 show some seasonal variation but unfortunately these values are based on only one and two samples, respectively.

Distribution of ^{55}Fe in Reindeer

To calculate the body burden and the distribution of ^{55}Fe in reindeer, meat, blood, liver, kidney, lung, spleen and bone were sampled from five animals during the winter 1964-65 when the ^{55}Fe level was at its maximum. Results are given in Table 2. The body burden of ^{55}Fe in reindeer was 2 μCi . This value is in agreement with the estimation, 1.5 μCi , made by Persson (1967) in Swedish Lapland, but about twice the maximum value of 0.95 μCi obtained for caribou in Alaska (Palmer *et al.*, 1968). The lower value in caribou is in agreement with the lower content of ^{55}Fe in lichen found in Alaska in 1964 (14 nCi per kg dry wt.; Palmer and Beasley, 1965) as compared to the values obtained for lichen during the same period in Swedish and Finnish Lapland (40-100 nCi/kg dry wt.; Persson, 1969; Jaakkola, 1969). According to Table 2, 74 per cent of the body burden of ^{55}Fe is in blood. The specific activity of ^{55}Fe (pCi/mg Fe) was the same and within the limits of the biological variation in all organs and tissues analyzed, except in meat. The value in meat was 40 per cent lower than in other tissues and organs. This indicates a different turnover rate of iron in hemoglobin and myoglobin. The studies of the ^{55}Fe level in various tissues were continued during 1965-1971 (Table 3 and Fig. 2). Since 1966, no systematic difference in the specific activity of ^{55}Fe (pCi/mg Fe) has been found among the diverse tissues and organs of the same animal. After 1966 the ^{55}Fe content of muscle samples is slightly higher than that of blood, but due to the small number of blood samples analyzed and to the individual variations, the difference found is not significant. Applying the results of the ^{55}Fe content of reindeer blood and lung samples for the period of 1962-1965 in Figure 2 and Table 2, 150 days was estimated to be the biological half-time of iron in reindeer blood (Jaakkola, 1969). Persson's (1969) estimation for the biological half-time of iron in reindeer was the same, 150 days.

Decrease Rate of ^{55}Fe in Reindeer

Based on the ^{55}Fe values in Figure 1, 1.5 years was estimated to be the effective residence half-time of this radionuclide in reindeer muscle tissue. This value is slightly lower than that in lichen (1.3 years). As can be seen from the standard deviations of the mean given for four points in Figure 1, the values of the individual determinations vary considerably and thereby decrease the accuracy of the residence half-time estimation. An essential reason for these individual variations may be the different ages of the animals

TABLE 1.--⁵⁵Fe content in reindeer meat in Finnish Lapland during 1965-1971.

Number of animals	Sampling date	mg Fe per kg fresh wt.	pCi ⁵⁵ Fe/mg Fe mean	(range)	nCi ⁵⁵ Fe per kg fresh wt.
4	March 1965	33.6	224±4.4 ¹		7.5
2	December 1965	30.2	226	(190-261)	6.8
9	March 1966	36.2	195±3.8 ¹		7.1
4	August 1966	36.6	201	(241-179)	7.4
6	March 1967	34.6	176	(205-105)	6.1
10	March 1968	42.4	118±2.1 ¹		5.0
1	November 1968	40.8	46.0		1.9
7	March 1969	48.4	89.1	(26.7-166)	4.5
2	September 1969	36.8	42.2	(38.7-45.6)	1.5
7	March 1970	49.1	44.2	(21.3-79.2)	2.2
13	March 1971	50.9	27.9	(15.8-37.0)	1.4

¹⁵⁵Fe content of pooled sample ± standard deviation of radioassay (one δ).

TABLE 2.--Distribution of ^{55}Fe in reindeer, December 1964. The data are based on analyses of samples from five animals.

Tissue or organ	Weight ² (kg)	mg Fe/kg ¹ fresh wt.	mg Fe/whole tissue or organ	^{55}Fe		
				pCi/mg Fe ¹	nCi/whole tissue or organ	%
Meat	28	35.4±2.5	990	206±53	204	10.2
Blood	7.5	593	4440	332±10	1470	73.8
Liver	1.6	263±57	422	306±37	129	6.5
Kidney	0.2	55.8±12.6	11.2	322±40	3.6	0.2
Lung	1.8	165±53	297	324±54	96.2	4.8
Spleen	0.08	156±52	12.5	283±55	3.5	0.2
Bones	8	-	260	332	86	4.3
Total accounted ³	47.2	-	6430	-	1992	100

¹Standard deviation (one δ) for the biological variation is indicated. Standard deviation for radioassay varied from 1 to 4 per cent.

²The weights of the different organs are based on weighing at a slaughter house.

³The average live weight of animals in question was estimated to be 70 kg.

TABLE 3.--Comparison of ^{55}Fe concentrations in various organs and tissues of reindeer in Finnish Lapland during 1965-1971. The ^{55}Fe results are indicated as pCi per mg Fe.¹

Sampling date	Muscle		Blood		Liver		Kidney	
December 1965	226	(2)	280	(10)	-		-	
March 1966	195	(9)	259	(12)	240	(3)	193	(1)
August 1966	201	(4)	215	(2)	216	(3)	-	
March 1967	176±41 ²	(6)	175±37 ²	(6)	162±42 ²	(6)	-	
November 1967	124	(5)	119	(5)	118	(5)	-	
March 1968	118	(10)	-		115	(10)	-	
March 1971	27.9	(15)	28±12 ²	(5)	24±2 ²	(4)	39.6	(2)

¹The figures in parenthesis indicate the number of samples.

²Mean values ± standard deviation of the mean (one δ).

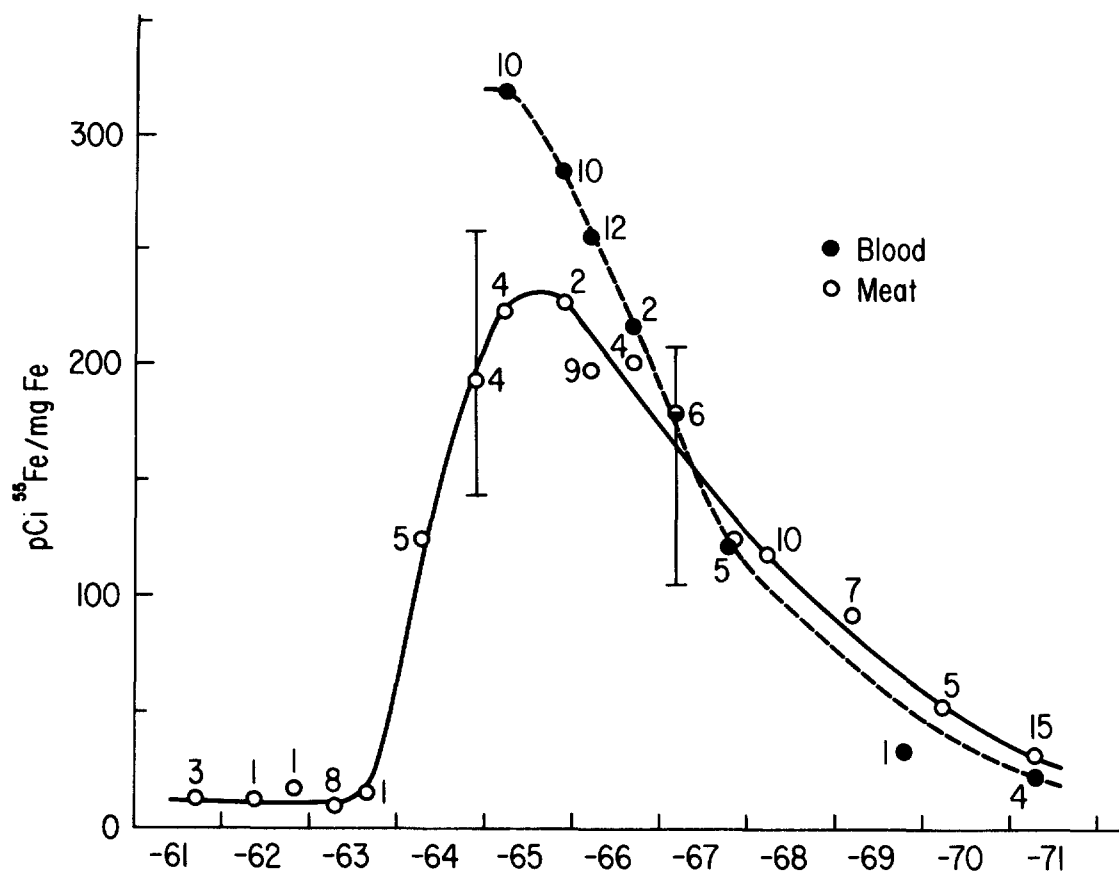


Fig. 2.— ^{55}Fe in reindeer meat and blood in Finnish Lapland in 1961-1971. The figures at the dots indicate the number of samples pooled for each analysis.

analyzed (1-12 years). The ^{55}Fe content is higher in reindeer that grow during the years when the ^{55}Fe concentration in lichens was high and especially during 1963 and 1964 when the ^{55}Fe content of the summer diet was also high, compared to the animals grown during the low ^{55}Fe content of diet. Langford and Jenkins (1971) have reported a residence half-time of one year for cattle blood in the State of Washington (USA).

The maximum body burden of ^{55}Fe in man was found in 1966. At that time the body burdens of ^{55}Fe in the fish-eating natives of Bethel, Alaska and Tokai-Mura, Japan were approximately five times higher than those in the Swedish and Finnish Lapps (Palmer and Beasley, 1967; Persson, 1969; Jaakkola, 1969). Thus, the accumulation of ^{55}Fe along the food chain sea-plankton-fish-man was higher than along the food chain lichen-reindeer(caribou)-man. However, the effective residence half-time of ^{55}Fe in the fish eating natives is faster than that in the Lapps. Jenkins (1971) has reported an effective residence half-time of approximately one year for ^{55}Fe in salmon-eating Eskimos. According to Jaakkola (1972) the effective residence half-time of ^{55}Fe in the blood of Finnish Lapps varied from 3.6 to 4.8 years for males and from 2.4 to 3.5 years for females. Jenkins (1971) reported that salmon-eating Eskimos of Alaska had ^{55}Fe body burdens of nine to 137 nCi in March 1969. Two years later, in 1971, the body burden of ^{55}Fe in Finnish Lapps ranged between 15 and 115 and averaged 52 nCi. Thus, in 1971, the body burdens of ^{55}Fe were probably higher in Lapps than Eskimos.

⁵⁵Fe in Predators Feeding on Reindeer

The results of ⁵⁵Fe analysis of tissues and organs of a wolverine and of a wolf are shown in Tables 4 and 5. Both the animals were reported to have killed reindeer before being shot.

TABLE 4.--⁵⁵Fe and stable iron concentrations of a wolverine (*Gulo gulo*) in Finnish Lapland (Inari) in March 1966.

Tissue or organ	Weight kg	mg Fe per kg fresh wt.	⁵⁵ Fe ¹	
			pCi/mg Fe	nCi/kg fresh wt.
Blood	-	522	158±4.6	82.2±2.5
Liver	0.26	146	165±3.8	24.1±0.6
Muscle	5.52	38.6	73.5±3.4	2.8±0.1
Muscle		45.1	69.6±6.9	3.1±0.3
Lung	0.21	224	154±3.8	34.6±0.9
Spleen	0.021	181	153±12	27.6±2.2
Kidney	0.058	98.3	150±7.4	14.7±0.7

¹The standard deviation of the radioassay (one δ) indicated.

TABLE 5.--⁵⁵Fe and stable iron concentrations of a wolf (*Canis lupus*) in northern Finland (Ylitornio) in March 1966.

Tissue or organ	Weight kg	mg Fe per kg fresh wt.	⁵⁵ Fe ¹	
			pCi/mg Fe	nCi/kg fresh wt.
Blood	-	586	54.1±1.9	31.6±1.1
Liver	0.68	246	50.7±2.0	12.4±0.5
Muscle	13.7	64.4	44.0±12.5	2.8±0.8
Muscle		55.0	43.4±5.7	2.4±0.3
Lung	0.45	410	53.1±2.2	21.7±0.9
Spleen	0.065	588	55.2±1.7	32.5±1.0
Kidney	0.25	91.7	44.6±4.5	4.1±0.4

¹The standard deviation of the radioassay (one δ) indicated.

The specific activity of ⁵⁵Fe (pCi/mg Fe) of the wolverine was the same in all tissues and organs except in muscles which contained only 46 per cent of the ⁵⁵Fe level of other tissues. The high ⁵⁵Fe content of the wolverine and the great difference between muscle and other tissues shows that this animal had fed on large amounts of reindeer meat and organs during the period just before sampling.

The low specific activity of ⁵⁵Fe in the wolf indicates it had eaten considerable amounts of iron containing meat and organs other than reindeer. The fact that the specific

activity of ^{55}Fe was slightly lower in muscle than in other samples of the wolf implied that the accumulation of ^{55}Fe occurred during a relatively long period of time.

Radiation Doses

According to Wrenn and Cohen (1967), the total dose rate to the erythrocytes of man is: $D = 1.83 \text{ rad/week/pCi/mg Fe}$. Although the iron content of reindeer blood is somewhat higher than that of man a good estimate for radiation dose to reindeer erythrocytes is obtained using this formula. The maximum ^{55}Fe level (330 pCi/mg Fe) obtained gives the total dose rate of 30 mrad per year to the erythrocytes of reindeer. This value is low compared to the radiation dose due to the natural radionuclide of ^{210}Po , i.e., 100 mrad/year to gonads of reindeer and 500 mrad/year to liver (Kauranen *et al.*, 1971). These dose rate levels are probably too low to result in detectable genetic effects.

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**SOME CONSIDERATIONS ON THE POSSIBLE EFFECTS
OF LOCAL AND GLOBAL SOURCES OF AIR POLLUTION ON LICHENS
GRAZED BY REINDEER AND CARIBOU**

Edmund Schofield
Institute of Polar Studies
The Ohio State University
Columbus, Ohio 43210
and
U. S. IBP Tundra Biome Program

ABSTRACT—Considerable evidence shows that local sources of air pollution eliminate most lichens from the immediate vicinities of urban and industrialized areas in temperate regions. Pollutants (e.g., SO_2) appear to be transported hundreds of kilometers from Britain and central Europe to Scandinavia. While there appear to be no reliable data or observations that link pollutants transported on a global scale to the deterioration of lichens there (primarily because the possibility has not been pursued), all of the ingredients necessary for lichen damage are present. Scattered comments and circumstantial evidence in the literature suggest that global pollution — in addition to local pollution — will adversely affect lichens grazed by reindeer and caribou. The accelerated industrialization of the Arctic makes this possibility of more than academic interest.

It has long been known that lichens have an aversion to urbanized and industrialized areas (e.g., Crombie, 1885; Arnold, 1891-1901), and the observation has been substantiated time and time again since the Nineteenth Century (e.g., Horwood, 1907; Jones, 1952; Skye, 1958; Fenton, 1960; LeBlanc, 1961; Gilbert, 1965; Fenton, 1965; LeBlanc and Rao, 1966; Brodo, 1966; Skye, 1968; Daly, 1970). Many mosses also appear to be adversely affected by airborne pollutants.

In most cases the toxic substance appears to be sulfur dioxide (SO_2) (Skye, 1958; Brodo, 1966; Rao and LeBlanc 1966, 1967; Coker, 1967), but fluorides are also toxic to lichens (Gilbert, 1971; Nash, 1971). Fruticose lichens tend to be more sensitive than foliose or crustose species (Fenton, 1960; Brodo, 1966). This is probably because they absorb moisture and nutrients from the atmosphere over a proportionately larger surface area than do crustose or foliose forms, which have only their upper surfaces exposed directly to the atmosphere.

The most sensitive lichens are affected by chronic concentrations of SO_2 at least as low as 0.02 ppm (cf. Skye, 1958). The number of species affected increases more or less directly with the SO_2 concentration.

Effects of SO_2 on Algal Chlorophyll

Sulfur dioxide is converted in the atmosphere to sulfurous and sulfuric acids. When acidic moisture is absorbed by lichens, or when SO_2 itself is absorbed by moist lichens, chlorophyll *a* is degraded to phaeophytin *a*. Apparently, the magnesium ions of chlorophyll molecules are displaced by the hydrogen ions released when SO_2 is oxidized to SO_3^{2-} and

SO_4^{2-} in the presence of water.

Morphological and Anatomical Effects

Rao and LeBlanc (1966) found that lichens exposed for 24 hours to 5 ppm of SO_2 developed sporadic brown spots on their chloroplasts. In addition, their algal cells were permanently plasmolyzed and their chlorophyll was bleached. Pearson and Skye (1965) found that a foliose lichen exposed to 100 ppm of SO_2 developed photosynthetic and morphological abnormalities similar to those of lichens from an industrial center in Sweden. Skye (1968) later reported that the thallus of the same lichen became progressively thinner with increased concentrations of SO_2 .

Osmotic Effects

Rao and LeBlanc (1966) found that the sulfate content of lichen thalli increased with increased humidity during the exposure period, and Gilbert (1965:43) found that the sulfur content of *Parmelia saxatilis* increased from only 225 ppm at a distance of 34 km from the center of pollution to 2870 ppm at a distance of only 6 km. As Rao and LeBlanc (1966) showed, SO_2 pollution has an adverse osmotic effect on lichen algae, in addition to its role in the degradation of algal chlorophyll.

Schofield (Schofield, 1972; Schofield and Ahmadjian, 1972) has observed that lichens in Antarctica are very sensitive to salinity; there was a very strong correlation between the absence of lichens and moderately high levels of salinity in the environment. There was a similar correlation for mosses. In view of Rao and LeBlanc's work (1966), it is possible that, under some conditions at least, the ambient salinity in some arctic microhabitats could be increased by sulfate and other ions contained in air pollution (cf. Kay, 1968).

Temperature Inversions and Ice Fogs

In addition to the intrinsic sensitivity of most lichens to SO_2 pollution, the problem may be more serious for lichens in the Arctic because very strong temperature inversions occur there very frequently, especially during the winter (Hare, 1970; see also Schofield and Hamilton, 1970a, 1970b).

Both water and ice fogs (Robinson *et al.*, 1957; Benson, 1965, 1969, 1970) frequently develop during times of inversions. The associated water droplets or ice particles that form on contamination particles scavenge and absorb pollutants from the air. In this way, contaminants become associated with larger particles and do not diffuse away. When the fog particles impinge upon a surface, they tend to stick — either as dew or as hoar frost. As a consequence, contaminants — including scavenged SO_2 — could be deposited directly on sensitive lichens.

A further unexplored consequence of ice fog concerns the osmotic effects of sulfate and other ions in industrial emissions. This possibility is suggested by the work of Rao and LeBlanc (1966).

Benson (1965) reported, for example, that the electrical conductances of snow reached magnitudes as high as $138 \mu\text{mho}\cdot\text{cm}^{-1}$ in the center of Fairbanks, Alaska, where ice fogs are common in winter, and were as high as $50 \mu\text{mho}\cdot\text{cm}^{-1}$ some 2 km from the center of pollution. In outlying areas (more than about 10 km from the center), values were less than $10 \mu\text{mho}\cdot\text{cm}^{-1}$. The conductivities of two pure ice fog deposits in the center of Fairbanks ranged from 730 to 770 and 1600 to 1760 $\mu\text{mho}\cdot\text{cm}^{-1}$, respectively. In Antarctica, Schofield (Schofield, 1972; Schofield and Ahmadjian, 1972) found that lichens were

completely absent where the conductance of the surface few centimeters of soil was greater than about $125 \mu\text{mho}\cdot\text{cm}^{-1}$. While there is as yet no concrete scientific evidence to show that arctic lichens would be adversely affected by high levels of salinity, the possibility exists. Studies should be initiated to prove or disprove the hypothesis.

Global Versus Local Pollution

To date, most studies of lichen contamination by airborne pollutants have dealt only with the influence of local, or nearby, sources of pollution. Global pollution seems to have been ignored. However, there is already ample evidence that global-scale pollution has affected the environment of some regions in ways that are known to have adverse effects on lichens. Yet no studies have been undertaken to evaluate these effects.

The strongest indication that global air pollution could affect arctic and subarctic lichens is evidence that organisms in Scandinavia are being exposed to extremely acid precipitation (cf. Sullivan, 1972). Elgmork (1971) reports that the pH of snow deposited in Vassfaret, Norway, during the winter of 1970-71 fell as low as 3.8. He found that the lowest pH values in snow profiles made in 1969 (Elgmork, 1969) and 1971 (Elgmork, 1971) were invariably associated with dark bands in the snow due to pollutants. He also reported that the 'electrolyte contents' of the bands were as high as 70. (Elgmork does not indicate the units, but they most likely are micromhos per centimeter.) In addition to lower pH and higher conductivity, there were greater quantities of sulfate, lead and iron in the dark bands. Elgmork attributed the pollution to industrial effluents from Great Britain and middle Europe, hundreds of kilometers to the southwest and south. Thus, conditions that are known to afflict lichens on a small scale also exist on a very large, global scale.

Elgmork's data are consistent with data reported by many other Scandinavian workers. For example, Skye (1968:79) states that pH values as low as 2.8 have been recorded in rainwater on the west coast of Sweden, and Skogland (Mr. Terje Skogland, personal communication, July 1972) reports that a similar value of pH 2.9 was measured in black snow on a mountain plateau in Norway during the winter of 1971-72. He states that the plateau (Hardangervidda) is the winter range of wild reindeer. (See also Reiquam, 1970b.) Likens *et al.* (1972) present evidence for increased acidity of precipitation in the northeastern United States.

Elgmork's suggestion that the source of the pollutants in Scandinavia is the British Isles and middle Europe is supported by data summarized by Likens *et al.* (1972), and Reiquam (1970a) has developed computer simulations of weather patterns that also support the suggestion. But despite the high probability that reindeer lichens might be adversely affected by such very acidic precipitation, the idea appears to have been entertained only by journalists (e.g., Palmstierna, 1969).

Possible Consequences for Reindeer and Caribou

Many environmental factors undoubtedly influence the degree to which SO_2 affects lichens, including rainfall regime and other meteorological and hydrological parameters. The details will vary from area to area. Nevertheless, the existing evidence justifies a concern for the health and survival of arctic lichens. There appears to be no reason why forage lichens will not be harmed by air pollution eventually. Global pollution is increasing rapidly. Likens *et al.* (1972) report that the acidity of Swedish rivers is increasing at an annual rate of 8 to 24 per cent. Local pollution will increase because the Arctic itself is undergoing intense development. The long-term likelihood is that arctic lichens will be bombarded by progressively greater quantities of pollution from both local and global sources. As a

consequence, reindeer and caribou that require lichens at critical times of the year will undoubtedly be affected. Lapps, Eskimos and other northern peoples who depend upon reindeer or caribou will suffer in their turn.

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Note added in proof

During the summer of 1973, the author and Dr. Ronald M. Atlas obtained evidence in laboratory and experimental field studies at Barrow and Prudhoe Bay, Alaska, that SO₂ stimulates or depresses respiration in *Cetraria nivalis* at concentrations of 0.1 and 1.0 ppm or 10 ppm, respectively, and depresses photosynthesis in *C. nivalis* and *Peltigera aphthosa* at concentrations as low as 0.01 ppm.

SOME RESULTS FROM FEEDING EXPERIMENTS WITH REINDEER

E. Jacobsen and S. Skjenneberg
Norwegian State Domestic Reindeer Research Institute
Harstad, Norway

ABSTRACT—The main purpose of this work is to make the reindeer husbandry more independent of the variations of natural pastures. The work includes: (1) development of a substitutional food stuff, (2) determination of the nutritional value of lichens, (3) effect of different supplements to a lichen diet, and (4) the importance of the quality of winter nutrition on newborn calves.

(1) Different types of dietary substitutes were tested. The ration having the (a) best dietary effect, (b) slow consumption rate and (c) high energy content has this composition (coarse-ground, pelleted): barley 40 per cent, oats 17 per cent, wheat bran 15 per cent, young grass 25 per cent and soybean oil 3 per cent.

(2) Three male calves given a pure lichen diet were used for two digestion trials. The lichen was digested as follows: organic matter 74.9 per cent, ether extract 66.0 per cent, crude fiber 75.2 per cent, nitrogen free extract 79.7 per cent. Lost by digestion of 1 kg DM was 6.3 g crude protein. Estimated energy was 0.9 feed units/kg DM.

(3) Supplements (protein, minerals or energy) increased the intake of lichen, reduced digestibility of total ration (compared to lichen alone) and gave a positive growth response.

(4) Pregnant females were given protein and minerals as a dietary supplement to lichen from February 16 to May 6. This increased the live weight of female reindeer, milk yield and the growth rate of fawns, thus indicating a beneficial effect on normal winter pastures.

OBJECTIVE OF THE EXPERIMENTS

The reindeer pastures in Norway are of very changing quality, depending partly upon type of vegetation and partly on the climate which varies from the coast to the interior. The domestic reindeer area, covering approximately 40 per cent of the country, is divided into pasture districts. Each district or group of districts is meant to make a complete pasture for reindeer throughout all seasons, but this is not always so; in many cases there are a surplus of summer grazing areas. In some districts the rapidly changing weather conditions may suddenly 'lock' the pastures. Spring is often the most critical period. The demands for food are high but snow and other weather conditions often make fatal restrictions in the grazing possibilities. Reindeer have until now depended solely on natural pastures for their nutrients. Due to above factors, traditional reindeer husbandry has many elements of risk. It is the objective of our experiments to eliminate these risks, thus making reindeer husbandry more secure and profitable.

EXPERIMENTS

One of the first problems undertaken by our Institute was to develop a suitable substitute feed for reindeer. In our opinion and based on our experiments with various feeds, the ideal and practical feed should have the following properties: *Good tolerance*. It must ensure normal ruminal digestion — for example, as indicated by pelleted feces. *Slow consumption*. The change from a natural pasture to an 'artificial' diet is difficult, especially if the reindeer have been starving some time before the feeding is started. It is most important to start artificial feeding of reindeer early enough to avoid destruction of the ruminal microflora and to prevent lowering of the animals' energy reserves. To avoid an initial large intake before the ruminal microbes are adjusted to the new feed, the palatability of the feed should not be very high. This also gives the weakest animals a chance to get their share of the food before the cribs are emptied by stronger reindeer. *High energy content*. A starving animal is above all lacking in energy. However, the feed must also include nutritional constituents that will permit the animals to recover from the results of malnutrition. It must also allow for limited growth and especially for continued development of the foetus. *Simple composition*. To permit rapid compounding when urgent, feed should consist of ordinary components usually kept in stock. Several types of feed were tested and were rejected. Three examples of recently tested feeds are shown in Table 1. These feeds are discussed below in respect to their composition and their influence upon the condition of the reindeer.

TABLE 1.--Composition (%) and digestibility of three types of feed tested in feeding trials with reindeer.

<i>Ingredients</i>	67 - B	69 - A	71 - A
Barley, ground	14.0	9.1	40.0
Oats, ground	22.0	14.3	17.0
Wheat bran	7.0		15.0
Beet pulp		8.8	
Peat with molasses	6.6		
Young grass, ground		19.5	25.0
Grass, ground	33.0		
Straw, ground	15.0	46.7	
Soybean oil			3.0
Seaweed	1.0	0.67	
NaCl	0.4	0.36	
Ca ₃ (PO ₄) ₂	1.0	0.67	
<i>Nutrients (% of dry matter)</i>			
Crude protein	9.6	6.3	13.4
Crude fat	2.6		7.2
NFE	52.4	48.7	62.7
Crude fiber	18.8	23.9	11.0
Ash	5.9		5.7
<i>Digestibility (of org. matter)</i>	59.3	63.8	74.2

Feed 67-B. This formula resulted from several experiments. The feed was very palatable to the reindeer and was tolerated well. The composition is however too complicated for practical use as some of the ingredients are not common commodities. Also,

weight gains shown by the animals were unsatisfactory and may be related to the high content of crude fiber and the resulting low digestibility (see Table 1). This is explained under 69-A below.

Feed 69-A. This formula was developed from 67-B. We intended to replace the straw with tapioca to increase the amount of easily digestible carbohydrate and decrease the level of crude fiber. Without our knowledge, the tapioca was excluded and the amount of straw doubled (relative to 67-B) giving a crude fiber content of nearly 24 per cent. As a result several animals died, although maintaining a voracious appetite to the end. On autopsy they showed emaciation and ulceration of the abomasum. One animal had multiple, perforating ulcers. These findings suggested mechanical irritation, probably from the straw, and starvation.

Feed 71-A. This feed satisfies all the requirements stated above. It was tested in a feeding trial with six animals from February 17 to April 2, 1971 and gave the following results: mean gain of weight per animal 4.70 kg; mean daily intake per animal 1.45 kg. It was given a practical test during the winter 1971-72 in a reindeer herd of about 300 animals suddenly 'locked out' from the pastures by heavy layers of crusty snow. The animals were fed every day from December 22 to January 26 with some other types of feed. The quantities given were too small, causing the weakest animals to starve and many others to show varying degrees of diarrhea. When changed over to sufficient quantities of 71-A, under a more proper feeding regime, the symptoms disappeared and there were no deaths in the herd for the last 2½ months of the feeding period which lasted to May 1. The reindeer owners reported that the fawns that spring were unusually vigorous.

Nutritional Value of Reindeer Lichen

Lichens play an important part in the winter feeding of reindeer — amounting to 51-88 per cent of daily dry matter intake according to Gulchak (1954) and Druri and Mitushev (1963). In Norway, Skjenneberg, *et al.* (1975) and Gaare *et al.* (1970) estimated by means of esophageal fistulas the part that lichens play in the winter nutrition of reindeer. Lichen intake ranged between 61 and 98 per cent of total food consumed.

To estimate the digestibility of reindeer lichen, two trials were carried out (January 19-29 and March 5-15) using mainly *Cladonia alpestris*. Three male calves were fed pure lichen *ad lib*. They were offered up to 1 kg dry matter daily from December 22 to March 15, but the consumption never reached that level. The mean daily consumption per animal was 818 g and 701 g respectively in each trial. Throughout the entire period the animals lost weight averaging 46.7 g/day/animal. Chemical composition of the lichen dry matter was as follows: organic matter 98.6 per cent, crude protein 3.1 per cent, nitrogen free extract 61.2 per cent, crude fiber 32.6 per cent, ether extract 1.7 per cent, ash 1.4 per cent.

The variation in digestibility is higher between animals than between trials. Thus, estimated means of mean deviation are smaller than they might have been with six different animals in one single trial. During digestion there is a loss of crude protein, Ca and P (Table 2). Fattening feed units (F.F.U.) were estimated on the basis of the chemical composition of the lichen and the digestibility of lichens from our trials. It was done according to the Kellner-Mollgaard method. We used a reduction of 1.04 NKF (net calories for fattening) per g undigestible org. matter. The negative protein value in lichen (Table 2) was not considered in the estimation which gave the value 1435 NKF of 0.9 f.f.u./1000 g dry lichen matter. This is very similar to that found by Nordfeldt *et al.* (1961) and Lenvik and Fjellheim (1970).

TABLE 2.--Digestibility of lichen nutrients (90% *Cl. alpestris*).

	Trial A (%)	Trial B (%)	Trials A+B (%)
Organic matter	74.6	75.2	74.9±1.03
Ether extract	65.0	67.0	66.0±1.69
Crude fiber	74.6	75.8	75.2±1.33
NFE	78.6	78.9	78.7±1.29
Digestibility: (g/1000 g dry matter of forage)			
Crude protein	-6.8	-5.7	-6.3
Ash	-5.9	-5.9	-5.9
Ca	-0.63	-0.97	-0.80
P	-0.30	-0.33	-0.32

Effect of Protein, Minerals and Energy Supplements upon Reindeer Calves Fed a Lichen Diet

Considering the low content of protein and minerals in reindeer lichen, the question arises if there is any effect of supplementing the winter diet with these constituents. Analysis of winter forage plants carried out by Persson (1962) and Scotter (1972) show that plants eaten in addition to lichens do not increase protein or mineral content to any extent. Skjenneberg *et al.* (1972) found by chemical analysis of 18 forage samples from reindeer with esophageal fistulas that the protein in dry matter of winter forage varied from 2.8-4.5 per cent, averaging 3.54 per cent. As the average intake of lichens was 76.9 per cent, it is obvious that plant protein other than from lichen does not enhance the diet significantly.

The weight loss of a reindeer through a winter season may approach 20 per cent according to records with the Norwegian experimental herd. The effect of this weight loss on the total economy of reindeer industry is not known. Important economic factors are loss of animals during winter, survival of fawns in spring and slaughter weights in the fall. Loss of calves from the experimental herd is approximately 15 per cent from birth to registration during July. The loss of calves through the first winter is of similar magnitude. Losses of calves during the first year are obviously of great importance and therefore we studied the effects of winter nutrition on the losses.

Our experiments were carried out with 26 calves separated into seven groups. The trial was repeated after six weeks to test if there was any influence on the utilization of the feed over a long period of intake. Table 3 gives details of the seven groups and feeding regimes. The mean daily intakes of the various rations and their constituent nutrients are listed in Tables 4 and 5.

The supplements gave a marked increase in appetite and thus lichen intake. There was an increase from a mean daily intake of 2320 g in Group I (lichen) to a maximum of 2896 g in Group VI (TF-69).

It appears from Table 6 and Figure 1 that all the groups given supplementary protein gained weight. Group III (Energy addition) showed no gain. Analysis of variance on the groups (Group VII not included) showed a statistically significant difference at the 1 per cent level. A significant difference was also shown between Groups III and IV on the 1 per cent level but not between IV and V (Students t-test). From these results it can be

TABLE 3.--Feeding groups and feeds (all groups on a basic lichen diet, trial lasted 83 days).

Group	Number and sex	Supplementary feed*
I	2♂ + 2♀	None
II	" "	None
III	" "	Barley (150 g/day)
IV	" "	"Urea-barley" (170 g/day)**
V	" "	Soybean meal (160 g/day)
VI	" "	"TF-69" (130 g/day)***
VII	2♂	Urea (24 g/day)

*All groups except Group I and II were fed 30 g of mixed minerals daily.

**Heated barley with 12% added urea.

***TF-69 has this composition: 42% mixed minerals, 16% urea, 10.5% soybean meal, 16% corn, 5.5% wheat bran and 10% molasses.

TABLE 4.--Mean daily intake of supplementary feed and mixed minerals, g/animal.

Group	Feed type	Intake (g/day/reindeer)	
		Supplementary feed	Mixed minerals
I	lichen	0	0
II	lichen + minerals	0	16.2
III	lichen + minerals + barley	148.4	18.2
IV	lichen + minerals + "urea-barley"	136.0	16.3
V	lichen + minerals + soybean meal	147.3	11.5
VI	lichen + "TF-69"	100.3	42.1
VII	lichen + minerals + urea	24.0	30.0

concluded that protein was the most beneficial additive, and there was a better gain with 'natural' protein than with urea.

Digestibility of the total ration is given in Table 7. Except for Group III (Barley) there are only small differences between the digestibilities when the two trials are compared. Ether extract shows a higher digestibility in the second trial in all groups.

The most interesting feature in Table 7 is that the digestibility values are considerably lower in all groups given supplementary feed than in those given pure lichen. We can speculate upon the reason for this lowered digestibility; it may either be caused by a very low digestibility of the supplementary feeds, or by an interaction between the lichen and supplementary feed leading to a reduction of lichen digestibility alone or of both lichen and supplement digestibility.

The connection between digestibility of organic matter in the total ration and Ca in the total ration. In the balance trials, there were no positive balances of minerals and the

TABLE 5.--Mean daily intake of f.f.u., crude protein, Ca, P and Mg.

Group	I Lichen	II Lichen Minerals	III Lichen Minerals Barley	IV Lichen Minerals "Urea-Barley"	V Lichen Minerals Soybean Meal	Lichen TF-69*	VII Lichen Minerals Urea
f.f.u. in lichen	0.698	0.745	0.746	0.842	0.846	0.878	0.868
f.f.u. in supplement	0	0	0.148	0.128	0.145	0.050	0
f.f.u. total	0.698	0.745	0.894	0.970	0.991	0.928	0.868
crude protein, g	24.5	26.4	42.2	78.1	101.6	74.4	100.2
% protein from urea	0	0	0	46.2	0	48.9	69.1
Ca, g	0.7	2.6	3.1	2.8	2.6	6.7	4.4
P, g	0.4	1.7	2.3	2.2	2.3	4.5	2.8
Mg, g	0.2	0.7	0.9	1.0	1.0	1.9	1.1
Apparently digested crude protein, g	-4.6	-7.0	2.4	36.2	58.5	35.1	61.0

*TF-69 includes minerals.

TABLE 6.--Weights and weight gain in the different groups
(83 day trial).

Group	I	II	III	IV	V	VI	VII
Number of animals	4	4	4	4	4	4	2
Initial weight, kg	39.4	39.8	40.8	39.8	41.8	38.8	43.5
Final weight, kg	35.2	37.2	38.7	41.1	43.4	41.0	43.7
Gain, kg	-4.2	-2.6	-2.1	1.3	1.6	2.2	0.2
Gain, g/day	-50.6	-31.3	-26.3	15.7	19.3	27.9	1.2

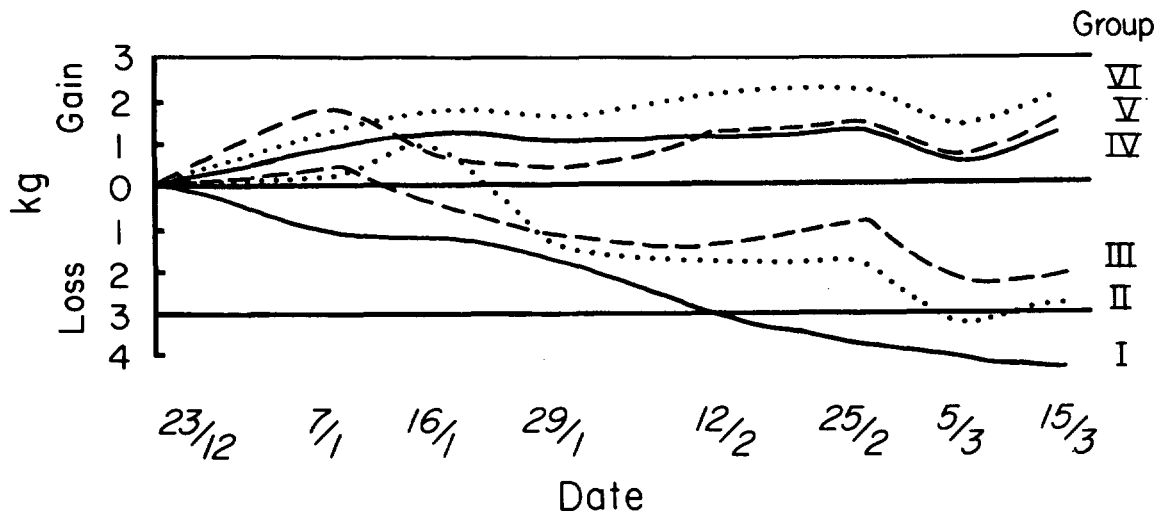


Fig. 1.--Changes in body weight in supplemented and non-supplemented reindeer calves fed a basic lichen ration.

minerals were shown to be excreted in the feces. We thus speculate that the minerals may have caused the reduced digestibility. The possibility that some indigestible salts of lichen acids and minerals are formed will be studied separately. The correlation between intake of Ca and digestibility of organic matter was calculated to be -0.501 in trial A and -0.684 in trial B.

The N-balance. The N-balance from the two trials is given in Table 8. Real growth is characterized by an increase in the body depots of protein, minerals and water; thus fattening is not growth (Maynard and Loosli, 1969). By means of N, Ca and P balances we may estimate real growth. Here we shall discuss the connection between the N-intake and the N-balance as displayed in Figure 2. When the object is to compare protein quality, it is recommended that the offered N is kept slightly lower than the demand and that the other nutrient requirements are fulfilled. If the protein in the different feeds is of equal digestibility and of equal biological value, a linear correlation would be expected between N-intake and N-balance when the balances are negative or slightly positive. The correlations between N-intake and N-balance are: trial A: $r = 0.95$, trial B: $r = 0.90$, and between apparently digested N and N-balance: trial A: $r = 0.94$, trial B: $r = 0.88$.

TABLE 7.--Digestibility of the components of the total ration.

Group		I	II	III	IV	V	VI	VII
Supplemental feed*				Barley	Urea-barley	Soybean meal	TF-69	Urea
Organic matter	Trial A	74.6	67.9	70.1	67.3	69.4	64.9	68.5
	" B	75.2	67.0	75.1	68.6	69.2	65.2	67.5
	Mean	74.9	67.4	72.6	68.0	69.3	65.0	68.0
Ether extract	Trial A	65.0	61.9	60.6	61.9	57.2	61.8	60.0
	" B	67.0	68.3	77.6	67.0	61.0	69.7	64.5
	Mean	66.0	65.1	69.1	64.4	59.1	65.8	62.2
Crude protein	Trial A	-20.8	-42.3	-13.2	42.4	55.3	47.6	58.9
	" B	-25.5	-37.3	12.3	50.3	59.8	46.8	61.3
	Mean	-23.6	-39.8	-0.4	46.3	57.7	47.2	60.1
Crude fiber	Trial A	74.6	72.3	67.6	65.0	67.5	65.4	66.4
	" B	75.8	66.7	72.4	69.5	66.8	64.1	67.4
	Mean	75.2	69.5	70.1	67.2	67.1	64.8	66.9
NFE	Trial A	78.6	70.0	76.0	69.7	73.0	69.3	71.9
	" B	78.9	71.2	80.1	74.3	72.2	69.5	71.0
	Mean	78.7	70.6	78.0	72.0	72.6	69.4	71.4

*All groups except I given minerals.

TABLE 8.--N-balance (g).

Trial A										
Group	I		II		III		IV		V	
Animal no.	83	75	131	110	84	129	128	74	89	86
N in feed	3.406	3.589	2.974	3.496	4.341	5.827	13.827	11.642	16.744	17.632
N in feces	3.934	4.530	4.206	4.976	5.626	5.637	7.174	7.365	6.554	8.885
N in urine	1.197	1.485	1.109	0.878	1.386	0.058	4.930	4.168	8.719	7.101
N-balance	-1.725	-2.426	-2.341	-2.358	-2.671	-0.668	+1.723	-0.109	+1.501	+1.646
Group	VI		VII							
Animal no.	115	104	88	77						
N in feed	7.451	14.003	16.170	16.232						
N in feces	7.006	7.339	6.317	6.461						
N in urine	2.455	6.046	8.614	8.975						
N-balance	-2.010	+0.618	+1.239	+0.796						
Trial B										
Group	I		II		III		IV		V	
Animal no.	83	75	131	110	84	129	128	74	89	86
N in feed	2.605	3.098	2.301	3.373	5.158	5.546	13.499	13.101	16.288	17.038
N in feces	3.142	4.029	2.789	4.630	4.714	4.542	6.728	6.499	0.066	7.342
N in urine	0.970	1.304	1.165	0.594	1.235	0.807	6.235	5.737	8.765	7.299
N-balance	-1.507	-2.235	-1.653	-1.851	-0.791	+0.197	+0.536	+0.865	+1.457	+2.397
Group	VI		VII							
Animal no.	115	104	88	77						
N in feed	11.334	13.778	15.787	15.818						
N in feces	6.610	6.622	6.110	6.122						
N in urine	4.581	6.811	8.941	9.422						
N-balance	+0.143	+0.345	+0.736	+0.204						

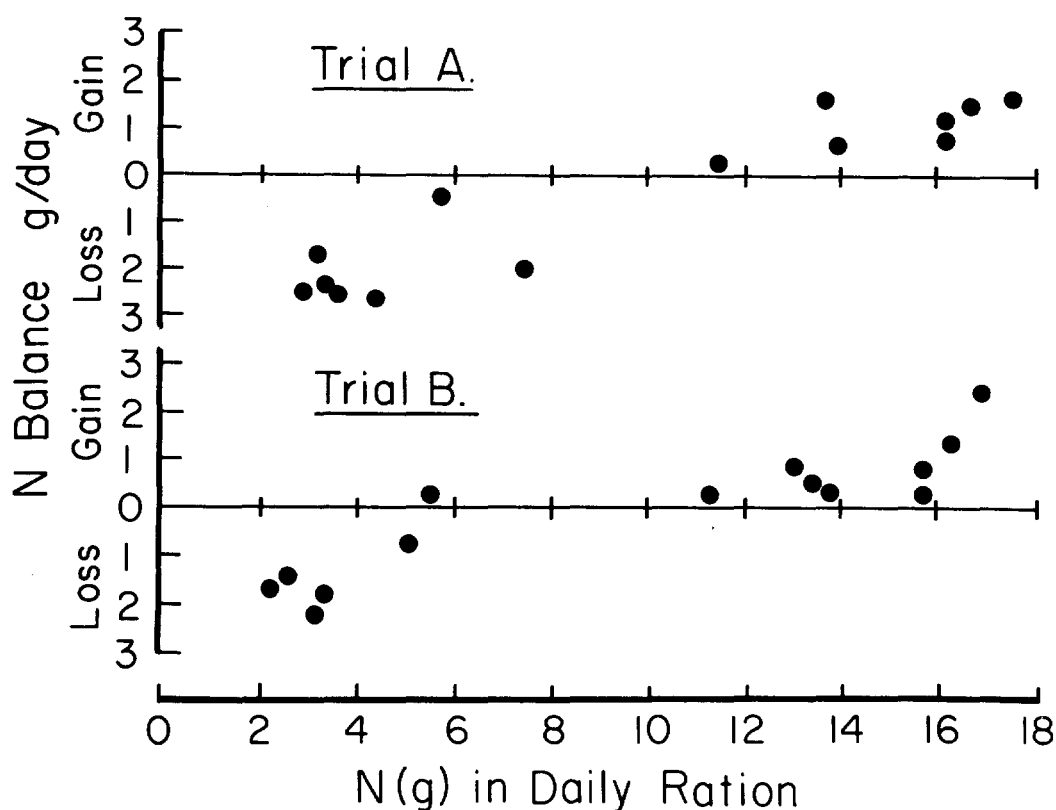


Fig. 2.—N-intake and N-balance in two balance trials with reindeer calves.

The ability of reindeer to grow during winter is not fully known. According to McEwan and Whitehead (1970) there is a decrease in the growth rate of caribou in winter. Our aim is to prevent weight loss from skeletal components and internal organs rather than to obtain growth. A drawback in our experiments is that the amount of essential nutrients has been to some degree insufficient; no vitamins were given and the intake of minerals was quite different between groups. With no reliable data for metabolic and endogenous N being available, the utilization of nitrogen is expressed as N-balance in per cent of N-intake and N-balance in per cent of apparently digested N (see Table 9).

By comparing Group V (soybean meal) and Group VII (urea) which have approximately the same N-intake, it is obvious that the reindeer in Group V utilized the nitrogen better than in Group VII. The difference is greater, however, when expressed as a per cent of apparently digested N and is probably due to greater biological value of the soybean meal protein.

Ca and Mg in blood plasma. Blood samples were taken from all animals at the end of the experiments and analyzed for Ca and Mg. The results are presented in Table 10. Eight samples were collected from each animal over a period of two days and the figures shown are means of the animals in each group.

These data show that the differences in Ca values are small whereas in contrast supplemental feeding distinctly affected the Mg value.

In addition to the animals of Group I, three other animals consumed very small amounts of minerals, and again we determined that plasma Mg-content was distinctly lower

TABLE 9.--N-balance.

Group	IV		V		VI		VII	
Animal no.	128	74	89	86	115	104	88	77
N-balance as % of total N-intake:								
Trial A	12.5	0.9	8.9	9.3	-0.27	4.4	7.7	4.9
Trial B	4.0	6.6	8.9	14.1	1.3	2.5	4.7	1.3
N-balance as % of apparently digested N:								
Trial A	25.9	2.5	14.7	18.8	-456.9	6.5	12.6	8.1
Trial B	7.9	13.1	14.3	24.7	3.0	4.8	7.6	2.1

TABLE 10.--Ca and Mg in blood plasma (mg/100 ml).

Group	Type of supplementary feed	Ca	Mg
I	None	9.37	1.11
II	Minerals	9.30	1.96
III	Minerals + barley	9.90	1.93
IV	Minerals + "Urea-barley"	9.65	2.29
V	Minerals + soybean meal	9.90	2.38
VI	TF-69	9.43	2.33
VII	Minerals + urea	9.44	2.38

than the mean of the supplemented groups. Consequently a pure lichen diet seems unable to support normal concentrations of Mg in blood.

Supplementary feeding of pregnant females. A preliminary study was undertaken to investigate the effect of an improved winter diet on the weight of the females during the winter and the growth of the calves during the ensuing summer. The experiment was carried out with 20 pregnant female reindeer which were kept on an *ad lib.* lichen diet from January 27 to June 13. During the period February 16 to May 6, 10 of the animals were offered TF-69 (see Table 3), after which time it was discontinued. The fawns were born from May 9 to June 1, with all the females calving. During calving the animals were kept in a large fence where they could eat small amounts of pasture in addition to the lichen provided. Even with the additional pasture, their food intake was estimated as lower than when on normal spring pastures.

Live weight of the females was determined five times during the trial. The fawns were weighed when 1, 4, 9 and 16 days old and on July 17 and September 19. Milk samples were taken at 4 hours and 13 days after calving and on July 17. Before sampling the mothers were isolated from their calves for 4 hours and before milking given 50 i.u. oxytocin intravenously. The milk yield from these samples was considered as indicative of the milk producing ability.

Some mishaps, however, reduced the number of mother-calf pairs to six in the supplementary fed group and to only four in the control group. Thus the numbers are too small for a statistical treatment. The data obtained were nevertheless so striking that we list

them in Tables 11-13.

TABLE 11.--Change in body weights of female reindeer and daily consumption of feed (kg).

	Change in body weight (kg)	Daily food consumption (kg)	
	(February 2 - May 5)	Lichen	TF-69
Lichen only	-3.65	4.225	
Lichen + TF-69	+3.50	6.326	0.117

TABLE 12.--Milk yield of female reindeer and body weights of reindeer calves.

Age of calf	Milk yield (g)			Mean weight of calves (kg)					
	4 hrs	13 days	July 17	1 day	2 days	9 days	16 days	July 17	Sept. 19
Lichen only	20	66	110	3.74	4.04	4.79	5.64	14.97	33.40
Lichen + TF-69	63	118	191	4.37	5.03	6.22	7.43	18.54	39.30

TABLE 13.--Mean daily weight gain (g) of calves.

Age period:	1-4 days	4-9 days	9-16 days	16 days- July 17	July 17- Sept. 19
Lichen only	101	149	121	280	281
Lichen + TF-69	221	238	172	322	293

The relatively small amount of supplementary feed caused a nearly 50 per cent increase in the *ad libitum* intake of lichen.

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SYLVICULTURAL PRACTICES AND REINDEER GRAZING IN NORTHERN SWEDEN

Olof Eriksson
Institute of Ecological Botany
University of Uppsala
Sweden

ABSTRACT—The most obvious immediate effect of large scale logging is the large quantity of slash that produces physical obstruction to winter grazing. Bioclimate, plant cover and availability of forage plants during winter are altered radically after clear cutting large areas. Beneficial effects of logging are an enlarged supply of epiphytic lichens immediately after the felling, and sometimes an increased growth of higher plants during following years. Reforestation methods also have an impact on the reindeer grazing resource. Controlled burning of clear cut areas, that destroys lichen stands for decades but that for some years may stimulate a rich growth of certain higher plants, is now almost abandoned. Mechanical preparation of the seed bed may destroy forage plants and reindeer herds also are reluctant to move across treated areas. Today, the use of herbicides to control deciduous growth in planted areas is restricted, since aerial application is prohibited. Aerial fertilization is practiced widely in Sweden. Little is known about the effect on plants used by reindeer. However, this method is used only on rich lands to make fast growing trees grow still faster the last few years before harvest. These rich lands are normally not of great importance to the reindeer industry. Although little research concerning interactions between logging and reindeer husbandry has been carried out so far, it seems reasonable to suspect that the reindeer husbandry will suffer if the existing silvicultural practices are not changed to some extent.

The part of Sweden utilized by the reindeer industry is the northernmost third, where the coniferous forests produce the main part of the winter grazing lands. These forests are not very valuable from the standpoint of forestry, because of high costs of transportation and problems with reforestation, and for other reasons. In spite of this a considerable amount of logging is done. The need of the local saw mills and pulp industries for raw material will probably affect the level of lumbering, as will the risks of unemployment among the local people.

Conflicts of interest between forestry and the reindeer industry arose several decades ago, when clear cutting became the dominant method of logging and burning of cut-over areas increased in popularity.

There are two types of reindeer herding in Sweden; the high mountain type where the reindeer migrate from summer pastures in the high mountains to the winter range in the coniferous forest, and the woodland type with migrations within a fairly restricted area in the coniferous forest region. Thus logging mainly affects the winter grazing for the mountain reindeer whereas it may have a year-round influence on the woodland reindeer.

This paper deals mainly with circumstances within the winter range north of the Lappmark border in the counties of Norrbotten and Västerbotten, the part of Sweden that is probably the most intensively utilized by the reindeer industry; moreover, only in this

region do the forest-statistical units coincide with the reindeer range (Figs. 1 and 2).

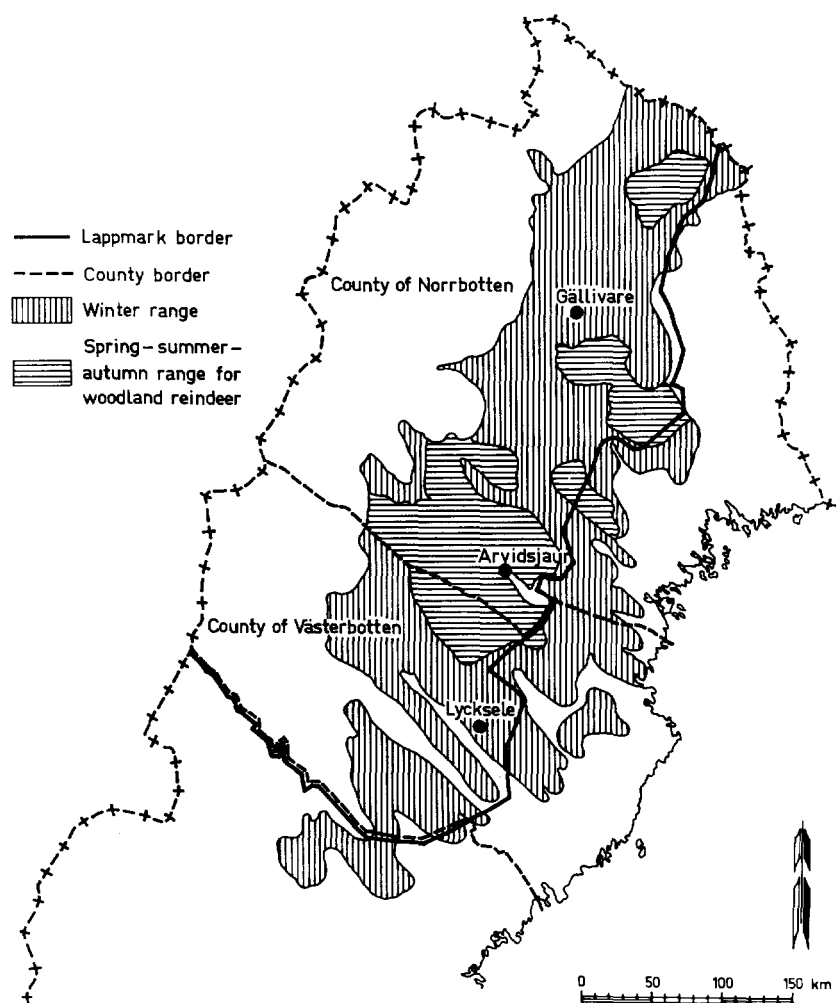


Fig. 1.—The distribution of range types within the coniferous forest region.

Logging

Availability of lichen range is of utmost importance for reindeer during winter. Nevertheless the diet also contains sedges, heath shrubs, such as *Empetrum hermaphroditum* and *Vaccinium myrtillus*, and grasses (Skuncke, 1963; Eriksson, 1972).

Thus while the most important winter ranges in the coniferous forest region are to be found in lichen-rich pine forests; pine forests with mosses, *Vaccinium vitis-idaea* or *Vaccinium myrtillus* and with patches of lichens are also of great importance.

As one can see from Table 1, about half of the lichen-rich pine forest north of the economic limit for artificial reforestation remains unlogged, while below this limit only 20-30 per cent remain. From the standpoint of reindeer grazing one should add to these remaining areas some forests under reforestation that now have reached such an age (20-30 years) that they once again may be looked upon as fair reindeer range. The most important

TABLE 1.--Occurrence of different winter range types in the counties of Norrbotten and Västerbotten of Lappmark. Figures in thousands of hectares. Skogsbruksutredningen (1969).

County	State of the forest	Pine, rich in lichens	%	Pine, with mosses, <i>Vacc. vitis-idaea</i> and patches of lichens	%	Pine, or spruce with mosses, <i>Vacc. myrtillus</i> (and patches of lichens)	%	Total
Norrbotten	clearcut	19.0	11.5	15.0	9.1	6.2	4.9	40.2
north of the	reforest.	62.8	37.9	53.1	32.1	42.5	33.9	158.4
limit of econ.	virgin	83.8	50.6	97.4	58.9	76.6	51.1	257.8
reforestation	Total	165.6		165.5		125.3		456.4
Norrbotten	clearcut	41.9	11.2	48.0	12.3	29.5	11.0	119.4
south of the	reforest.	212.8	57.0	212.0	54.4	130.8	48.9	555.6
limit of econ.	virgin	118.6	31.8	129.7	33.3	107.2	40.1	355.5
reforestation	Total	373.3		389.7		267.5		1,030.5
Västerbotten	clearcut	0.5	17.2	3.1	8.9	1.4	5.2	5.0
north of the	reforest.	0.8	27.6	13.9	40.1	9.4	35.1	24.1
limit of econ.	virgin	1.6	55.2	17.7	51.0	16.0	59.7	35.3
reforestation	Total	2.9		34.7		26.8		64.4
Västerbotten	clearcut	11.2	9.1	28.6	10.2	27.6	8.9	67.4
south of the	reforest.	83.2	67.6	178.0	63.4	178.9	57.4	440.1
limit of econ.	virgin	28.7	23.3	74.1	26.4	105.3	33.8	208.1
reforestation	Total	123.1		280.7		311.8		715.6

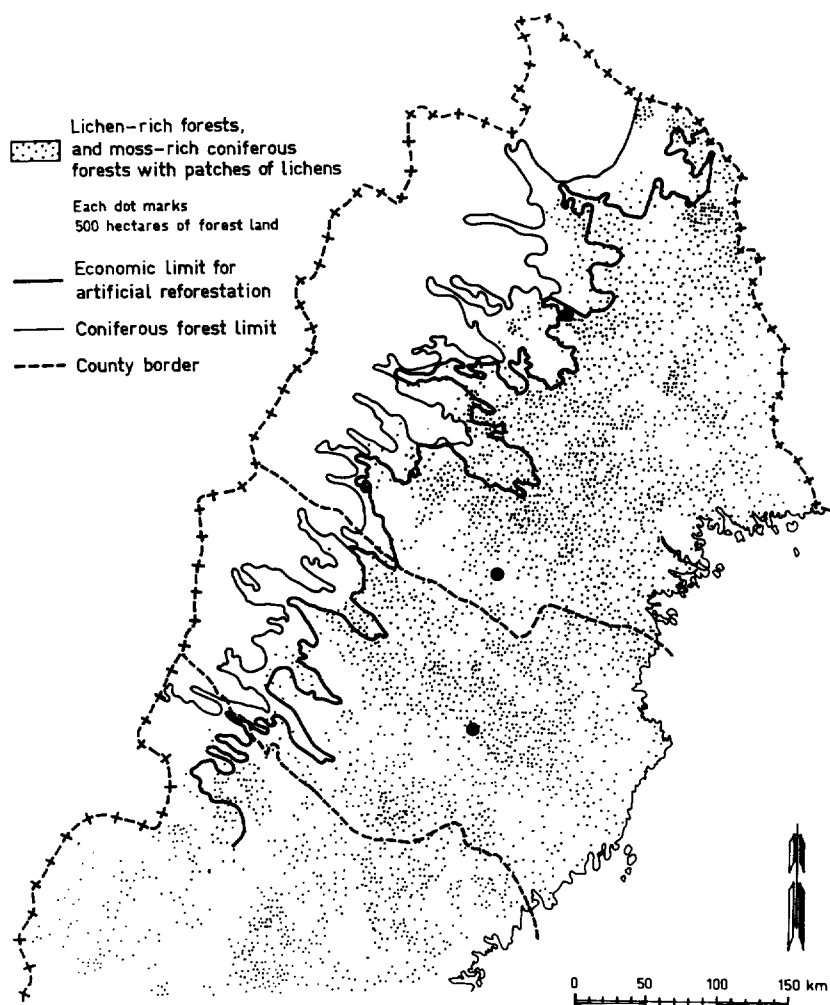


Fig. 2.—Dominant areas with lichen-rich forests.

winter range types (in reality forest types) occur both north and south of the limit of economic reforestation (Skogsbruksutredningen, 1969).

Today almost all logging is done as a complete clearcut or as a semi-clearcut (seed-type stand), where a certain number of pine trees (70-100/ha) are left to produce seeds to self-regenerate the forest.

The complete clearcut is utilized under the following conditions: (a) when the development of seeds is retarded or plant growth is delayed by a thick undecomposed layer of raw humus or by luxurious grass or forb growth, (b) when seed producing pine trees of good quality are lacking, (c) where there is great risk of wind-throw (mainly in spruce forest; only pine is used as seed-trees) and (d) where one wants to change the dominant species (usually from spruce to pine).

Seed-tree stands are utilized under the following conditions: (a) in areas where self-reproduction is easy, especially dry pine forest sites, (b) where the risk of wind-throw is small, (c) when a sufficient number of seed producing trees are at hand and (d) on very low-producing lands where planting is too expensive in relation to the value of the future

product (i.e., the profit to be expected).

Selective logging, in which only the most valuable trees were cut, is today more or less abandoned, partly because it is too expensive in terms of labor and transport costs and partly because the remaining trees usually are more or less damaged by the large machines that are used to haul out the logs. This method is also considered to make efficient reforestation impossible (Ebeling, 1972).

From the standpoint of reindeer grazing, there is no great difference between the two types of clear cutting. In both cases large quantities of slash remain. For some four or five years this slash makes grazing difficult. Lichens protected by the slash, however, may grow rather swiftly.

At present large scale experiments are made with machines that cut the trees and bring them to centrally located processors that in turn remove the branches and cut the logs to proper dimensions. Thus the slash is concentrated in large piles.

Microenvironment

Few studies have been made that reveal the connection between changes in micro-environment and the amount of vegetation available to the reindeer both before and after logging. A project was, however, started in the summer of 1971 in the parish of Arvidsjaur, county of Norrbotten, within an area that was to be logged during 1972. Effects of this logging operation, undertaken in October 1972, on the biomass of vegetation available to reindeer, have, of course, not yet been observed. Certain changes in microenvironment between earlier logged and unlogged sites have, on the other hand, been recorded. For example insolation, reflection, wind speed and maximum temperature during daytime in summer have increased, whereas humidity and minimum temperature have decreased (Eriksson, 1972).

Studies where changes in climate after logging have been recorded were published by Odin and Perttu (1966), Odin (1971) and Perttu (1973). Some of the results from their studies on clearcut areas and in adjacent, somewhat scattered forest close to the treeline in Gällivare parish, county of Norrbotten, may be synthesized as follows:

- (1) No obvious difference in temperature at standard level (200 cm) between a clearcut area and the surrounding forest.
- (2) Close to the ground (less than 50 cm) the clearcut area was warmer in daytime and colder at night than the surrounding forest.
- (3) The number of night frosts during summer was greater in the clearcut area than in the forest.
- (4) Surface temperature in the clearcut area was about 15°C higher than in the surrounding forest on a hot summer's day.
- (5) The capacity for evaporation from the ground vegetation was about 40 per cent higher in the clearcut area than in the forest.
- (6) Wind speed in the clearcut area was 80 per cent higher than in the surrounding forest.
- (7) Net insolation during a cloudless summer's day was 50 per cent higher in the logged area than in the forest.
- (8) Snow cover thickness in the clearcut area varied greatly due to exposure to wind as follows:

Snow cover thickness	Clearcut	Surrounding forest	Surrounding forest
		south side	north side
1964-68	42-64 cm	52-89 cm	50-90 cm

(9) The average snow density during the winter of 1965 varied as follows:

Date (day/month)	Clearcut	Surrounding forest south side	Surrounding forest north side
20/01	0.23	0.22	0.23
05/02	0.32	0.28	0.30
17/02	0.37	0.30	0.27
03/03	0.40	0.37	0.40
22/04	0.32	0.29	0.27
\bar{X} , N=3	0.33	0.29	0.29

In districts where the climate is naturally harsh large clearcut areas may contribute to make the climate still worse; in places this may cause the tree line to move down to lower altitudes (Söderström and Hopfgarten, 1971).

The Availability of the Range

Usually open areas, such as clearcut areas and mires, tend to have a thinner snow cover than surrounding forests. This is a natural consequence of the fact that the winds are stronger and snow drifting is more pronounced over open ground than in forest (Rodhe, 1965; Eriksson, 1972).

An occasional spell of mild weather may cause a thin snow layer to thaw right down to the ground. When cold weather later returns, the wet snow on the ground will freeze to an icy crust that will make grazing more or less impossible. Consequently there is a greater risk of getting hard snow cover than in forests (Rodhe, 1965). Layers of icy snow (Sw. 'skare') or tough compressed snow also tend to develop more often on open ground than in forests (Rodhe, 1965; Eriksson, 1972).

Figure 3 shows the snow situation on a partially logged site and in an adjacent pine

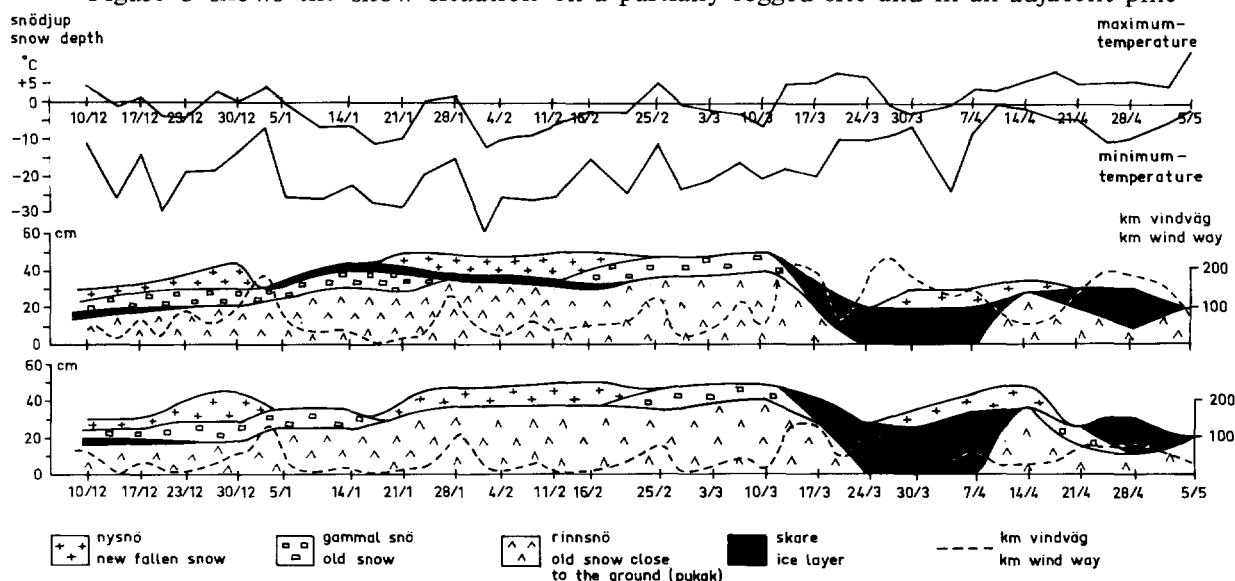


Fig. 3.—Time sequence of temperature, wind and snow conditions on a clearcut area (above) and in an adjacent pine forest (below).

forest during the winter of 1971-72 in a study area close to Arivdsjaur in central Lapland. Note that the thick layer of icy snow (Sw. skare) which developed the first of January next to the ground on the cut-over site did not vanish until late February; in the surrounding forest the snow was soft all the time (Eriksson, 1972).

Biomass

Post-logging changes in the biomass of the ground vegetation obviously have been considered of only secondary interest, therefore few investigations have been made and then mostly in high-yielding forest types, usually outside the reindeer country. Nykvist (1971), for example, has investigated changes in biomass in the ground vegetation in a spruce (*Picea abies*) forest about 40 km south of Lycksele, county of Västerbotten.

This forest type is not prime winter range although it is extremely important during winters with bad snow conditions since it provides arboreal lichens as emergency food. Nykvist's work showed that a clearcut may cause obvious changes in biomass as early as two years after cutting. Before logging (1967) there were 1,580 kg of vegetation biomass/ha in the field and bottom layers. Of this amount 1,080 kg or 69 per cent were mosses and 520 kg or about 30 per cent were *Vaccinium* spp. After two years only 700 kg of biomass/ha remained. The mosses had diminished dramatically to only 120 kg or 17 per cent, whereas *Vaccinium* had diminished to only 365 kg/ha, which now was not less than about 50 per cent of the total biomass in the field and bottom layers. The amount of small deciduous trees and herbs (ca 140 kg/ha) had about doubled during the two years after logging. The growth of grass had also flourished from near zero to about 100 kg/ha. One might think that from the standpoint of reindeer herding this vegetation had, to a certain point, developed positively, since a considerable amount of *Vaccinium* remained and the herb and grass growth had increased. Herbs and grasses are useful to the reindeer only if they are in the neighborhood at the time these plants are available. Among *Vaccinium* only blueberry (*V. myrtillus*) seems to be grazed in large quantities (Skuncke, 1963; Eriksson *et al.*, 1971).

Lichen Growth

Kärenlampi and Tammisola (1970) have shown that the growth of certain lichens is governed mainly by precipitation, humidity and net radiation. Too high and too low a level of insolation will diminish lichen growth, as will drought. Hence a clearcut area is a poor environment for lichens since insolation is unrestricted and humidity is lower than in a forest (Odin, 1971; Eriksson, 1972; Perttu, 1973).

Measures of Reforestation

After logging and eventual cleaning up an area may be left for natural reforestation if good seed producing trees are at hand and if the type of ground is considered easily reforested, or if costs for artificial reforestation are considered to be higher than the future yield. This way of reforestation is utilized on 50-100 per cent of the lichen-rich range and the areas with mosses, *Vaccinium vitis-idaea*, and patches of lichens north of the economic limit for artificial reforestation in Lappmark (Skogsbruksutredningen, 1969). From the standpoint of reindeer grazing, this method is of course superior to any other method utilized.

Controlled Burning

Usually one has to promote reforestation actively if one wants to get a new productive forest in a logged over area within reasonable time.

The oldest method is controlled burning, a method that is now more or less abandoned since on one hand it is fairly expensive and on the other hand it gives uncertain results. During 1970 only 736 ha were burned over in Lappmark (Skogsstatistisk årsbok, 1970).

According to Domänverket (1972) burning is a biologically useful method in northern Sweden on moist ground with a thick layer of raw humus; that is, on ground that is not of prime importance as winter pasture.

If one burns a pasture rich in lichens the area so treated will be useless as a winter range for a long period of time.

Uggla (1958) has studied the effect of wildfires in lichen-rich pine (*Pinus silvestris*) forests in Muddus National Park, county of Norrbotten. He has reported a regeneration period of more than 40 years for reindeer lichens (*Cladonia* spp.). Holmbäck and Malmström (1947) have burned some study plots when making experiments in order to improve seed beds in lichen-rich pine forests in North Sweden. After 10-12 years only a few lichen thalli were to be seen. Fairly soon after a burning there is, however, an increased growth of certain higher plants that are eaten by reindeer. Among these are, for example, *Deschampsia flexuosa*. These plants, however, have their annual period of optimum production when there are plenty of other plants available for reindeer to eat and when the larger part of the reindeer population does not use this range.

Preparation of Seed Beds

According to Domänverket (1972) the goal, among other things, is to remove the humus layer in order to give the seeds a more suitable seed bed, to raise ground and air temperatures, to reduce competition from surrounding vegetation and to make planting easier.

Conventional preparation gives evenly distributed patches of exposed mineral soil with an area of about 0.4 m². This method should be utilized where the raw humus is thin or normal (average). Sometimes this method is needed also on fairly dry soil but never on the driest types of soil.

Radical preparation of seed beds gives considerably larger patches of exposed mineral soil (0.75-1.5 m²). It should be used in sites with a thick layer of raw humus.

Harrowing gives continuous 0.5 m wide stripes of bare mineral soil. These stripes are about 2-3 m from one another.

Plowing is an extremely thorough measure of reforestation. A ditch, about 40 cm deep, is created, flanked by two ridges of exposed mineral soil 2 m wide (Figs. 4 and 5). These ditches are cut about 4.5-5 m from each other. Increased ground temperature, less risk of summer frosts and local drainage give the seedlings of trees a greater chance to survive.

It has been proven by Söderström and Hopfgarten (1971), Kohn (1970) and MoDo (1970, 1971, 1972) that the environmental conditions offered to tree seedlings are favorable after correctly executed plowing. This method, however, also has its drawbacks, as have been stated by Söderström and Hopfgarten (1971) and Troedsson and Utbult (1972).

Winter range that is plowed will have for a considerable time a very low value as winter pasture. First, the vegetation cover will be reduced by more than 50 per cent by the exposure of the mineral soil and by the ridges of slash and raw humus that will develop between the trenches. Secondly one must suspect that the system of ridges and trenches



Fig. 4.—Low level aerial view of plowed cut-over area in Gällivare Forest Rangers District, county of Norrbotten. Photo by Pål-Nils Nilsson/Tio.

will affect negatively the distribution of the snow cover. This, however, has not been investigated. For how long a period a plowed area will have a reduced value is unknown, but the experiments by Holmbäck and Malmström (1947) show that after 10-12 years practically no regeneration of lichens had occurred on a lichen range worked over with shovels so that the mineral soil had been exposed.

Plowing is a silvicultural practice that is primarily executed on moist soils with a thick layer of raw humus (i.e., second rank winter pastures). Plowing, however, is also allowed on dry soils with extremely severe climatic conditions (Domänverket, 1972). These types of areas are fairly frequent within the reindeer winter range and originally were often good winter pastures.

Among the methods of preparing seed beds, radical preparation, harrowing and plowing are the ones that can cause the reindeer industry a great deal of trouble. First, considerable amounts of pastures are destroyed by the exposure of the mineral soil and by the quantities of slash and raw humus that are deposited between the exposed patches or strings of mineral soil. The traffic of all-terrain vehicles needed for the mechanical preparation of seed beds also causes considerable damage to the lichen cover, especially if it is dry.

Secondarily, technical difficulties develop after plowing, since it becomes very difficult to traverse the area. Persuading a reindeer herd to traverse a plowed clearcut is certainly not



Fig. 5.—Close up of plowed cut-over forest land shown in Figure 4. The area is also reindeer winter range. Photo by Pål-Nils Nilsson/Tio.

an easy task.

One must hope that the worries felt by the reindeer herders over the future development of plowing cut-over coniferous forest are somewhat diminished after the Secretary of Agriculture, replying to a question in Parliament, stated that it is completely unlawful to plow areas utilized by Lapps as winter pasture (Bengtsson, 1972).

During 1970 a total of 6,369 ka were exposed to some kind of mechanical preparation of seed beds in Lappmark (Skogsstatistisk årsbok, 1970). Skogsbruksutredningen (1969) has estimated the yearly need for mechanical preparation of seed beds (in recently cut areas) as shown in Table 2.

To the reindeer industry the areas treated for self reproduction (6,300 ha) should be of prime interest. One might think that treated areas in the order of 6,300 or even 17,200 ha/year should be of minor importance. One must realize, however, that large continuous areas are those usually treated. Thus the damage caused to a single Lapp community might be considerable although the treated area might seem small compared to the total range.

For example, in 1971 and 1972 in the three northernmost districts administered by the Royal Board of Forestry, 2,397 ha and 1,734 ha respectively, were plowed (Director Häggström, Royal Board of Forestry, oral comm.). During these two years in the Forest Rangers district of Gällivare, 575 and 550 ha, respectively were plowed. These areas are situated almost entirely in the Lapp community of Norrkaitum (Skum, N., unpub. data).

TABLE 2.--Estimation of areas to be exposed each year to mechanical preparation of seed beds in future cut-over areas in Lappmark.
Figures in thousands of hectares.

County	Yearly cut-over areas	Mechanical preparation of seed beds for self reproduction, planting & seeding				Total
		%		%		
Norrbotten north of the limit of economical reforestation	8.8	1.1	13	1.0	12	2.1
Norrbotten south of this limit	14.9	2.8	19	3.6	24	6.4
Västerbotten north of this limit	4.1	0.4	9	0.5	12	0.9
Västerbotten south of this limit	15.4	2.0	13	5.8	7.8	
Total	43.2	6.3		10.9		17.2

Judging from the almost unanimous opinion of the forest experts, some kind of mechanical preparation of seed beds seems necessary in areas with difficult conditions for spontaneous reforestation. From the standpoint of reindeer grazing one would wish that there were a machine to be used for preparation of seed beds like the one that was suggested by Troedsson and Utbult (1972). The visible result of its activity would be small, 30-40 cm high piles of mixed humus and mineral soil. These piles would then serve as seed beds.

Use of Herbicides to Reduce Deciduous Growth

The use of fenoxi-acids (mainly 2,4-D and 2,4,5-T) within forestry was for one year totally prohibited. However, since February 1, 1972 their use on the ground has been allowed.

Strict regulations have now been established in order to prevent people and large animals from being exposed unwillingly to the compounds used. Thus, aerial treating of cut-over areas is prohibited.

According to Häggström (1972) the vertebrate fauna is not affected by the herbicides used in Sweden. Each year a little less than one-third of the total clearcut area is treated.

The reduction in deciduous growth is of course a drawback to the reindeer industry, since certain quantities of broadleaf browse are lost. This reduction, will however, not last very long and it is to some extent compensated for by an almost instant increase in grass growth (*Deschampsia flexuosa*, etc.).

The preparation of very large areas may, however, cause severe trouble to the individual Lapp community, especially in the woodland type, as these communities have all of their range within the boreal coniferous forest.

Fertilization of Woodlands

According to Friberg (1972) fertilization is used in order to increase the growth of wood in valuable middle age or older forest stands. Airplanes are almost exclusively used to distribute the nitrogen fertilizers over about 1½ per cent of the forests of Sweden every year.

The effect on the ground vegetation is visible in terms of increased growth of heath shrubs. Friberg also noted that the higher fauna seems to prefer plants from fertilized areas to those from non-fertilized areas. Experiments have shown that game does not willingly eat fertilizers as such.

As fertilization is not applied today in the low producing forests within the reindeer area and as the ground vegetation in dry forest types does not seem to respond easily to fertilization, this method should be tolerated from the standpoint of the reindeer trade.

DISCUSSION

As one can see from Table 1 a considerable part of the central winter range in Lappmark now has been logged and is either clearcut or in a state of reforestation.

Clearcutting will in itself cause considerable problems to the reindeer industry. These problems will be rather prolonged as the regeneration in the marginal or near marginal forest regions is very slow and somewhat hazardous. A clearcut area probably will not become fair range again until about 20-30 years after logging.

If the speed with which old mature forests are clearcut is not reduced, it seems obvious that the reindeer industry will encounter still larger problems as more areas will be reduced in value. Areas already clearcut will not return to good winter pastures nearly as fast as mature forests are logged. At the present rate of cutting only small unlogged areas will remain by the turn of the century.

One cannot escape the conclusion that the decrease in the reindeer population that has hit many Lapp communities is caused, at least partly, by a decrease in range available to the reindeer.

If the use of mechanical preparation of seed beds on prime winter range continues (in spite of what the Secretary of Agriculture declared in Parliament), it will also have a severe effect.

One way of stopping the rapid decrease in the available reindeer range would be a modification of the boundaries of the area economically suitable for artificial reforestation. First, it should include all marginal forest lands, privately owned as well as public, in areas where reforestation is uncertain or where it demands brutal encroachment on vital winter range. North of this limit all logging should be of a conservation type, where short-sighted economic aspects should not be allowed to direct the methods utilized.

There should be an extended consultation between the forest and the reindeer industries, especially on the local level so that no major encroachment on the grazing resources is made before an agreement is concluded as to how to diminish the consequences.

Too little research has been done so far into the effects of silvicultural practices on reindeer range. For example we know very little about changes in vegetation biomass and in its accessibility.

It seems reasonable to claim that no encroachments like the ones here described should be allowed in vital areas before it has been determined how much environmental damage they would cause and for how long this damage would stay.

SUMMARY

The most obvious though not long-lasting effect of clear cutting is the amount of slash that is accumulated which makes it difficult for the reindeer to get at the ground vegetation during winter. Microenvironment and biomass also are radically changed.

An increase in certain higher plants may occur.

The measures of reforestation also affect the grazing resources. Burning of clearcut areas, a practice that destroys the lichen carpet for decades, but that stimulates the growth of some higher plants for a number of years, has been abandoned almost entirely.

Mechanical preparation of seed beds destroys a certain amount of winter pasture and will also give difficulties to reindeer in moving across the area.

As the use of herbicides to kill off deciduous growth now has been regulated and one has not yet been able to prove damage to the vertebrate fauna in Sweden, it should be tolerated by the reindeer industry, provided that not too large continuous areas of importance to the individual community are treated at the same time.

Fertilization is a very common silvicultural practice in areas with middle age or old forest. The rich forest types that today are treated with fertilizers usually are only of secondary interest as winter range. Unfortunately, very little is yet known about how the ground cover of winter range types would react to fertilization.

So far very little of the total amount of research has been devoted to the conflict between forestry and reindeer herding. In spite of this one may state that the reindeer industry will be affected negatively if the present silvicultural practices in Lappland are not altered to a certain degree.

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CHANGES IN LAPPISH REINDEER HERDING IN NORTHERN FINLAND CAUSED BY MECHANIZATION AND MOTORIZATION

Ludger Müller-Wille
Library
Westfälische Wilhelms-Universität
Münster, Federal Republic of Germany

ABSTRACT—Anthropological field research totalling 16 months (1968-71) in Utsjoki, Finnish Lapland, concentrated on the effects of the introduction of snowmobiles and motorbikes into reindeer herding. Since 1962, Lapps have been using these vehicles ever more extensively and efficiently. The mechanization has caused severe changes in the picture of reindeer herding: rationalized working methods, reduced manpower requirements, large capital investments, shift in economic position and power and concentration of animal capital forcing smaller owners to leave herding. Motorization has influenced the inhabitants' attitude toward their natural environment and has affected the ecology and animal behavior. Because Lapps were able to integrate elements of Western technology into their age-old system, reindeer herding has received a more expansive position and prestige in Finland's national economy. During one decade, single technological innovations have, thus, given the impetus for a trend from a traditional, family oriented subsistence level activity to a modern competitive meat industry.

This year it will be 10 years since Lappish reindeer herders in Utsjoki (Lapp. Ohcijohka), the northernmost county of Finland, introduced snowmobiles into their herding work. Since its introduction in 1962, the handy one-person snowmobile, developed in Canada in the late 50's, has revolutionized the reindeer economy. Reindeer herding has been a main factor in the life of the native peoples of the North from the Lapps to the Chukchee on the Eurasian mainland.

This increasing mechanization and motorization of the main branch of the native economy in these areas is just a link in the chain of events underway in the arctic and subarctic during the past three to four decades. The technological revolution has caused tremendous changes in the local socio-economic situation and the traditional technology. The introduction of various technical devices poses very difficult problems of reorientation and re-evaluation if these elements of Western civilization are to be used meaningfully by the peoples in question.

The Lapps have shown an admirable flexibility in adjusting socially and economically to meet this new situation. Their problems have not been eased by the fact of their being an ethnic minority in the Scandinavian national societies (Finnish, Norwegian and Swedish).

The relationship between technology and social change, which holds special interest for the social scientist and anthropologist, has unfortunately been rather neglected (Bernard and Pelto, 1972). At present we are in the fortunate position of being able to observe and document the developments in the traditional reindeer herding of the Lapps in Northern Scandinavia during the last 10 years. The 'snowmobile revolution' in Lapland is characterized by its unplanned, micro-technological aspect brought about by individual decision making and adoption. This process is in contrast to such macro-technological

changes as planned housing projects in arctic settlements (Honigman, 1972).

The data presented here were gathered during anthropological field research in Utsjoki between 1968 and 1971 (see Acknowledgment). They are based on participant observation, systematic interviews with reindeer herders and connected people and the records of the local reindeer associations (Finn. paliskunta). The history and present situation have been treated in more detail elsewhere (Pelto *et al.*, 1968; Sammallahti, 1969; Müller-Wille, 1971; Müller-Wille and Aikio, 1971; Müller-Wille and Pelto, 1971; and others).

In the fall of 1962, a few well-off Lappish reindeer herders bought the first snowmobiles in Utsjoki and began using them to herd their animals. Others rapidly followed suit with such success that within two to three years the snowmobile had become indispensable. The official records report 26 'snowmobile working days' driven by association herders in 1962-63, and more than 1,000 per year since 1967-68. The family herding system was abandoned along with reindeer sleds, herds were allowed to roam freely and new herding and roundup techniques were developed which depended almost entirely on the use of snowmobiles. Motorbikes for summer marking roundups (since 1968) and other technical devices such as telephones and walkie-talkies also have their places in the new setting. Four features have been noticeably affected by these innovations after 10 years of application: herding management and techniques, economic structure, natural environment and social structure.

HERDING MANAGEMENT AND TECHNIQUES

In Finland, reindeer herding is organized by associations and herds of members are restricted to the associations' territory and must be kept within these boundaries (Alaruikka, 1964). In the Kaldoaivi reindeer association, the eastern part of Utsjoki county, some 40 motorized herders are hired by the association to keep track of herd movements. These men commute daily or every few days up to 60 km to the herds. The association, often in agreement with neighbor associations, schedules six to 10 roundups in the winter months.

When a roundup is to be held, eight to 10 snowmobilers search the 2,000 km² Kaldoaivi district for the small, scattered herds of reindeer and drive them to a prearranged point. When 1,000 to 1,500 head have been gathered, snowmobilers at the rear and sides of the herd drive it to the corral. This drive may take two or three days. A herd can travel about 25 km a day in this way.

The success of the drive into the roundup corral depends on the proper placement of the funnel-shaped fences leading into the corral (Fig. 1). They must take advantage of hills and valleys that the deer follow naturally and open country where the snowmobilers can maneuver the herd well. The location of these fences is especially important because the snowmobiles have very limited maneuverability in the funnel. Here the herd begins to circle and the final drive is accomplished by a chain of men afoot and several snowmobiles driven at some distance to the rear.

In 1969, 34 active snowmobilers drove an average of 35 days each to round up about 7,300 reindeer, which is about 215 deer for each driver. Today, an active reindeer herder in Utsjoki spends 50 to 60 work days in the mountains watching the herds. This includes some 15 to 20 motorbike days during the summer.

Motorization has made herding more efficient — animals can be controlled and gathered faster — although the effect on the deer is still debated.

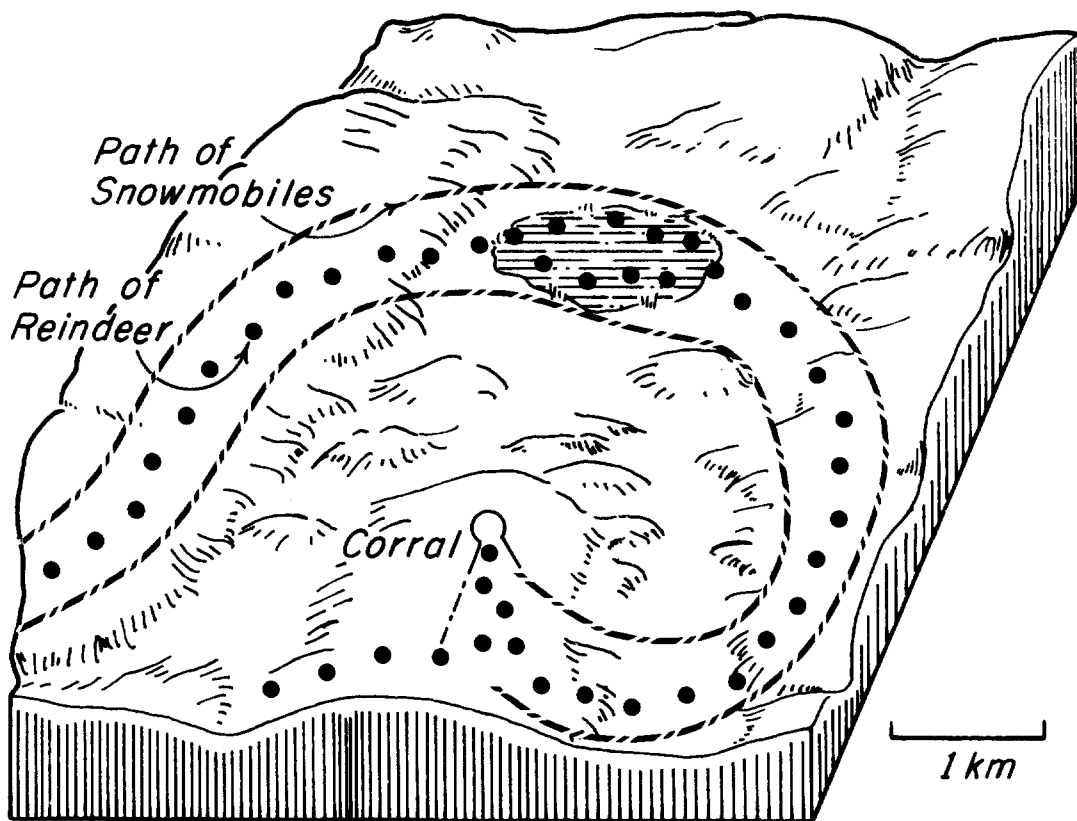


Fig. 1.—Snowmobilers drive reindeer herd into corral in Utsjoki, Finland, 1968 (drawing by Linna Müller-Wille).

ECONOMIC STRUCTURE

Very striking is the fundamental change from a subsistence economy to a monetary, labor and market oriented economy. In the traditional setting, there was a strong emphasis on a local network for the exchange of products. Few external socio-economic contacts for marketing existed. Most products were for family consumption and along with fishing, hunting and small farming, provided the economic base. At the single general roundup at Christmas time, where all the family groups and their herds met, there was an opportunity for exchange of products. Northern Finland was isolated until the 1950's when the first roads were built and, thus, the area experienced no modern economic development until after this time.

The use of snowmobiles and other technical devices necessitates large amounts of cash for buying, maintenance and operation. Many smaller herders were forced to leave the reindeer business and to sell their livestock because they could not compete without one. This caused concentration of animal capital. The remaining owners were forced to oversell up to 10 to 15 per cent above the normal reproduction replacement rate in order to meet the new cash requirements. Now, after 10 years of experience, this practice seems to be levelling off.

With the rationalized working methods reindeer herding has acquired a better status in both the local and national economy. The continuing development of a road

communication system has led to better local, national and even international marketing of reindeer meat. These developments in turn resulted in meat control and, thus, higher meat quality. Today, reindeer herding has found itself in a competitive position in the national meat industries.

Even so, reindeer herding still cannot provide a complete living base for the herder and his family. He must still supplement with fishing, hunting and even tourism. The fact that he is motorized means that he now is able to spend more time on these important side activities. Unfortunately, many of the former herders, who could not follow the snowmobile trend, were not able to find work in their local communities and had to migrate to the south where there are more job possibilities.

NATURAL ENVIRONMENT

Since the introduction of motor vehicles into the mountain regions of northern Scandinavia, there has been a change in man's attitude toward his environment and his concern for animals. The vehicles enable herders to take large loads of provisions into the mountains, but there are no adequate places for disposal. Also, random driving has an effect on the vegetation cover. Local people, however, are still more concerned about their environment than the intruding tourists. We do not have much data on the influences of motorbikes and snowmobiles on the ecology (Wanek, 1971) and the behavior of the reindeer and other animals (Klein, 1971). After a drive by snowmobiles, the reindeer seem to be quite exhausted in the corral and become nervous and easily frightened. The harmful effects are still debated.

SOCIAL STRUCTURE

Concerning the socio-cultural situation, the quick and more frequent communication afforded by snowmobiles has brought about somewhat closer social relations among the local people. The position of the reindeer herder in the family has been changed since he no longer is in the mountains for extended periods. Along with the development of a communications system and the strengthened economic position there has been at least an overt assimilation of the Lapps into the national societies. On the other hand, this position and the closer local contacts have in turn increased their consciousness as an ethnic group.

Because of the early stage of the technological revolution in subarctic and arctic regions and the opportunity of observing these processes, there is a need for more basic material and analysis and for information which could enable the native peoples to direct the application of innovations and thus simplify their problems of adaptation.

ACKNOWLEDGMENTS

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THE INTERNATIONAL HERDS: PRESENT KNOWLEDGE OF THE FORTY-MILE AND PORCUPINE CARIBOU HERDS

Robert E. LeResche
Alaska Department of Fish and Game
Fairbanks, Alaska 99701

ABSTRACT—Present knowledge of the two major caribou herds shared by Alaska and Canada is minimal despite recorded observations dating back to the 19th Century. Sizes of both herds have fluctuated from apparent 20th Century highs of over half a million to present numbers of 100,000 (Porcupine Herd) and less than 10,000 (Fortymile Herd). Interchange of animals with other herds has taken place, and changes in distribution have occurred several times in recorded history. Both herds have temporarily occupied much larger areas than at present. Although both herds are healthy at present, a return to former high numbers is unlikely in the future because of new land ownership and use patterns and increasing northern development.

Since 1950, studies of caribou (*Rangifer tarandus granti*) in Alaska have considered the animals in terms of 'herds', or groups of caribou sharing a common calving area in most years. Skoog (1968) formalized the concept, with his contention that all Alaskan caribou comprised one population (i.e., that interbreeding occurred between 'herds'), but could be considered as 13 separate herds. Hemming (1971) summarized the present state of general knowledge of the six major herds (commonly referred to as the Arctic, Porcupine, Fortymile, Nelchina, McKinley and Alaska Peninsula herds), five minor herds (Delta, Mentasta, Mulchatna, Beaver and Chisana) and two introduced herds (true biological populations) on Adak Island and the Kenai Peninsula (Fig. 1).

Two major groups, the Porcupine and Fortymile herds, winter predominately in Canada and calve in Alaska. Coincidentally, these two groups are, among Alaska's 13 herds, the most likely to be severely affected in the near future by increased human activity and changing land use-ownership patterns in the north. Both the direct effects of gas pipeline and road construction and the indirect impact of increased human presence and utilization may drastically change conditions for these caribou in the next few years.

Numbers, movements and distribution of both herds are still but sketchily known, although past work has defined them somewhat. Virtually nothing is known about population dynamics or habitat of these animals.

Any review of caribou in Alaska must draw heavily from Skoog's (1968) extensive treatment of historical material and Hemming's (1971) summary and updating of knowledge of movement patterns and distribution. Therefore I have begun by summarizing material presented by these two authors. Olson's (1957, 1958, 1959) work provided much of the background for discussion of the Fortymile Herd. All additional and more recent data, except when noted, are from Alaska Department of Fish and Game files (unpublished), notably those collected by L. Jennings and from my own studies currently underway.

PORCUPINE HERD

Knowledge Before 1970

Information concerning caribou associated with the present range of the Porcupine Herd (Figs. 1 and 2) dates from early explorations of the arctic coast (Franklin, 1826; Dease

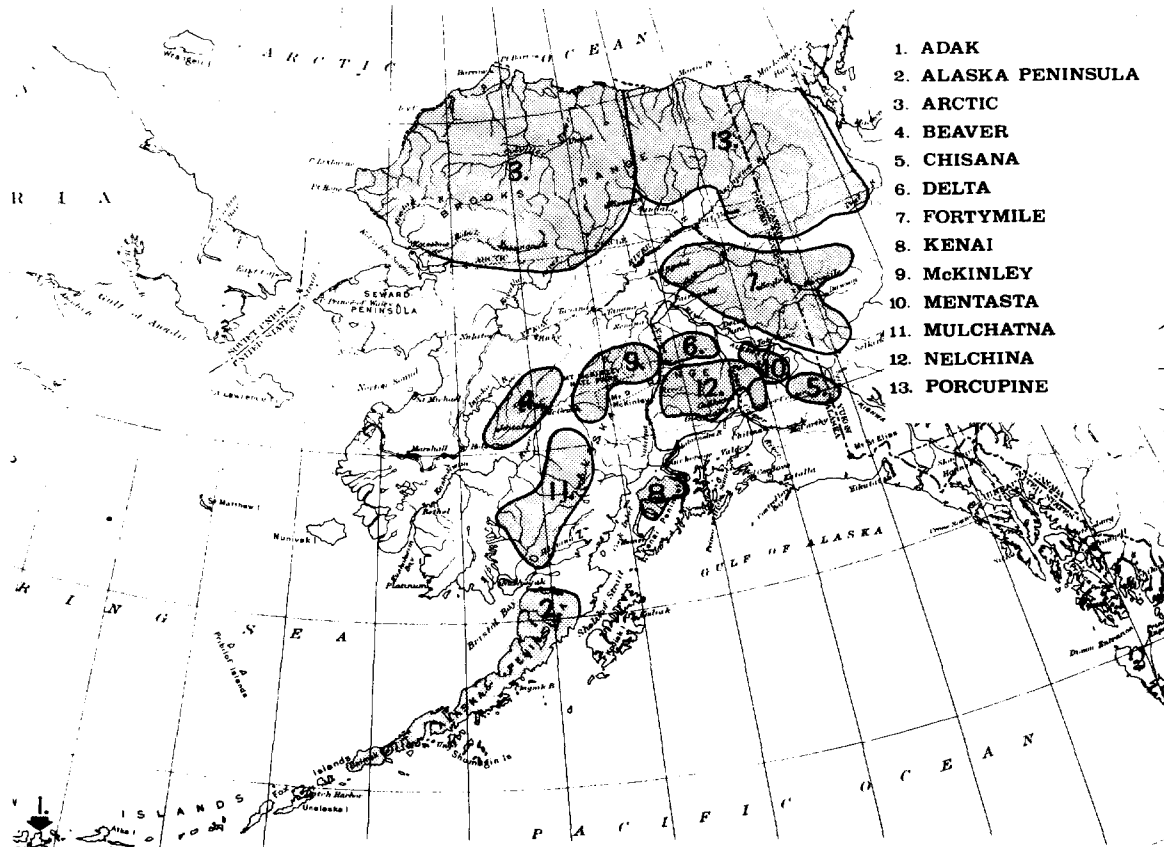


Fig. 1.—Alaska's caribou herds, showing approximate ranges of the Porcupine (13) and Fortymile (7) herds. From Hemming (1971).

and Simpson, 1838; Simpson, 1843; Isbister, 1845; Russell, 1898; Pike, 1892), when caribou were reported by whalers between Demarcation Bay and the MacKenzie River delta. Interesting reports indicated caribou were common year-around at Herschel Island, and that these animals intermixed with caribou east of the MacKenzie (Russell, 1898). Nineteenth Century reports from winter ranges (Funston, 1896; Russell, 1898) indicated distribution similar to today's, with semi-annual crossings at the lower Porcupine River and some animals wintering near Arctic Village.

From 1900 until about 1950, the herd apparently increased in numbers and expanded wintering areas westward into the central Brooks Range (Skoog, 1968; Hemming, 1971). Murie (1935) indicated caribou were common in the Koyukuk-Chandalar area from 1917-1930. He related a harvest occurred at Fort Yukon in 1925, for the first time in a hundred years. Porsild (1945) described a huge southward migration ('millions') in 1927 along the eastern Richardson Mountains; and, in the 1930's fall harvest increased steadily at

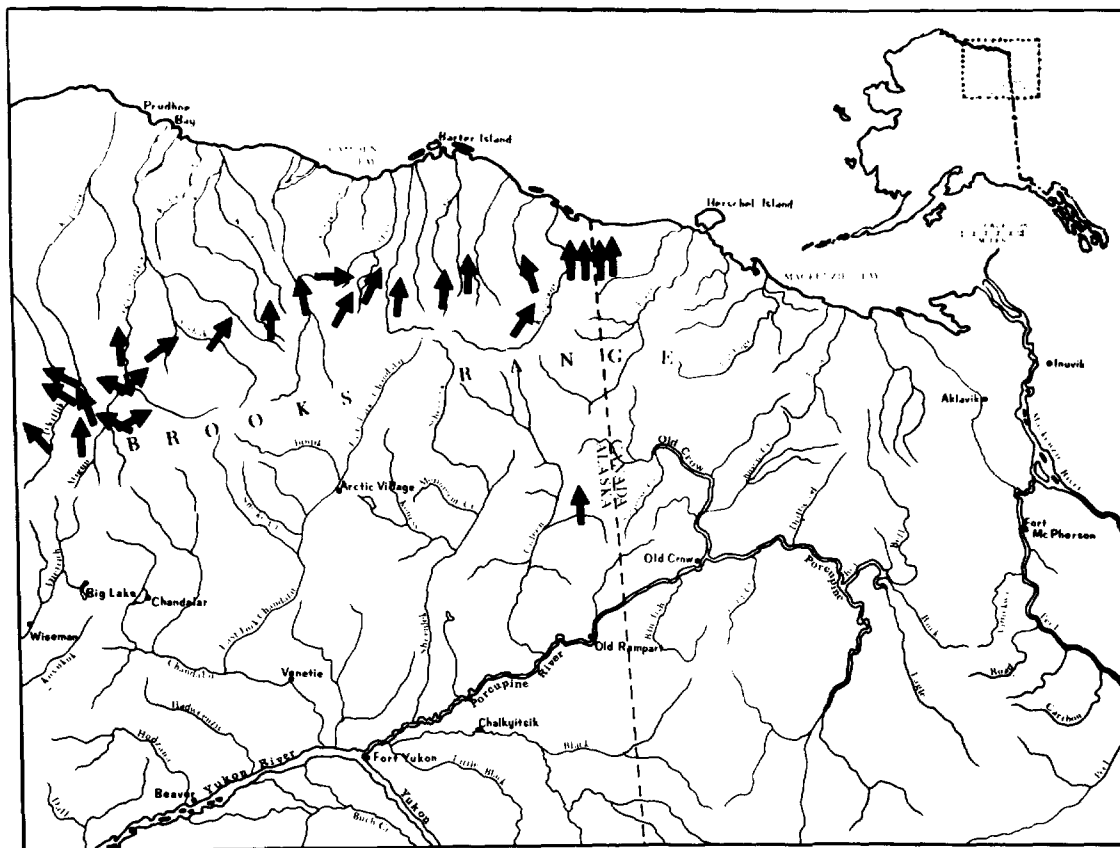


Fig. 2.—Present range of the Porcupine Herd, showing spring migration routes as observed 22-24 May, 1972. West-turning caribou probably are western Arctic Herd animals. Major Canadian migration routes are not shown.

Fort Yukon. Hemming (1971) cites a resident of Anaktuvuk Pass, in the central Brooks Range, as saying caribou migrating through this pass turned eastward (i.e., to the calving grounds of the Porcupine Herd) from about 1900-1920. Animals using the pass since have headed predominately westward, toward the Arctic Herd's calving grounds. Skoog (1968) suggested that the herd was actually two herds during this period: a northeast group and a central Brooks Range group. No good estimate exists of the total number reached. In any event, a 'drastic' (Skoog, 1968) decline in numbers occurred following a population peak in the mid-1940's. Skoog attributed the decline to migration to the Arctic Herd and across the MacKenzie into the Northwest Territories.

Scott (1953) was the first to consider animals wintering from the Chandalar River to the Richardson Mountains as one herd. Since that time the Porcupine Herd has increased in numbers and established the patterns of distribution and movements we are currently observing.

Two occurrences in the 1950-1970 period merit special note here: (1) repeated ingress of animals from the Fortymile Herd and, (2) occasional wintering and rutting in the east-central Brooks Range. In 1957 and again in 1964, substantial numbers of Fortymile Herd caribou migrated north from the northwestern Ogilvie Mountains with the Porcupine Herd (Olson, 1958; Skoog, 1964). The latter interchange was well documented and involved about 20,000 animals. It is unknown whether any of these animals rejoined the Fortymile

Herd in succeeding springs. Olson (1957, 1959) reported that, in 1956 and 1958, many caribou migrated southward past the headwaters of the Ivishak and Sagavanirktok Rivers to winter in the Big Lake-Chandalar area. This may have been an atavistic distribution from days of more westerly distribution, or it might continue to occur periodically.

RECENT KNOWLEDGE (1971-1972)

Distribution and Movements

Studies over the past one and a half years (Calef and Lortie, 1971; Thayer *vive voce*; LeResche, unpub.) show the Porcupine Herd is distributed generally as described by Hemming (1971). Calving occurs on the north coastal foothills east of the Canning River and west of the Babbage, and post-calving concentration occurs on the arctic coastal plain or eastward and southward into the northern British Mountains. Fall migration generally proceeds east of the Kongakut River, and most animals occupy winter ranges in the northern Ogilvie Mountains and the head of the Porcupine River, with a few wintering in Alaska in the Arctic Village-Chandalar area. Calef and Lortie (1971) have followed the Porcupine Herd since April, 1971, and the Alaska Department of Fish and Game, with cooperation from U. S. Bureau of Land Management, initiated studies in May, 1972. The following information is based on these studies. In addition, Renewable Resources, Ltd. has spent considerable effort since April 1971 (Yukon Territory) and March 1972 (Alaska) in extensive aerial surveys, and the Canadian Wildlife Service began a major study in April 1972.

Calef and Lortie reported spring migration was apparently two months delayed in 1971, but that it followed the ridges of the Richardson and Keele Mountains, with animals probably also moving through the Babbage, Firth and Kongakut River drainages. In 1972, migration was similarly timed, with most cows not reaching the coastal plain until late May, and many bulls not arriving until July. We documented movement through mountain passes in Alaska and onto the coastal plain from 22 to 24 May, 1972 (Fig. 3), and demonstrated that the line of separation between the Arctic (west-turning) and Porcupine (east-turning) herds occurred at the Sagavanirktok River and Atigun River drainages. All passes and drainages from the international border to the Chandler River (where our survey ended) were used by caribou. Nevertheless, the majority of the calving herd of approximately 60,000 reached the coastal plain inside Canada, with only an estimated 10,000 moving northward in Alaska. In early July, 20,000 to 25,000 bulls descended onto the coastal plain from the foothills down the Kongakut, Egaksrak, Aichillik, Jago, Okpilak and Hulahula Rivers, and 5,000 to 10,000 more were first observed in the northern foothills of the Sadlerochit Mountains, near Katakturak River. Many of these animals were probably present in the large bull groups observed in the foothills of the British Mountains in mid-June, and moved westward in mountainous terrain.

Some calving occurred in northern Yukon Territory in 1971, almost exactly as it had in 1952 (Alaska Fish and Game files). In 1972, calving occurred in the north-sloping foothills from the Blow River on the east to the Hulahula River on the west, with large concentrations occurring south of Herschel Island and between the Okerokovik and Hulahula Rivers, south of Barter Island. With the exception of a few hundred animals in the Prudhoe Bay-Kavik area, virtually no calving occurred between this group and the calving grounds of the Arctic herd, 600 km to the west. Peak of calving probably occurred between 8 and 13 June, for our classification counts on 8 June between the Okerokovik and Hulahula Rivers indicated 55 calves:100 adults (n=2525) with only 28 per cent of adults antlerless and an antlerless:calf proportion of 0.51 (460/896). Calef (*vive voce*) reported

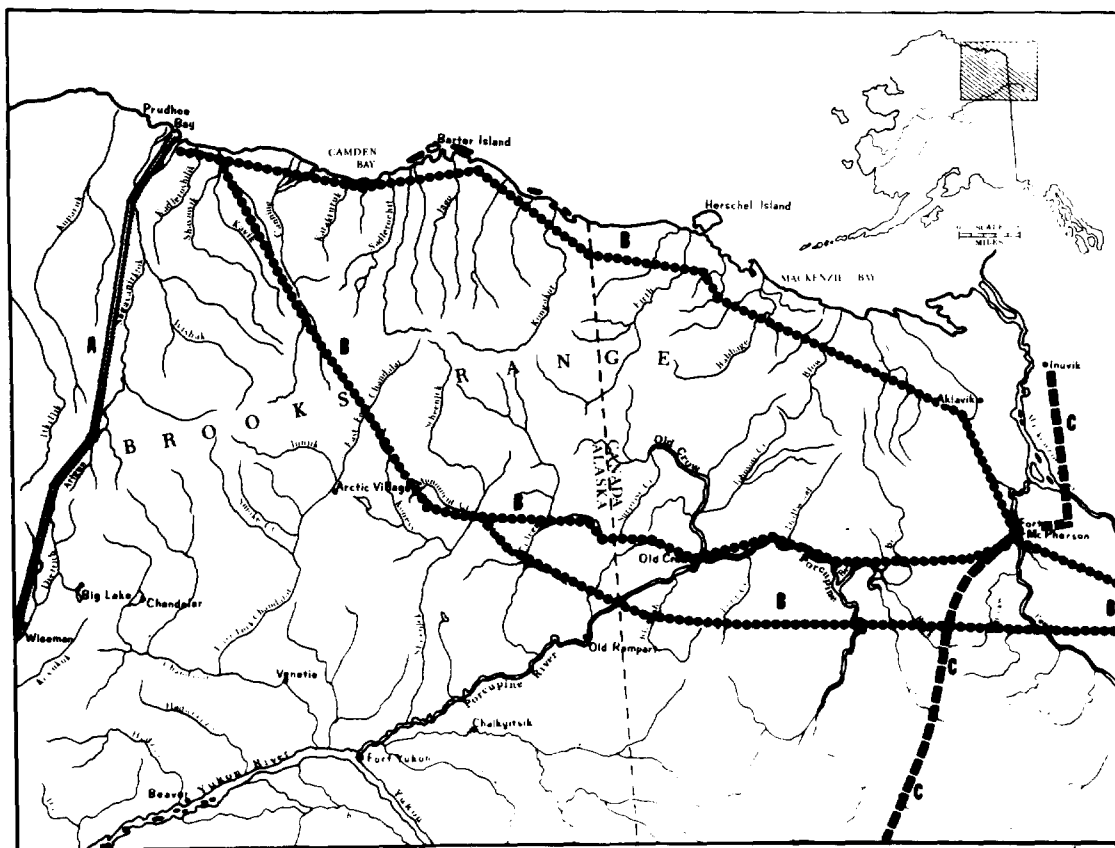


Fig. 3.—Present range of the Porcupine Herd, showing locations of (A) the proposed TransAlaska oil pipeline, (B) alternate routes of the proposed Prudhoe-MacKenzie gas pipeline and (C) the Dempster Highway.

calf:adult proportion peaked at 43:100 ($n=5376$) on 13 and 14 June, between Herschel Island and Okerokovik River.

A post-calving aggregation of approximately 60,000 animals was observed by Calef and Lortie (1971) in the southeast British Mountains on 20 to 26 July, 1971. The Alaska coastal plain was not surveyed that year. On 30 June, 1972, we located a concentration of approximately 30,000 animals in the foothills between the Okpilak and Hulahula Rivers and another 40,000 to 60,000 in the foothills of the Katakturuk River. On 2 July both groups had moved to the Arctic Ocean, aggregated more closely and begun to move eastward. This closely aggregated group of about 90,000 animals occupied the coastal plain between Camden Bay and the Aichillik River for at least 10 days before dispersing and moving eastward into the British Mountains and southward into the Brooks Range. Reportedly a group of 40,000 caribou crossed the international border eastward at Clarence River on 10 July. During the entire month of July, coastal areas were very important to the insect-harrassed animals, which were observed wading in tidal flats as much as 1.5 km from shore, and congregating on shore fast-ice.

Calef and Lortie (1971) reported that most animals from the Porcupine Herd wintered in 1970-71 in the northeast Ogilvie Mountains and south of the Peel River. Fall migrations tended to follow spring migration routes. Winter distribution in 1971-72 was similar, and several hundred animals, at least, wintered in the Junjik Valley near Arctic Village in Alaska

(Thayer, *vive voce*).

Productivity

Calef and Lortie estimated spring and fall calf proportions in the herd of 16 per cent, and remarked that this was midway between Skoog's (1968) estimates for the increasing Nelchina Herd and Kelsall's (1968) for declining Canadian Arctic Herds. Lent (1966) reported a similar 17 per cent calves for the Arctic Herd in July, 1961, when it was probably increasing.

On 4 July, 1972, we classified 12,921 caribou in post-calving concentration. Of these, 3,052 were calves and 6,357 were adult cows, indicating a calf:adult cow ratio of 0.48. Extrapolating on the assumption that cows represent 50 per cent of the adult-yearling herd (Pegau and Hemming, 1972, estimated this for the Arctic Herd in 1970), calves represented 24 per cent of the herd three weeks after calving, suggesting a healthy herd in terms of productivity.

Numbers

Skoog (1961) estimated that the Porcupine Herd numbered between 110,000 and 117,000. Lentfer (1965) estimated 140,000 in 1964. In July 1972, we initiated an aerial photo-direct count — extrapolation census (Pegau and Hemming, 1972) of the herd, and the current estimate, based on analysis of these photographs, indicates the population contains a minimum of 101,000 individuals.

Human Impact on the Herd

Hunter use of the Porcupine Herd has to this time been insignificant although residents of Old Crow, Arctic Village, Kaktovik, Inuvik and Aklavik depend upon the animals for subsistence in most years. Northern extension of the Dempster Highway to Fort McPherson (Fig. 3) has caused some concern for increased use of the wintering herd by sport hunters, but restrictive regulation by the Yukon Territorial government promises to keep harvest far below production. Current harvest is about 300 at Old Crow and 'slightly more' on the Dempster Highway (Sinclair, pers. comm.). There is practically no sport hunting use of the Porcupine Herd in Alaska.

Three major projects, the TransAlaska Oil Pipeline, the Prudhoe Bay-MacKenzie River gas pipeline and the Dempster Highway, have great potential for altering the present environment of the Porcupine Caribou Herd (Fig. 3). No one can predict the eventual effects of habitat alteration on caribou distribution, movements and population dynamics (c.f. Klein, 1971), but potential areas of conflict are apparent. Fortuitously, the present ranges of the Porcupine and Arctic herds meet at the Sagavanirktok, Atigun, Dieterich River pass, the route of the proposed oil pipeline. With the exception of the small, rather isolated group (probably fewer than 5,000) that uses the Prudhoe Bay area, very few animals calve along the pipeline route, and few (in relation to total numbers) have crossed it during spring and fall migrations in most recent years (Hemming and Pegau, 1970). However, were the pipeline to present any sort of barrier, it could preclude any future westward expansion of the Porcupine Herd into areas utilized in the 1900 to 1930 period, or any exchange with the Arctic Herd.

The proposed gas pipeline routes coincide considerably with areas of habitat critical to caribou. The coastal alternative, which would pass through the Arctic National Wildlife Range, would cross areas used for calving and post-calving concentration in 1971 and 1972.

If it presented a summer barrier, it could restrict use of the Arctic coast, so important during insect season. The southern alternatives both cut across spring-fall migration routes along their entire distance west of the MacKenzie River. They cross wintering areas from the Chandalar to the Peel Rivers. Were a gas line along either southern route to restrict free movement of caribou, the Porcupine Herd would doubtless be drastically reduced in numbers, despite vast areas of unaltered range north of the lines.

Similarly, the Dempster Highway crosses current wintering areas in the upper Porcupine and Eagle River drainages. In addition, it lies between eastern winter ranges and calving/summer areas. Both the Nelchina and Fortymile herds in Alaska have coexisted with lightly-traveled highways for as long as 30 years. In recent years, however, both herds have declined in numbers and shifted in distribution concurrently with increased highway travel. A multitude of factors are involved, and most may have no relation to the roads. Nonetheless, the fate of these herds gives cause for somber reflection on the ultimate influence of the Dempster Highway on the Porcupine Herd.

FORTYMILE HERD

Knowledge Before 1965

Very few records of the Fortymile Herd before 1950 exist, but enough are extant to establish that caribou have inhabited the area between the Yukon and Tanana Rivers and the White Mountains (Figs. 1 and 4) for 100 years. Skoog (1956) summarized all printed

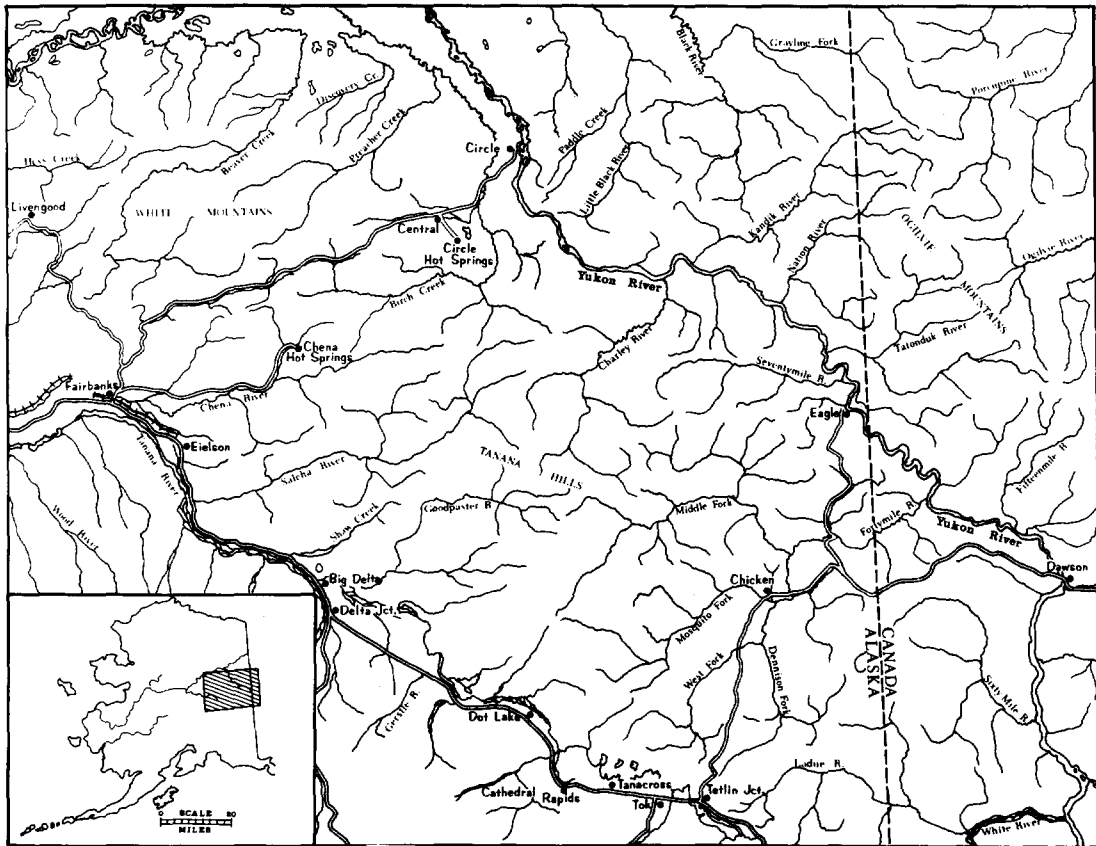


Fig. 4.—Present range of the Fortymile Herd.

and many verbal records from this period. The earliest indicate distribution before 1900 was further east than at present, and caribou were abundant throughout the Klondike country. Crossings of the Yukon River near the international border, however, have occurred regularly since the first records.

Murie (1935) summarizes the herd's increase to a tremendous population peak in the mid-1920's, when he estimated it numbered over one-half million caribou (Table 1). During

TABLE 1.--Estimated numbers of Fortymile Caribou Herd, 1920-1972.

Year	Population estimate	Source
1920	568,000	Murie 1935
Early 1940's	10-20,000	Skoog 1956
1953	40,000	Skoog 1956
*		
1963	30,000	Skoog 1968
*		
1964	20,000	Lentfer 1965
1969	20,000	Alaska Dept. of Fish and Game
	(8-10,000 post-calving)	files
1970	10,000 maximum	Jennings (unpubl.)ADF&G files
1972	10,000 maximum	Jennings (unpubl.)ADF&G files

*Suspected egress to Porcupine Herd.

the period of increased population, the herd's range expanded in all directions. Large fall migrations occurred in the Fairbanks-Circle region between 1906-1913 (Palmer, 1941). In the early 1900's many caribou wintered near Dawson (Sheldon, 1911), and in 1918 there were 'unprecedented numbers' in the Fairbanks area (Riggs, 1919). Perhaps the most significant result of this expansion of range was the winter movement of caribou across the Tanana River southwest to the head of the Delta River, where they may have added significant numbers to what we now call the Delta and Nelchina Herds. Murie (1935) suggests these movements persisted at least until the late 1920's, when more northeasterly movements became the rule. During the same period (1924), many caribou wintered near Whitehorse (Murie, 1935), and a spring-fall migration occurred for about 10 years through Nenana, west of Fairbanks.

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From 1930 to 1965, the Fortymile Herd decreased in numbers (Table 1) and extent of range (Skoog, 1968; Hemming, 1971). The herd became generally confined in its present range between the Yukon and Tanana Rivers and decreased in numbers to between 30,000 and 40,000 in 1960 and to 20,000 in 1965 (Table 1). From 1950 to 1965 the calving area of the herd shifted progressively east and south, across the Steese Highway (Hemming, 1971). Also during this period, egress of animals to the Porcupine Herd occurred twice (1957 and 1964).

PRESENT KNOWLEDGE (1966-1972)

Distribution

Present distribution of the Fortymile Herd is well illustrated by Hemming (1971). The major wintering area is between Dawson on the east and the Taylor Highway on the west,

and extends northward into the Ogilvie Mountains, where the animals may mix with Porcupine Herd caribou. A few caribou remain in the vicinity of the Taylor Highway into late winter (300 observed on February 12, 1969), and a few range as far south as the Alaska Highway (250 at Tetlin-Northway in winter, 1971).

Calving has occurred since 1966 in the Tanana Hills in the area of the headwaters of the Salcha, Goodpaster, Charley and Middle Fork Fortymile Rivers, and post-calving concentrations were observed in 1969 through 1972 between the heads of the Chena and Charley Rivers (Fig. 4).

Fall migration has occurred regularly in September and November, with most animals moving eastward across the Taylor Highway in October.

Productivity

In 1960 and 1961 Skoog (1961) estimated June productivity of 68 calves:100 adults (n=8524) and 66 calves:100 adults (n=1976) (adults include 12-month-old animals in this comparison), or 78:100 adult females and 74:100, respectively. Previous estimates (1954-1959) (Skoog, 1961) had varied from 38:100 (1957) to 78:100 (1954) and indicated good productivity at that time.

Numbers

The Fortymile Herd probably numbers fewer than 10,000 animals at present, although no census has been accomplished since 1964, and the best available enumeration (1953; Skoog, 1956) was made from ground observations. More recent estimates derive from extrapolation from estimates of numbers of animals in post-calving concentrations (3,000 to 5,000 in 1970, 4,000 to 6,000 in 1971, 3,000 to 5,000 in 1972).

Human Impact on the Herd

The Fortymile Herd has been hunted regularly since gold rush days and, unlike the Porcupine Herd, may have been altered in numbers or composition by human utilization. Skoog (1956) cited an estimated (Alaska Game Commission 1934, 1935) harvest of at least 10,000 annually for dog food by trappers in the Fort Yukon district in the 1930's. Skoog concluded that a harvest of such magnitude alone could not have initiated the decline in number from more than half a million animals; however, he believed subsistence hunting might have become a 'serious factor' once the decline began.

From the early 1950's until the present, the Fortymile Herd has been an important recreational hunting resource in Alaska (Table 2). Through 1966 animals were killed as they migrated near the Steese Highway in August and September. Since that time, caribou crossing the Steese have been too few to attract a significant number of hunters. Hunting on the Taylor Highway has increased in recent years and, depending upon timing of the migration and closing of the road by weather, harvest has varied from 500 to 2,500 annually. In addition, a small harvest of Fortymile Herd animals occurs some years in the Yukon Territory.

Skoog (1956) calculated a minimum annual increment of 10 per cent for this herd and believed it did not exceed 15 per cent. His calculations were based on a spring herd size averaging 44,500 and included average hunting harvest of 1,500 over a three-year period (1953-1955). Using his method of calculation (1956; Table 10), which includes calf to yearling survival of 50 per cent, initial calf production of 60:100 cows (1954-1960 mean), wolf predation of 2 per cent and miscellaneous mortality of 1 per cent, and assumes 46 per

cent of the herd are cows; annual increment of a herd presently estimated at 10,000 maximum is 1,080 animals before hunting. Thus, a harvest of 1,386 in Alaska (1970) likely exceeds the maximum allowable harvest for herd maintenance, and the 1971 harvest of 2,363 possibly doubles it. I emphasize that this calculation is based on a patchwork of data most of which are 10 years out-dated, and on an estimate of total numbers that is little more than a guess at present. However, there is little current information to add optimism to the picture.

TABLE 2.--Human harvest of Fortymile Caribou Herd in Alaska, 1935-1970. (Based on Alaska Dept. of Fish and Game files)

Year	Male	Female	Total ¹
1935			10,000 ⁷
1954	462	467	984 ⁶
1955	816	747	1,624 ⁶
1956	316	241	607 ⁶
1957	257	143	403 ⁶
1960	670	564	1,234 ⁶
1961	790	854	1,648 ⁶
1962	(170) ²	(120) ²	640 ³
1963			335 ⁴
1967			503 ⁴
1968	191	96	579 ⁴
1969	260	79	492 ⁵
1970	601	275	1,386 ⁵
1971			2,500 ⁸

¹Includes sex unknown animals.

²Taylor Highway only.

³Includes 35 on Steese Highway, 315 in Yukon Territory.

⁴Estimated from harvest tickets.

⁵Estimated from harvest tickets, extrapolated to non-returned tickets.

⁶Checked at check station.

⁷Estimated (Skoog, 1956) subsistence kill.

⁸Alaska harvest of 2,363 estimated from harvest tickets extrapolated to non-returned tickets and estimated Yukon harvest (slightly more than 300 from Dempster Highway).

The decline in numbers since 1956 to the present level cannot be attributed to hunting any more than could the initial share of the decline in the 1930's and 1940's. Skoog (1956) described the declining condition of the Fortymile Herd's range after 1930 and laid the blame on fires and settlement (chiefly mining). Fires continue to be an almost annual cause of habitat destruction.

Development and human habitation in the remote portions in the range of the Fortymile Herd is perhaps less intense than during the 1930's, 1940's and 1950's. However,

settlements on the peripheries of the range have persisted, and some have become towns. Trails have become highways. The Dempster Highway is the newest addition, cutting across the northeast corner of the herd's winter range.

CONCLUSIONS

Land use decisions being made today will determine whether huge herds of caribou will exist in the future. Present trends suggest the days of tremendously large herds are past in eastern Alaska and western Canada. Further, the days of moderately large herds of 100,000 or more appear numbered. Little by little, development and civilization have restricted movements of the Porcupine and Fortymile Herds, and the potential exists for rapidly accelerated increase in such disruption.

Changing patterns of land ownership are the bases for the fate of these herds. Implementation of the Alaska Native Claims Settlement Act will partition vast areas of land into small parcels under private, state and federal ownership. Such partitioning will almost inevitably result in increased development of resources for human use and decreased land available for caribou use through projects such as roads and pipelines that may cause shifts in caribou movement patterns. This will also result in increased demands on caribou as a recreational resource. Caribou will survive these changes, but, since uninhibited movement and interchange seem a prerequisite to attaining extremely high numbers, they will probably never again achieve the numbers reached periodically in the past.

No biologist concerned with caribou has failed to wonder at the vast areas covered by the animals in their annual movements, and at the much vaster expanses utilized over a century of population growth, interchange and decline. Skoog (1968) felt all the caribou in Alaska were one population and recognized that (1956: 136): "The erratic and continued movements of caribou are difficult to understand." Hemming (1971: 3) stressed, "They visit some areas annually, and may utilize others only once in a decade. Even preferred areas are used only a few weeks each year." Individual subpopulations (herds) have never been stable in terms of numbers or range. Yet in the past, recovery of range from overuse and of caribou from population lows has occurred repeatedly, largely because other habitat was available.

The range of the Fortymile Herd at its most recent zenith (1920-1930) was probably in excess of 256,000 km² (100,000 miles²). The Porcupine Herd presently utilizes almost 358,000 km² (140,000 miles²) of Alaska and Canada. Reservation of such large areas for the exclusive use of caribou is not likely to occur in the future. Yet, without this much land, peaks in numbers equivalent to past highs are not possible.

Extremely high caribou populations are not needed to maintain a closely managed consumptive or nonconsumptive recreational resource. Properly managed sport hunting does not contribute to the decline of herds, but maintains them relatively constant at highly productive levels which are well below maximum size. Allowing herds to reach peaks is profligate use of the range compared to a closely managed annual sustained-yield herd.

It is unlikely the TransAlaska oil pipeline, the Prudhoe-MacKenzie gas pipeline, the Dempster Highway or any similar project, properly constructed, will pose an absolute barrier to caribou movement. Nevertheless, every human development presents a barrier of some order to potential caribou movement. Some (highways, railroads, elevated pipelines) may be high-order barriers; others (settlements, roads, buried pipelines), low-order barriers. All affect movement and distribution at least slightly (Klein, 1971), and all new human constructs restrict potential caribou expansion somewhat. Skoog (1956: 3) believed it was "doubtful whether [caribou] can, or will, exist alongside of populated areas."

If Alaskan caribou are one population, restricting some subpopulations will affect others eventually. Large populations have repeatedly led to exchange with and nurturing of

adjoining herds. The Porcupine Herd gained more than 20,000 animals from the Fortymile Herd in 1957 through 1964 and could potentially add several thousand to the Fortymile Herd some winter in the future. The modern Nelchina Herd, which for several years provided more recreational days of hunting than any other single resource in Alaska, likely received impetus from an abnormal movement of part of the Fortymile Herd through the Alaska Range in 1920 to 1925 (Scott *et al.*, 1950). Such exchanges would likely never have occurred were these subpopulations restricted in numbers and movements as they promise to be in the near future.

The status of the international herds is reasonably healthy in 1972, but they both require closer scrutiny in the next decade than they have ever received in the past. Proper stewardship of the Porcupine Herd requires description and evaluation of botanical aspects of its present range, mapping present and past migration routes and careful analysis of the potential effects of pipeline construction. Priorities for management of the Fortymile Herd include close control of harvest, censuses, determination of productivity and a qualitative analysis of the productivity of its range.

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DISTRIBUTION AND MOVEMENTS OF THE PORCUPINE CARIBOU HERD IN THE NORTHERN YUKON

R. D. Jakimchuk and K. H. McCourt
Renewable Resources Consulting Services Ltd.

ABSTRACT—Intensive aerial and ground surveys have been carried out on the Porcupine herd since April 1971. The population wintered south of 67°N latitude in three main subgroups in 1971. Winter distribution in 1972 extended further southward and subgroups were less discrete. Subgroups migrate north to calving grounds via two main routes: the 'Old Crow' route (in the vicinity of the village of Old Crow) and the 'Richardson' route (over the Richardson Mountain Range). These major routes were also utilized in the fall migration in 1971. Spring migration patterns were variable. The timing of fall migration in 1971 appears to be fairly consistent with previous observations indicating that caribou reach the vicinity of Porcupine River in early September. Major summer movements coincided with aboriginal 'caribou fences' discovered in 1971. Surveys confirm that the northern Yukon caribou population interacts as a single population several times a year despite variations in winter distribution and the use of two distinct migration routes.

Until 1971, the Porcupine herd had been the least studied caribou population in Canada. However, recent industrial developments, notably proposals for arctic pipelines, have spurred intensive studies on this herd.

The Porcupine herd is an international resource. Major movements take place between Canada and Alaska at least twice annually. The size of the herd establishes it as a major population both in Canada and the United States. Our studies in 1971 estimated 70,000 caribou in the northern Yukon while Lentfer (1965) estimated 140,000 animals in the entire population.

Caribou of the Porcupine herd are the subspecies *Rangifer tarandus granti* Banfield, (1961). Their habitat differs from that of populations east of the Mackenzie River (*R. t. groenlandicus*) in two main characteristics. They occupy and traverse mountainous terrain throughout much of the year and calve on the coastal plain or adjacent snow free uplands, in contrast to calving ground characteristics described by Kelsall (1968) for eastern populations.

The Porcupine herd occupied a position of significant economic importance in the Arctic during the days of whaling and mining in the late 19th century (Kevan, 1970). This herd continues to be an important resource to native peoples in the northern Yukon and Northwest Territories, notably those of Old Crow, Aklavik and Ft. McPherson, as well as several villages in Alaska.

This paper summarizes the movements and distribution of the herd since initiation of an intensive study in March 1971 and compares current data with previous observations.

THE STUDY AREA

The study area includes essentially all of the Yukon Territory north of 64°N latitude, an area of approximately 180,000 km². Two major river systems, the Porcupine and the

Peel rivers, drain the central part of the study area. This region, consisting of the rolling hills of the Porcupine and Peel plateaus, is bounded on the south and west by the Ogilvie Mountains and on the east by the Richardson Mountains (Fig. 1).

The plateaus are underlain by permafrost and are vegetated primarily by black spruce (*Picea mariana*) and white spruce (*Picea glauca*) communities depending on local drainage conditions. Deciduous growth including birch (*Betula papyrifera*), poplar (*Populus balsamifera*) and alder (*Alnus sp.*) is largely restricted to water courses and relatively recent burns.

North of the Porcupine River is a low-lying, lake-studded area known as the Old Crow Flats. The northern and eastern boundary of this area coincides with the northern limit of trees. The Old Crow Flats are separated from the arctic coastal plain by the Barn and British mountains.

METHODS

Field work was undertaken throughout the months of April to October in 1971 and has been continuing since March of 1972. Operations in the Yukon were based out of the village of Old Crow. In 1972, a second study crew was established at Arctic Village in Alaska. Their purpose was to undertake concurrent surveys in order to determine relationships of caribou in the Yukon with those in the Brooks Range in Alaska and to monitor the movements of the Porcupine herd in Alaska.

Data were gathered primarily through aerial surveillance with a Cessna 185 aircraft and Bell 206 helicopter and at ground camps. In 1971 a total 486.5 hours of fixed-wing aircraft and 12.9 hours of helicopter time were flown in actual survey. Survey efforts of comparable intensity have been underway since March 1972.

Delineation of winter range was accomplished using the fixed-wing aircraft to follow the perimeter of areas showing caribou sign. Tracks, feeding craters and presence of animals provided evidence of winter range utilization. Some aspects of range characteristics (e.g., snow conditions) were studied using the helicopter for transportation. Migration routes were determined by following trails in the snow and locating animals with both fixed-wing aircraft and helicopters. Ground camps at strategic locations enabled the collection of data on numbers and composition of migrating herds. Summer movements were traced by following trails across the tundra, while numbers of animals which made the trails were visually estimated from an aircraft. Fall migration routes were determined by following trails in the snow.

RESULTS

Winter Distribution

The winter range of the Porcupine herd encompassed approximately 26,000 km² in 1971. Two major population subgroups were identified. These are: (1) the 'Ogilvie group' which wintered in the Ogilvie Mountains north and east of the Yukon River and (2) the 'Central group,' or largest wintering component, wintering from the Ogilvie Mountains to the south, north throughout the headwaters of the Porcupine River drainage (Fig. 2). The Trevor Range-Bonnet Plume group is part of the central group winter distribution but has been separated on the basis of its migratory route northward in the spring.

The eastern portion of the 1970-71 winter range included both mountainous terrain and spruce-lichen forests south of the Peel River and into the headwaters of its tributaries from the Blackstone River on the west to the Snake River on the east. In the spring of 1971,

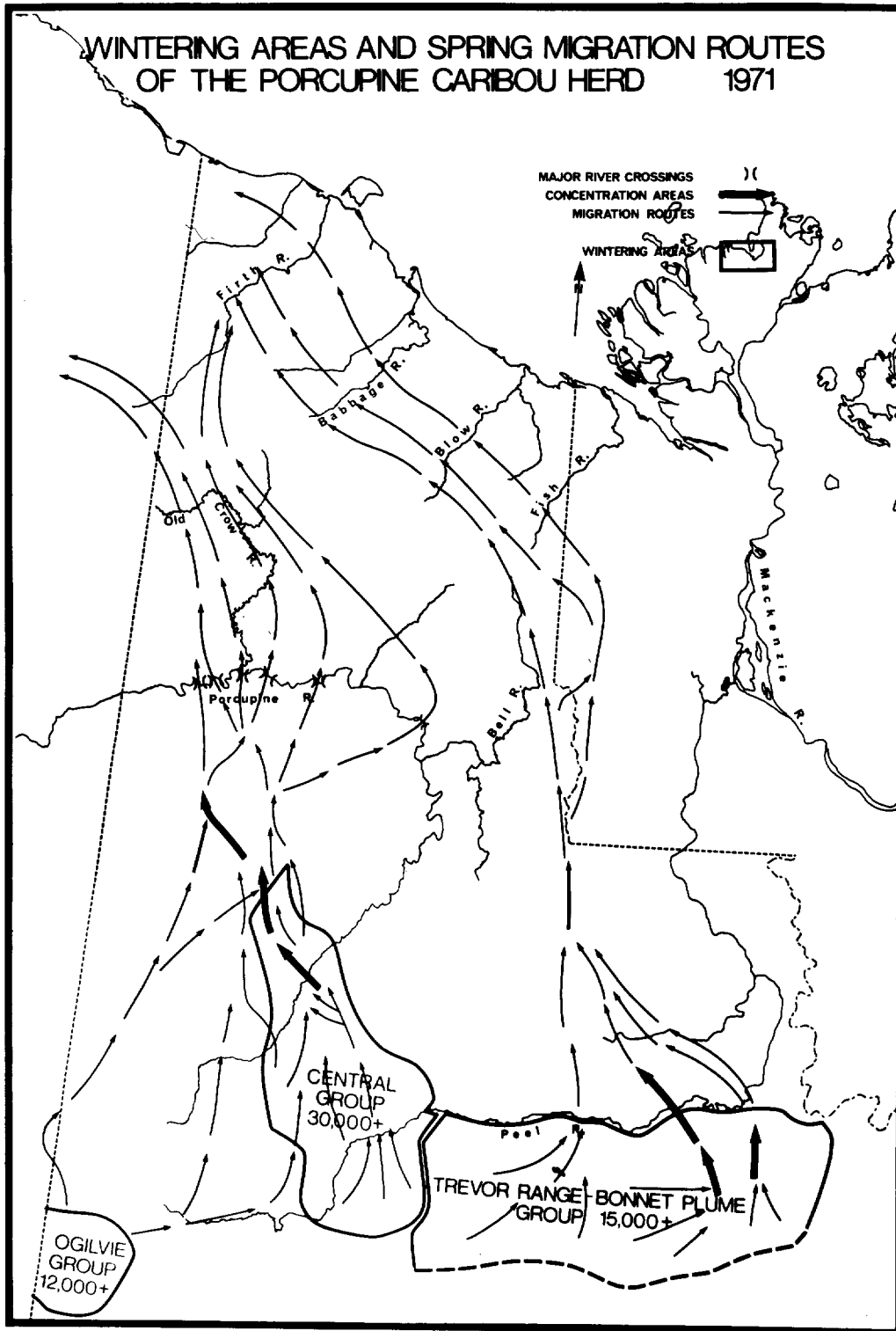


Fig. 2.

Lepp (pers. comm.) reported a wintering population of 2,500 caribou in the headwaters of the Stony, Rat and Vittrekwa rivers.

In the winters of 1971 and 1972, both alpine tundra range and open spruce taiga were utilized. Forested areas were dominated by the black spruce-lichen (*Cladonia* sp.) association. Habitat utilization ranged from rolling benchland to high mountain ridges above timberline. We observed one wintering group of some 5,000 animals which remained in a localized area of ridge tops on the Knorr Range from April 12 to May 19, 1971 probably as a result of deep snow in surrounding lowlands. This group was first observed a week earlier by A. Pearson (pers. comm.).

As illustrated in Figure 3, the winter distribution of caribou in 1971-72 was again primarily in the region of the upper Peel River including the area drained by its major tributaries, the Snake, Bonnet Plume, Wind, Hart and lower Ogilvie rivers. A northward extension of the foothills of the Ogilvie Mountains between the Miner and Whitestone rivers was extensively used. The Richardson Mountains and associated eastern and western foothills were also heavily utilized as far north as the headwaters of the Rock River. A discrete group (Ogilvie group) again wintered in the headwaters of the Tatonduk River in the Ogilvie Mountains.

Small groups were also observed at various locations within the northern Richardson Mountains and on the Old Crow Flats.

As in the winter of 1970-71, two distinct habitat types were used as winter range: the spruce forest and alpine tundra. Small groups of caribou averaging approximately 16 animals per group characteristically fed in craters excavated usually at the base of black spruce trees in medium dense stands. Snow cover in the forested area averaged approximately 64 cm to 74 cm in depth. The alpine tundra, being exposed to the wind, had a much shallower, but often crusted, snow cover. Relatively large groups of animals (averaging more than 100 animals per group) dug feeding craters where snow was only a few inches deep.

Spring Migration

Two major migration routes were used in both 1971 and 1972 in the northward spring migration. These are termed the Old Crow route, used by the Ogilvie and Central groups, and the Richardson route, used by the Trevor Range-Bonnet Plume group (Figs. 2 and 3). In 1971 the major movement along the Old Crow route commenced on May 11, began crossing the Porcupine River on May 21 and was essentially completed by June 10 along the Porcupine except for stragglers. The Ogilvie group covered the 300 km from their wintering area to the Porcupine River in 18 days.

The Trevor Range-Bonnet Plume group commenced moving north between May 13 and 16, although a herd of 2,000 animals started moving from the southern Richardson Mountains by May 10. An earlier drifting movement of some 3,000 caribou was observed in the northern Richardsons in April 1971. These were probably animals from the Stony Creek area. By May 23, caribou using the Richardson route were entering the Barn Range and joining with animals of the Old Crow route as they entered Alaska. Animals south of the Peel River had moved over 370 km of mountainous terrain in 10 days. The 1971 migration was characterized by periodic grouping of animals prior to a concerted movement then regrouping following movements. Dispersal occurred once the Old Crow route animals reached Old Crow Flats and those on the Richardson route reached the northern Richardson Mountains.

Areas of funneling of major portions of the herd occurred in the valley of the Fishing Branch River, across the Keele Range, along the Knorr and Trevor Ranges and across the east end of McDougall Pass in the Richardson Mountains (Fig. 2). The Porcupine River was

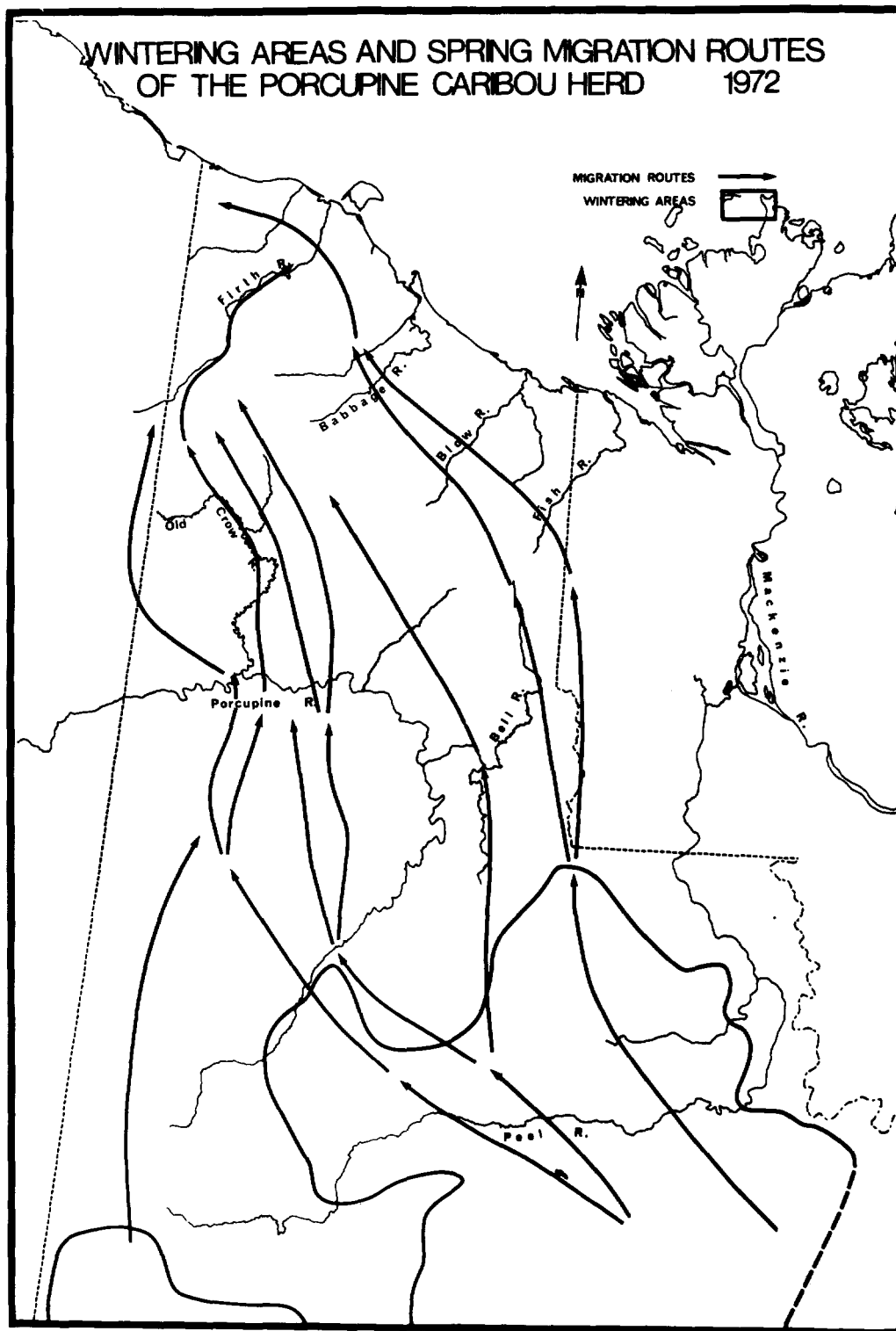


Fig. 3.

crossed at numerous points, although aerial surveys and ground camps revealed two major crossing points at 'Caribou Lookout' and 'Fish Camp' (Fig. 1). A total of 29,222 caribou were counted crossing these points within a 13 day period. Both Caribou Lookout and Fish Camp are known historical crossing points. The six main crossing points on the Porcupine River in 1971 are shown in Figure 2.

In 1972, caribou moving out of the headwaters of the drainages of the Richardson Mountains began migrating north on approximately March 15. From that time until the end of April, the animals traveled over the shallow crusted snow along the highest ridges. During the first half of May, the path of movement shifted to the western slopes apparently in response to the appearance of large areas of bare ground resulting from a thaw. After crossing McDougall Pass the animals dispersed in the northern Richardson Mountains but upon emerging, followed a narrow corridor of snow-free ground along the northern foothills of the Barn Range and British Mountains. The vanguard of animals traveling the Richardson route crossed the Blow River on May 2, the Babbage on May 10 and the Firth on May 16 (Fig. 3).

Caribou did not begin moving along the Old Crow route until the first week of May in 1972. The movement appeared to be triggered by warm weather during the first week of May which left snow depths at approximately one-half their original depth. The soft, shallow melting snow appeared to present little obstacle to caribou movement. During the second week of May, cold weather resulted in the formation of a crust on the snow, which also provided excellent traveling conditions.

The majority of animals west of the Richardson Mountains and the Wind River used the Old Crow route during the spring migration. The animals from the Tatonduk River (Ogilvie group) moved up the Ogilvie Mountains where they converged with animals on the Old Crow route during the spring migration. The animals on the Old Crow route moved north in much the same manner as they did in 1971. Animals south of the Peel River and east of the Wind River did not begin a concerted movement north until the first week of May, at which time snow conditions became favorable for movement across the lowlands of the Peel River to the Richardson Mountains.

The Old Crow route was not as restricted in 1972 as it was in 1971. Although the majority of the animals crossed the Porcupine River between the mouth of the Bluefish River and a point just east of the mouth of Lord Creek, as they did in 1971, a number of animals traveled up the Eagle Plains to cross the Bell River.

Upon crossing the Porcupine River beginning on May 14, one movement swung west into Alaska along the Old Crow Range, while a second major movement continued northwest across the Old Crow Flats as in 1971. Caribou which traveled across the Old Crow Flats moved north through the British Mountains with the major movement down the Firth River Valley, then west into Alaska along the northernmost portion of the British Mountains.

Calving in the Yukon

In 1971 we suspect that the bulk of calving took place in Alaska. Although surveys were limited, only a few cows with calves were observed in the Yukon prior to large numbers of caribou entering Alaska.

In 1972 the first calf was observed on May 28 and it is believed that most calving occurred during the first week of June. The main area used for calving in the Yukon in 1972 was bounded by the Spring River on the east, the United States border on the west, the Arctic coast on the north and northernmost foothills of the British Mountains on the south. Smaller numbers of calves were observed outside this area near the confluence of the Firth

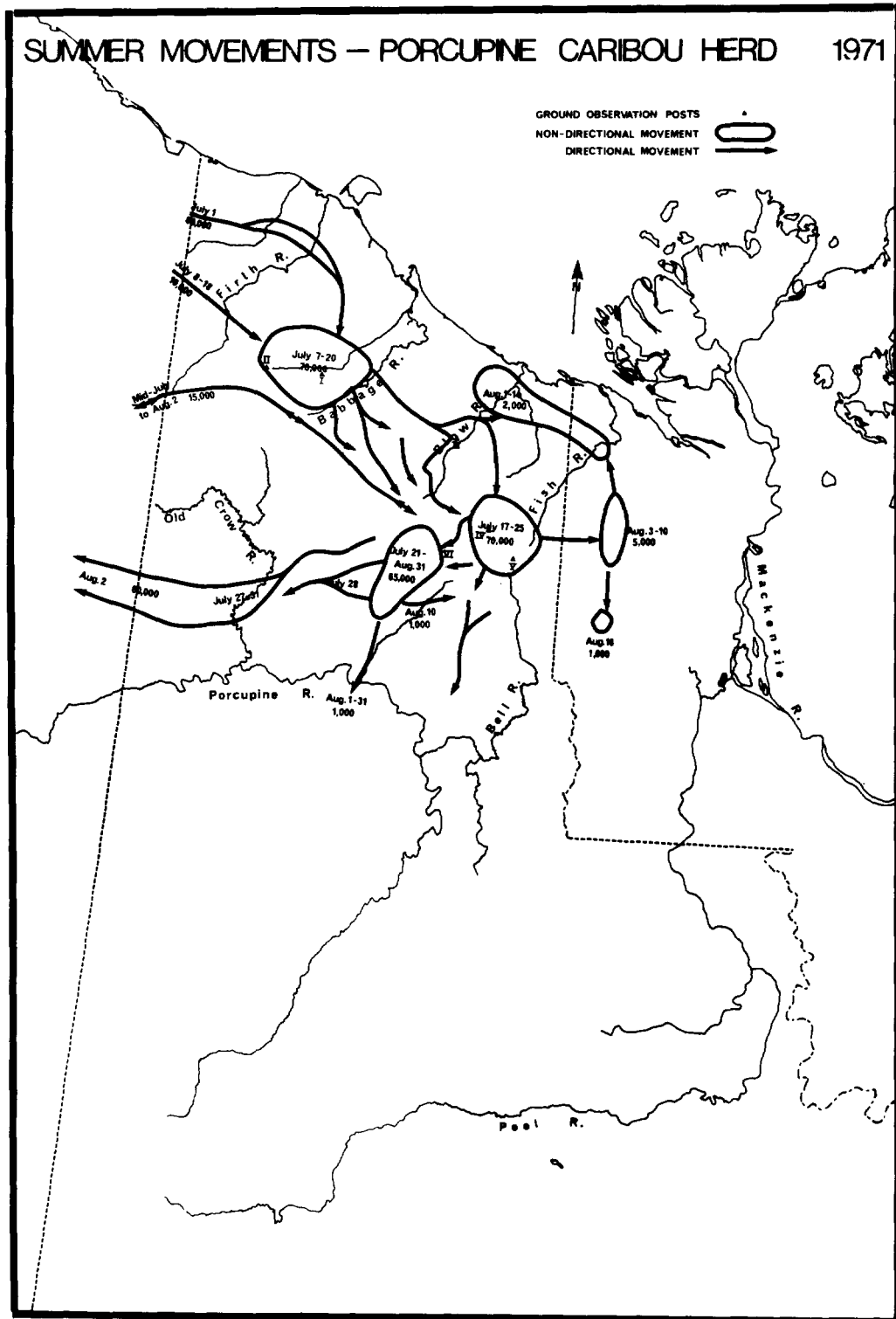


Fig. 4.

River and Joe Creek and on the Trail and Babbage rivers. On the basis of census attempts by transect flights, the size of the calving herd in the Yukon was considered to be not less than 16,000 animals and quite possibly considerably larger.

Summer Movements

On July 1, 1971 approximately 60,000 animals crossed the Yukon-Alaska border in the northern foothills of the British Mountains and moved southeastward (Fig. 4). An additional group of 10,000 entered further south on July 6 and joined the latter group. The combined group crossed the Blow River on July 17, entering the northern Richardson Mountains. On July 15 another herd of 15,000 animals entered in the Firth River area penetrating eastward as far as the headwaters of the Blow River before doubling back and returning to Alaska (Fig. 4). Thus three major groups returned from the calving grounds in Alaska. On July 28, the large group moved rapidly westward into Alaska, and by August 2 all animals (except approximately 10,000 dispersed throughout the Yukon) had re-entered Alaska.

Summer movements were characterized by post-calving aggregations that moved in a clockwise direction in the Yukon from July 1 to August 2. Periods of dispersal were short (Fig. 4) during this period with the exception of animals that remained scattered in the northern Yukon during August. The major August dispersal apparently occurred on or just following August 2, 1971.

In 1972, during the latter two weeks of June, virtually all the caribou remaining in the northern Yukon moved into Alaska along the North Slope. They did not return until July 10 at which time approximately 50,000 caribou in two large compact herds were observed just inside the Yukon Territory at the headwaters of the Clarence and Malcom rivers. These animals, which separated into several herds, moved steadily southeast through the British Mountains and Barn Range (Fig. 5). Characteristically, they spent the hottest part of the day in very compact herds on the tops of mountains or sometimes on snow patches. Movement and feeding occurred in late afternoon and evening. The majority of these animals had crossed the Blow River into the northern Richardson Mountains by July 21. Here, movement slowed considerably and the animals dispersed. During the first week of August the majority of caribou left the Richardson Mountains and began moving westward across the Old Crow Flats, exhibiting a pattern of movement identical to that of 1971.

Fall Migration

Caribou moving south during September and October followed the two basic routes used in the northward spring migration. The actual routes used are shown in Figure 6.

The first concerted southward movement was observed on September 7, 1971 when animals were crossing the Porcupine River between Salmon Cache and the Alaska border (Fig. 5). This movement lasted from about September 6 to 8. Retracing this movement through 15 to 20 cm of snow revealed that the movement originated in the Brooks Range in Alaska. Trails indicated a southward movement from the Kongakut to the Firth River area. Large numbers (estimated 30,000) crossed the Porcupine River between Caribou Bar Creek and Salmon Cache (Fig. 6) and moved south over the Keele Range, where they dispersed. On September 20, caribou south of the Keele Range reversed direction and began moving northward, stopping at three locations south of the Porcupine River, one of which was directly south of Old Crow. On September 30 a blizzard dropped 46 cm of snow on the northern Yukon. When surveys were resumed on October 2, animals had left their staging area in an apparently rapid movement. By October 26, caribou were well into winter range,

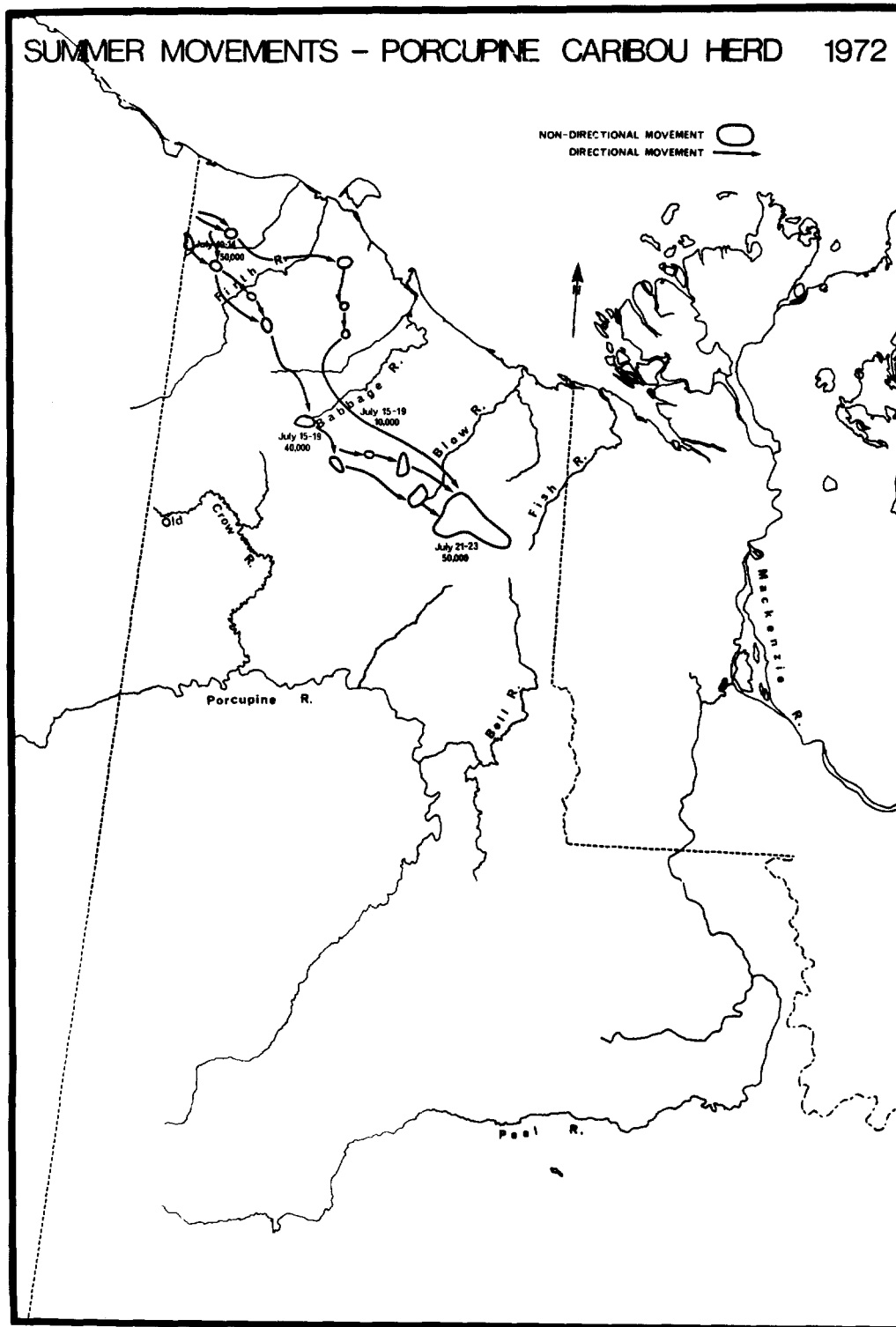


Fig. 5.

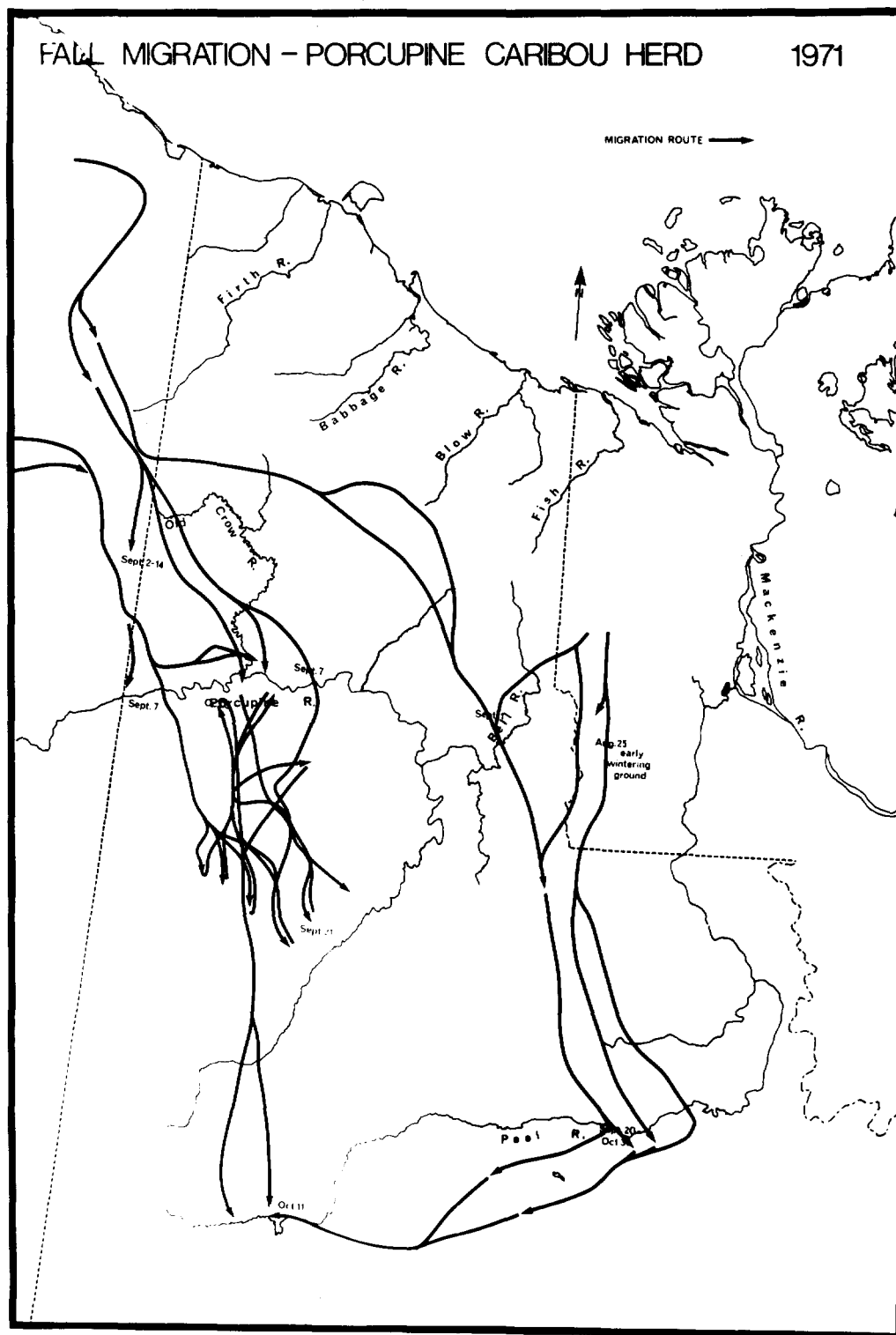


Fig. 6.

occupying the valleys of the Ogilvie, Blackstone and Hart rivers (Fig. 6).

Herds moving down the Richardson route were largely unobserved due to adverse weather conditions. No northward shift was evident in these animals. Southward movement was first noted on September 1 just north of the Bell River (Fig. 6).

By October 26, caribou of the Richardson route had penetrated winter range into the Bonnet Plume, Wind River and Hungry Lake region. Trails showed movement southwest into areas occupied by herds which utilized the Old Crow route.

DISCUSSION

Until recently the location of the winter range of the Porcupine caribou herd has been the subject of much speculation, as a result of the limited nature of past investigations and probable shifts in winter range location. Murie (1935) reported that caribou occurred on the headwaters of the Porcupine River and south of the upper Peel River. Stevens (1948) observed caribou of the Porcupine herd on the Peel River in October. On the other hand, aerial surveys by Munro (1953), the most complete observations prior to current research, suggested that the winter range was in the Keele Mountains. Hemming (1971) reported suggestions that the animals south of the Peel are not part of the Porcupine herd. However, systematic surveys during 1971 and 1972 now confirm that caribou of the Porcupine herd utilize a winter range which extends well south of the upper Peel River.

Hemming (1971) raised questions regarding the origin of populations along the drainages of the Ogilvie and Blackstone rivers. Flights in 1971 confirm that Porcupine herd caribou penetrate well into this region. On October 26, 1971 trails were followed from Old Crow to the upper Blackstone River (Fig. 6) and animals were observed on and adjacent to the Dempster Highway over a distance of 113 km.

The relationships and overlaps on this portion of range are somewhat confusing. Hemming (1971) shows part of the winter range of the Fortymile herd in the headwaters of the Tatonduk River (Fig. 1) during the period 1965-1970. We have termed caribou in this area the Ogilvie group which moved northward on spring migration via the Old Crow route in both 1971 and 1972.

Skoog (1964) (cited in Hemming, 1971) indicated that in 1957 and 1964 large numbers of Fortymile caribou moved north with the Porcupine herd. Either this group has always done so or it appears that a permanent shift has taken place and this population segment now may be considered as part of the Porcupine herd owing to its fidelity to a north slope calving ground.

The winter range of the Porcupine herd overlaps that of woodland caribou (*R. t. caribou*) and intergradation is a possibility although no taxonomic work has been carried out to examine this possibility.

The group of animals with calves observed by Hemming in July, 1964 (Hemming, 1971) may have been woodland caribou since it is now clear that the so called 'Dawson herd' is a wintering subgroup of the Porcupine herd identical to what we have referred to as the Ogilvie group.

A feature of winter range utilization common with Alaska caribou is extensive use of alpine tundra particularly in late spring. Some 5,000 caribou, increasing to 10,000, on the Knorr Range occupied the same slopes in 1971 for a period of six weeks – an extraordinary occurrence in caribou which are noted for their vagility. We are not aware of a similar restricted range use for such a lengthy period in the literature. This situation is attributed to record snowfalls in the Yukon in 1971.

Wind-swept slopes provide attractions for caribou, particularly in spring when snow in surrounding areas reaches its maximum depth and later when solar radiation crusts the

snow, making feeding and movement difficult. However, snow depths tolerated are greater than those tolerated by Keewatin caribou according to Pruitt (1959), who reported the thickness threshold there as being approximately 60 cm. In addition, temperature inversions moderate apparently severe exposures occurring in alpine areas. Inversions were frequently noted during surveys of caribou in alpine areas.

While three population subgroups have been identified on the basis of migration paths utilized, only two discrete wintering groups occur. The central and Trevor Range groups overlap in winter distribution and freely intermingle during the rut. The relationship between the Ogilvie and the other groups during the rut is unknown.

The onset of migration appears variable based on both previous observations (Kevan, 1970) and our own studies. Chatelain (in Kevan, 1970) recorded approximately 20,000 animals at the headwaters of the Firth and Colleen Rivers in May 1950, while McEwan recorded a similar number on March 25 along the Yukon coast. Aerial surveys in 1971 and 1972 indicated a variability in the onset of migration along the two major routes which offers an explanation for the discrepancy. In late March, 1972, caribou which had wintered in the southern Richardson Mountains began moving north with approximately 5,000 animals reaching the vicinity of McDougall Pass by April 15. Animals south and west of the Richardson Mountains (representing all those using the Old Crow route and some using the Richardson route) did not begin a concerted movement until the first week of May.

The more favorable traveling conditions over shallow crusted snow in the Richardson Mountains appeared responsible for the earlier onset of movement. In 1971, approximately 2,500 wintered in the Richardson Mountains and subsequently undertook an early movement along the Richardsons. Data presented by Munro (1953) indicate an early movement along the Richardson route and a later one along the Old Crow route. Chatelain's and McEwan's observations probably represent observations of animals using the Old Crow route and the Richardson route respectively.

The onset of migration along each of the two routes when considered separately is therefore probably not particularly variable. Along the Old Crow route, migration is apparently well under way in the first half of May while minor variations may result from variable traveling conditions dependent on weather or due to variations in the southern extent of the winter range. Migration along the Richardson route may be almost two months earlier if the winter range includes the Richardson Mountains. However, if animals have to travel across deep snow-covered lowlands to reach the Richardson Mountains, the onset of their movement will be delayed to coincide with that of caribou using the Old Crow route.

In any case, variability is not unusual for migrating caribou in the spring and appears to occur in all North American caribou populations (Skoog, 1968; Kelsall, 1968).

Observations of the Porcupine herd during the calving period in 1972 indicate a variation in both location and extent of the calving area from that reported by Hemming (1971). Hemming reports that the main calving area is located on the sedge meadows of the coastal plain between the Katakturuk and Kongakut Rivers. In 1972, the major calving area was between the Jago River in Alaska and Spring River in the Yukon. The more easterly distribution is attributed to the suspected delay in migration preventing caribou from reaching their destination before parturition. Parturient animals delayed by 10 days may be 240-320 km behind the vanguard of the movement. Once these animals had calved, further movement to the west was effectively curtailed by numerous swift-flowing rivers at right angles to the direction of movement. Few cows with calves attempted crossing major streams until the calves were at least 10 days of age.

In the latter part of June 1972 following calving, the caribou were observed to aggregate into large compact herds on the North Slope of Alaska before large numbers

re-entered the Yukon. Characteristically, summer movements of caribou appear to be very random in nature. However, post-calving movements of the Porcupine herd showed a remarkable consistency during 1971 and 1972. In both years, large compact groups moved southeast through the British Mountains and Barn Range during early July to reach the northern Richardson Mountains and disperse there in the latter part of July. By August 1, the caribou again began moving, this time westward across the Old Crow Flats.

This reversal in direction of movement has been reported previously for Porcupine caribou by Murie (1935). In addition, the locations of five aboriginal caribou corrals, discovered while following summer movements of the caribou, suggest the traditional nature of this route. A similar pattern of movement has been reported for the Arctic herd of northwestern Alaska by Lent (1966), who also commented on the remarkable similarity of post-calving movements of that herd in 1960 and 1961. The tendency to form large aggregations following calving and to disperse subsequently has been reported for several other caribou herds (Lent, 1966; Skoog, 1968; Kelsall, 1968).

Fall migration exhibits a greater consistency than the spring movement, contrary to the suggestions of Kelsall (1968) for Keewatin herds. Kevan (1970) gives the locality of scattered observations from 1949 to 1956, which place caribou in the vicinity of the Porcupine River from late August to early September. Our observations in 1971 showed a major movement on September 6 to 8 across the Porcupine River. Calef and Lortie (1971) observed additional movements in this area on September 9 and 10. Similarly timed movements apparently occurred across McDougall Pass. Hemming (1971) also reports that the first caribou reach Old Crow and McDougall Pass in early September.

Thus while the spring migration appears to be subject to considerable variation, especially between the two routes, the autumn migration appears to be fairly regular. This may be a result of the lack of difference in environmental conditions on the two routes during the fall as opposed to spring. A feature of the 1971 fall migration was a northern shift in late September following an initial southward movement. This took place by animals using the Old Crow route.

CONCLUSIONS

Two years of intensive studies of the Porcupine caribou herd have resolved several questions concerning the relationships of caribou in several parts of the southern extent of their range in the Yukon Territory. The discovery of two major spring migration routes and the apparent effect of differences in nival conditions on the onset of migration along the routes offer an explanation for the variability in timing of migration indicated in the literature. A notable feature of observations and indirect evidence to date, is the high degree of consistency in the annual pattern of movements.

ACKNOWLEDGMENTS

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The sponsorship of the Gas Arctic-Northwest Project Study Group has made this study possible. Finally we wish to thank the native people of Old Crow for their assistance and hospitality.

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THE STATUS OF WILD REINDEER IN THE USSR, ESPECIALLY THE KOLA PENINSULA

O. I. Semenov-Tian-Shanskii
Lapland State Reserve
Monchegorsk, Murmansk Province
USSR

ABSTRACT — The total number of wild reindeer in the USSR in 1969 amounted to 650,000, based on aerial counts. Some aspects of wild reindeer-domesticated reindeer relations are discussed. In the Lapland Reserve only 99 caribou were found in 1929, but in 1941 942 deer were counted here. Since the Second World War the numbers of caribou, as well as their range, considerably increased, amounting to 20,500 deer on 26,000 square km of range in 1967-1968. On Kola Peninsula the annual population increase in wild reindeer, free of harvesting, reaches 19 to 23 per cent. Bears and wolverines do not do much harm to wild reindeer, but promote natural selection in populations. In order to regulate numbers systematic harvesting of wild reindeer is introduced in some regions of the USSR.

The true wild *Rangifer tarandus* of the Old World is referred to in this paper as 'wild reindeer', in opposition to 'domesticated reindeer'. The corresponding names in Russia are 'dikii olen' and 'domashnii olen'. In both stocks tundra and woodland forms can be distinguished, analogous with American barren ground and woodland caribou.

By the middle of the 20th Century the numbers of wild reindeer in the USSR were considerably decreased. The main reason for this was the progress of reindeer industry, accompanied with forcing the wild reindeer onto the poorest northern ranges and, partly, excess hunting and habitat destruction (Druri, 1949; Heptner *et al.*, 1962). The decree issued by the Council of Ministers, RSFSR, November 1956, "On measures for Arctic animals conservation," forbids completely the killing of polar bear and at the same time strongly restricts walrus and reindeer hunting, making exceptions for local requirements of northern and far eastern natives (Borisov, 1957). As a consequence, the reindeer populations rapidly increased. We now have reliable information on wild reindeer numbers, for since 1957 censuses or estimates have been based on aerial counts.

The Taimir Peninsula holds the greatest population of wild tundra reindeer in the USSR; its numbers were determined to be about 100,000 in 1959 and 333,000 in 1969 (Andreyev, 1961; Pavlov *et al.*, 1971). In the Yakutsk Autonomous Republic the numbers of tundra wild reindeer are estimated as 95,000, on the Yamal Peninsula as 4,000 and on the Chukotsk Peninsula as 3,500 (Semenov-Tian-Shanskii, 1971). The total numbers of this form (*Rangifer tarandus sibiricus* Murr.) in 1967-1969 amounted to 440,000. The estimations of woodland wild reindeer numbers in forest and mountain parts of Siberia are about 180,000 (of them 100,000 in Yakutsk AR) and 38,000 for the northern parts of European Russia (inhabited by *Rangifer tarandus tarandus* L.). According to information produced at the Conference on Conservation and Rational Use of Wild Reindeer, held in the town of Dudinka, June 23-25, 1970, the total number of wild reindeer in USSR is close to 650,000 (the estimation made by Wildlife Management Board of RSFSR is somewhat less — 600,000). The total number of domesticated reindeer in USSR is at least 2,000,000.

As a consequence of wild reindeer population growth in Taimir the scope of their seasonal migrations enlarged, running up to 1,000 km each way. In the course of these migrations wild reindeer invade and degrade the winter range of domesticated reindeer, causing some losses of domesticated animals moving away with the migrants. Owing to this, the attitude of reindeer herdsman toward wild reindeer became aggravated. Pasture degradation from this overuse makes necessary the controlling of wild reindeer numbers. In Taimir, as well as in some other northern regions, measures are being taken for increasing wild reindeer harvesting. Reindeer hunting in tundras and the transportation of products from there are difficult and expensive. For this reason in Taimir and in the Lena Delta some experiments were undertaken for wild reindeer harvesting on river crossings along their migration routes (Semenov-Tian-Shanskii, 1971).

On the Kola Peninsula the last decades of the 19th Century were marked by rapid progress in reindeer raising. Estimates of domesticated reindeer numbers are 7,072 in 1866 and 58,601 in 1908 (Segal, 1962). In connection with this the Kola wild reindeer was nearly exterminated by the 1920's. Only a few herds remained in two separated areas, the western one, on Chuna-tundra and Monche-tundra ranges, and the eastern one, in the forest-tundra plains around the upper reaches of Pana, Varzuga and Strelna rivers. In the first of the regions mentioned the Lapland Reserve was established in 1930, primarily to protect the wild reindeer together with their typical habitats. In 1929 only 99 wild reindeer were found on this territory (about 1,600 km²). Put under protection, the wild reindeer population rapidly increased, reaching 942 individuals by 1941; this corresponds to an average annual increase of about 23 per cent.

Since World War II, as a consequence of the sharp decline of reindeer raising near the front-line (from 1940 to 1950 the number of domesticated reindeer in the west half of Murmansk Province reduced to one-fifth of the pre-war number), the wild reindeer numbers, as well as their area, considerably increased. This area is now seven times as large as the Lapland Reserve territory (Fig. 1).

In recent years, the wild reindeer census is carried out using a helicopter in the latter part of winter when wild reindeer are usually concentrated in large herds on the slopes of highland tundras. Herds over 30 animals must be photographed several times each with the usual 35- or 60-mm cameras (Fig. 2). Counts can be processed later using enlarged 18 X 24 cm copies. In snowy winters, when the wild reindeer are gathered on open tracts almost without exception, the technique mentioned provides a nearly absolute census. With poor snow cover some wild reindeer spend all the winter in the forest zone. In such winters the census is incomplete, for not all herds can be found and not all animals are photographed. In practice, in most years the wild reindeer census in Lapland Reserve is more or less incomplete. The census was considered complete in 1957 (1,964 reindeer), 1961 (4,396) and in 1967 (12,641; 98 per cent of animals on tundra). The annual population increase for these years in average is about 20 per cent. In 1972 only 9,756 wild reindeer were recorded, of them 40 per cent on mountain tundras, 40 per cent in pine forests, 17 per cent on bogs and 3 per cent on frozen lakes (Fig. 3). Perhaps thousands were not found at all. Very likely, the continuous population growth recently ceased and now its level is nearly stabilized. The western population density in 1967 was estimated to be 115/100 km², not much different from that for domesticated reindeer in Kola Peninsula.

The east Kola wild reindeer population inhabits rather open, flat country. Apparently they have no need for seasonal migrations. An aerial census was carried out at five year intervals. In 1958, 1,400 wild reindeer were recorded here, 3,559 in 1963 and 7,880 in 1968. The annual population increase in this case is about 19 per cent (Semenov-Tian-Shanskii, 1970).

The area of the western wild reindeer population is about 11,000 km² and that of the

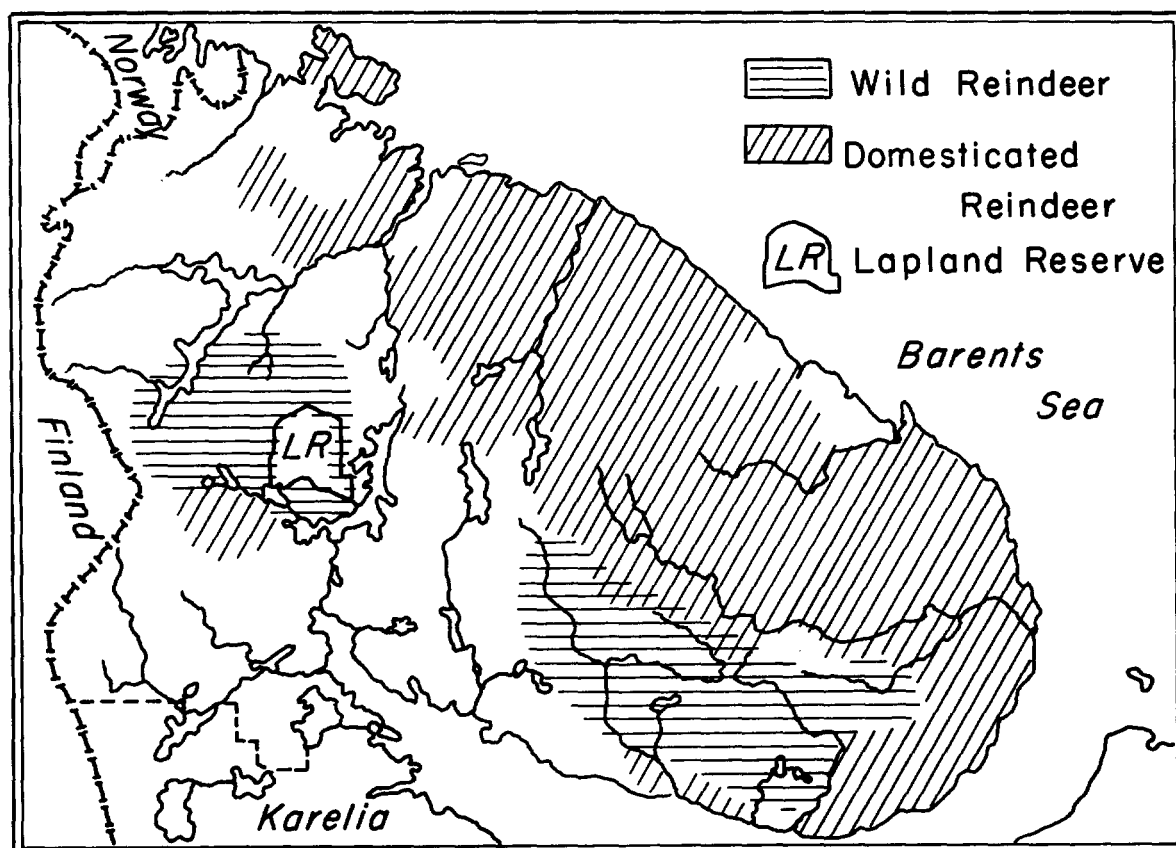


Fig. 1.—Present ranges of the wild and domestic reindeer in Murmansk Province, USSR (after Atlas of Murmansk Province, 1971).

eastern one about 15,000 km². Both populations have but few possibilities for further expansion, for the major part of Peninsula's area is already used for domestic reindeer.

Anthrax and brucellosis are unknown on the Kola Peninsula; so, the reindeer populations, both wild (about 20,000) and domesticated (about 80,000), are essentially limited by range carrying capacity, impeding their further growth.

Reindeer hunting has been closed in Murmansk Province since the 1920's. Recently some harvesting was recognized as necessary to regulate wild reindeer numbers. Hunting is carried out under special licenses. The kill limit is determined on basis of population numbers. Helicopters and snowmobiles are used for locating the herds and removing the production from the hunting grounds.

Reindeer domesticated long ago by the Lapps are of local origin and do not differ much from local wild forms in habitus; both are of the same ancestors. The domesticated tundra reindeer appeared on Kola Peninsula for the first time in 1887, being driven here from the Malozemelskaja tundra (the lower reaches of Pechora River). Modern Kola domesticated reindeer are, for the most, hybrids between local woodland and introduced tundra domesticated reindeer ('Izhemskii olen' is the Russian name for the latter). When lost, domesticated reindeer often join into wild reindeer herds. Being ear-marked such feral reindeer can be easily recognized among genuine wild reindeer.

In 1931-1941 the ear-marked reindeer made up 4 per cent of the wild stock, but in recent years this decreased to 0.4 per cent in the western wild reindeer area and to 1.1 per



Fig. 2.—Reindeer on the highland tundra in Lapland Reserve on April 6, 1962; herd numbers 2,086.

cent in the eastern one (Semenov-Tian-Shanskii, in press). Even when going feral, domesticated reindeer remain less wary compared with genuine wild reindeer; for this reason they are more likely to be killed by predators as well as by hunters. Consequently, the woodland reindeer habitus is well maintained in the Kola populations, in the west one especially, for it has less contacts with domesticated herds.

Among 4,196 wild reindeer observed in summer, we found the sex and age ratio to be



Fig. 3.—Bog moss pine forest is a typical reindeer habitat in the taiga zone of USSR (March 23, 1971).

as follows: adult males = 20 per cent, subadult males = 7 per cent, adult females = 40 per cent, subadult females = 10 per cent and fawns = 23 per cent.

Since wolves are nearly exterminated on the Kola Peninsula, the only predators of importance for reindeer are bears and wolverines. Over the last 14 years, remains of 17 reindeer killed by bears, 8 by wolverines and 2 by wolves were recorded in the Lapland Reserve. In kills by bears, males predominate over females (10:3) and older individuals over

younger (6:1). The bear obtains its victims, as a rule, by stealing up on them. Therefore, males and old animals, being less wary, are most likely to be killed. For similar reason the moose, in comparison with reindeer, is more vulnerable. The number of moose in the Lapland Reserve is about one-tenth that of reindeer. However, in kills by bears we found 19 moose and 17 reindeer. The brown bear obviously promotes natural selection in reindeer populations. The wolverine, feeding mainly on carrion, sometimes takes the chance to kill some sick or injured reindeer (and moose, in exceptional cases). In October, 1968 one wolverine attacked a lone female fawn and paralyzed it, having heavily injured its back around the shoulder blades. This fawn could not defend itself nor run away, for its hind foot joint was already injured (Fig. 4). In February, 1959 an adult male reindeer, worn out with



Fig. 4.—This wild reindeer fawn was found wounded by a wolverine, but still alive (October 26, 1968).

necrobacillosis, was killed by a wolverine. It is doubtful whether a wolverine can kill a reindeer in good health. Apparently both the bear and the wolverine should not be considered as major problems for reindeer. The general attitude toward wolves remains negative in USSR and efforts towards reducing their numbers are applied as formerly

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POPULATION GROWTH AND MOVEMENT PATTERNS OF THE NELCHINA CARIBOU HERD

J. E. Hemming
U. S. Bureau of Land Management
Anchorage, Alaska

ABSTRACT—The Nelchina caribou herd of south central Alaska has reached two peaks in the last 100 years, one in the mid-1800's and another in the early 1960's. The herd declined for about 70 years following the first peak, and then increased at a geometric rate from 1947 to 1962. As caribou (*Rangifer tarandus granti*) numbers increased, the frequency of shifts in range use and seasonal splitting increased, and the herd expanded its range. Conversely, as numbers decreased, the area occupied by the herd contracted toward the traditional calving area. The time between successive population peaks plus a relatively small area of occupancy no doubt allowed optimum recovery on many previously overused ranges. At the present time the population is declining. Distribution and movement patterns can be used as indicators of the relative abundance of caribou herds.

The Nelchina herd of south central Alaska ranges over the Copper River and Upper Susitna River basins and adjacent mountains. This is a diversified area of rugged, glacier-capped mountains, rolling uplands and broad forested plains. Four mountain ranges form the herd boundaries: the Alaska Range on the north, the Chugach Mountains on the south, the Talkeetna Mountains on the west and the Wrangell Mountains on the east. Calving occurs on the eastern slopes of the Talkeetna Mountains. Like other herds of Alaskan caribou (*Rangifer tarandus granti*) movements of the Nelchina herd center on traditional calving grounds regardless of population status. This herd is not isolated from neighboring populations and has at times shared winter ranges with portions of the Delta, Fortymile, McKinley and Mentasta herds. This paper describes the population changes and spatial relationships of this caribou herd from the mid-1800's to the present time.

PROCEDURES

Between 1948 and 1958, the U. S. Fish and Wildlife Service provided regular caribou census data to the Territorial Government. After Alaska achieved statehood in 1959, the responsibility for caribou research was assumed by the State of Alaska Department of Fish and Game.

Population estimates were obtained by aerial transect sampling from 1948 to 1955 (Watson and Scott, 1956), by extrapolation from 1956 to 1961 (Skoog, 1968), by aerial stratified random sampling in 1962 (Siniff and Skoog, 1964) and by aerial photo-direct count techniques in 1967 (Hemming and Glenn, 1968).

For the period prior to 1948, information concerning the general distribution of the Nelchina herd was gleaned from the literature and from interviews with long-time bush pilots, guides and local residents. In recent years seasonal movements were recorded by aerial surveys at monthly intervals. The location, direction of movement, trail patterns and approximate numbers of caribou were recorded on topographic maps at a scale of

1:250,000. Annual movements were determined by summarizing data from monthly surveys.

RESULTS AND DISCUSSION

Even though the historical record is fragmentary, it was possible to piece together the early population status and range of the herd. Sometime between 1848 and 1885, the herd was very abundant and ranged from the Talkeetna Mountains eastward over the entire Copper River Basin (Skoog, 1968). Suitable winter habitat must have been well saturated with caribou because even marginal areas, such as the Chitina River Valley that regularly receives heavy accumulations of snow, were utilized (Glenn and Abercrombie, 1899; Allen, 1900; Rohn, 1900). By 1885 only a few caribou moved as far as the Chitina and Copper River Valleys (Allen, 1900). At the turn of the century it was obvious that the herd was decreasing, and the remaining animals were found in ever closer proximity to the Talkeetna Mountains (Glenn and Abercrombie, 1899; Glenn, 1900; Mendenhall, 1900; Osgood, 1901).

The status of the Nelchina herd during the early 1900's is somewhat confusing because of the seasonal influx of caribou from the then abundant McKinley and Fortymile caribou herds (Skoog, 1968). However, remnants of the Nelchina herd apparently remained mostly within the Talkeetna Mountains from 1900 to 1945 (Osgood, 1901; Capps, 1927; Alaska Game Commission, 1925-1948). The first aerial count was made in November, 1948, but the accuracy was questionable due to uneven distribution of caribou and the inexperience of observers. Initial tallies resulted in a population estimate of 4,500 to 5,000 animals. However, continued refinement of aerial census techniques in the succeeding seven years revealed that the original estimate probably accounted for only about one-half of the animals present. Extrapolation backward from 1955 to 1948 yielded a revised population estimate of about 10,000 caribou for 1948 (Watson and Scott, 1956).

In 1950 the herd occupied an area of about 16,000 km² (10,000 mi²) and had begun to increase (Table 1).

TABLE 1.--Population estimates of the Nelchina caribou herd.

Year	Herd size**	Source
1948	10,000	Watson and Scott, 1956
1956*	45,000	Watson and Scott, 1956
1957	48,000	Skoog, 1968
1958	53,000	Skoog, 1968
1959	59,000	Skoog, 1968
1960	64,000	Skoog, 1968
1961	69,000	Skoog, 1968
1962*	71,000	Siniff and Skoog, 1964
1967*	46,000	Hemming and Glenn, 1968

*Years when census was conducted.

**All estimates exclude calves.

The cow-calf segment began to split seasonally into two or more groups after 1955. In succeeding years the range of the herd expanded as numbers increased, and by 1960 the herd utilized an area of about 52,000 km² (20,000 mi²). As a result of field studies in 1961 and 1962 Skog (1963a) stated, "The range is beginning to show signs of deterioration and

there is some indication that carrying capacity has been reached.”

Shifts in winter range use became increasingly common while areas of summer use remained essentially unchanged. Signs of emigration were observed each winter from 1962 to 1965 (Skoog, 1963a; Skoog, 1963b; Skoog, 1964; Lentfer, 1965; McGowan, 1966; Glenn, 1967). The annual distance traveled by the Nelchina herd increased from 600 km to 1,580 km (370 mi to 980 mi) between 1955 and 1964 (Skoog, 1968).

The census of 1967 revealed that the population had started to decline. Even though no census has been completed since 1967, field studies have suggested a continuous downward trend.

In order to analyze the relationship between caribou numbers and patterns of movement, I constructed a population growth curve (Fig. 1). The size of the Nelchina herd

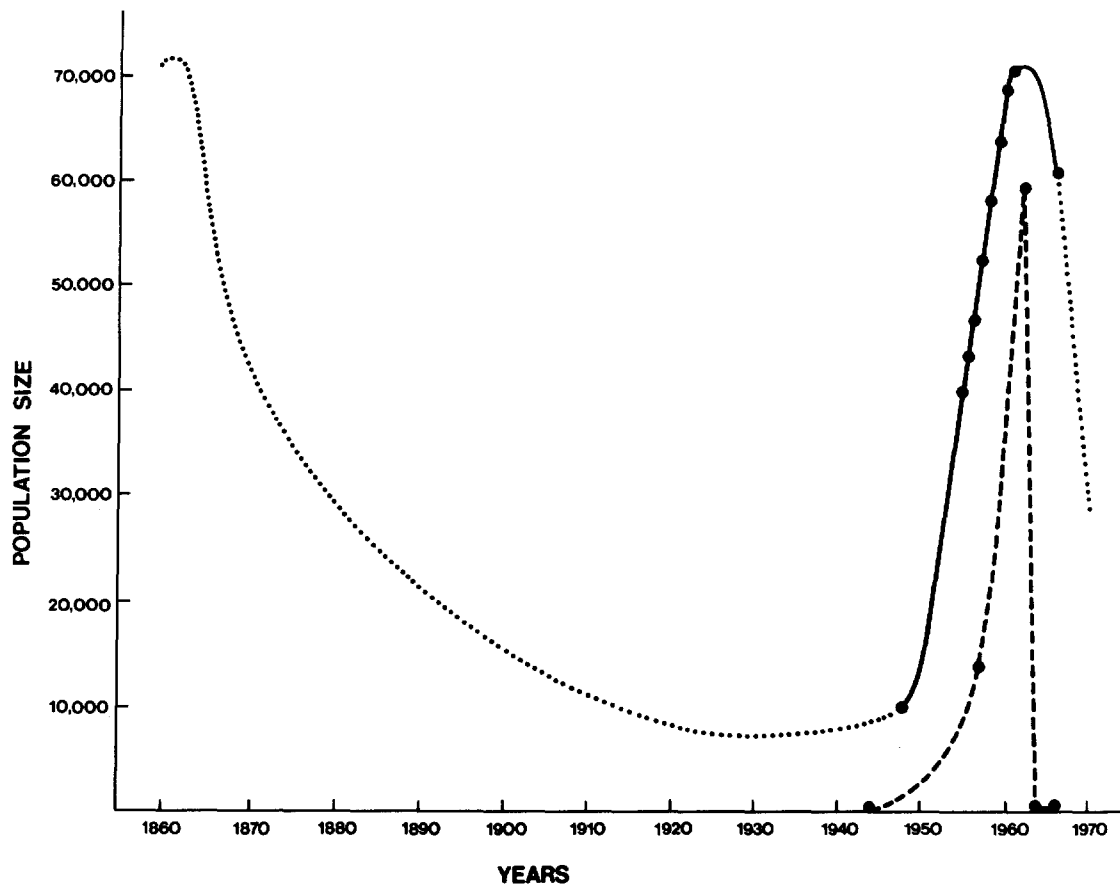


Fig. 1.—Population growth of the Nelchina caribou herd. The solid line represents documented population growth. The dotted line represents assumed population growth. *Lower curve*, population growth curve (dashed line) of the St. Matthew Island reindeer herd (from Klein, 1968).

in the mid-1800's could not be determined. However, due to the similarities of herd distribution in the 1860's and 1960's, i.e., caribou saturated suitable habitat in the Copper and Susitna River basins during both periods (Figs. 2 and 3), it was assumed that total numbers must have been quite similar.

One of the most interesting aspects of the population growth curve is the time between

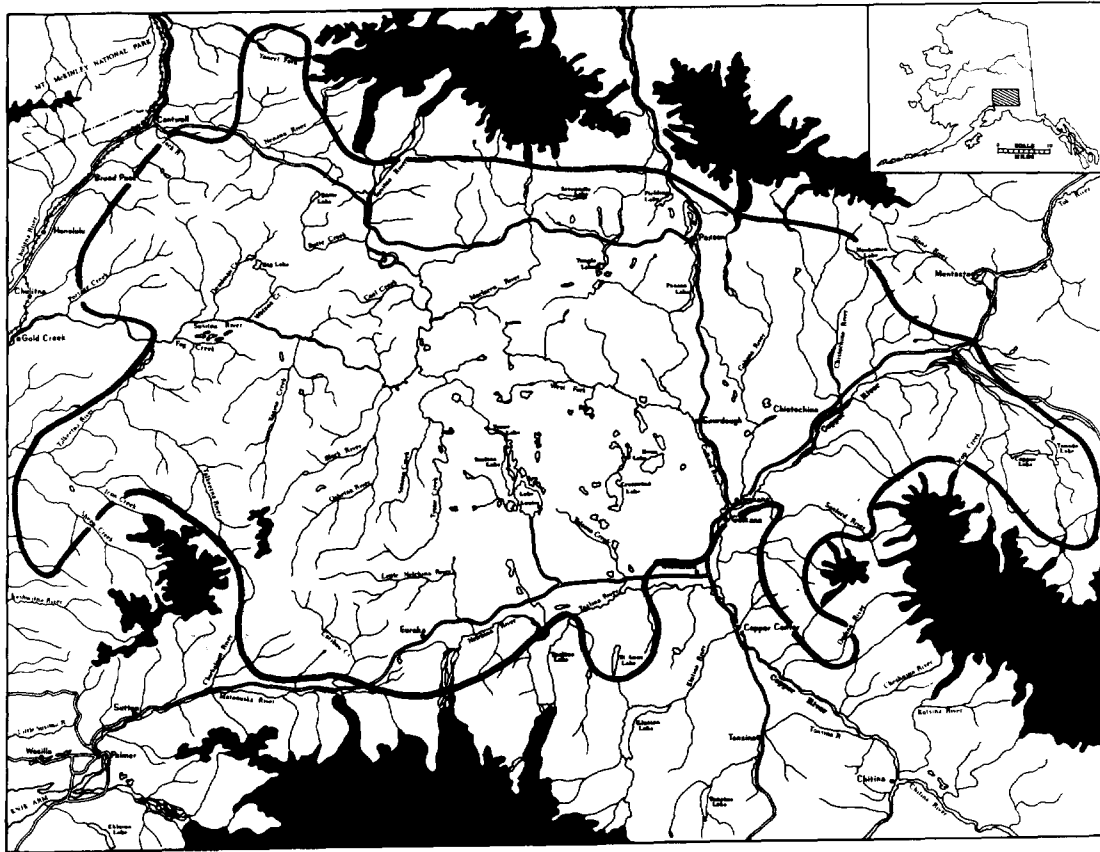


Fig. 2.—Range of the Nelchina caribou herd 1960-1970.

the two peaks. In the lower portion of the curve the population was relatively small and vast portions of the Copper River Basin were unoccupied by caribou (Fig. 4). With caribou distribution restricted for over 50 years, major portions of the range undoubtedly recovered from previous periods of heavy use. Palmer and Rouse (1945) concluded that 20 to 40 years are required for depleted lichen ranges to return to a robust condition.

Caribou appear to be unique among cervids in demonstrating oscillations with a time periodicity approaching 100 years. This is not to imply that caribou have a fixed cycle frequency. Any caribou population may be subject to random environmental factors that could cause the oscillations of the population to vary in both wavelength and amplitude. For example, the seasonal influx of large numbers of caribou from the McKinley and Fortymile herds in the early 1900's may have delayed the increase of the Nelchina herd by altering plant succession on portions of its range. Such shifts into vacant ranges of adjacent populations have also occurred in other areas. The Porcupine caribou herd of the eastern Brooks Range shifted into the range of the Arctic caribou herd in the early 1900's (Harrison, 1908; Porsild, 1945). This occurred at a time when the Arctic herd was greatly reduced and remained throughout the year in a small portion of the western Brooks Range (Birch, pers. comm.; Skoog, 1968). Around 1920 the Porcupine herd shifted eastward and later as the Arctic herd increased it expanded into the central Brooks Range again (Hemming, 1971).

With vast areas of productive caribou habitat, population growth and dispersal can proceed for long periods of time. In areas where the total available habitat is limited, initial



Fig. 3.—Approximate range of the Nelchina caribou herd 1848-1885. Prepared from descriptions of Glenn and Abercrombie (1899), Allen (1900), Rohn (1900) and Skoog (1968).

population growth can be expected to be quite similar to that of caribou herds with more open ranges, as suggested in Figure 1. However, if saturation time is short because of small areas of suitable habitat and rigid boundaries, social and feeding pressures can be relieved only temporarily by mechanisms of seasonal segregation, dispersal and emigration.

A classic example of the response of reindeer to a restricted range was described by Klein (1968) from his studies of an introduced reindeer population on St. Matthew Island in the Bering Sea.

St. Matthew Island has a land area of only 332 km² (128 mi²) compared with the Copper River-Upper Susitna River basins that encompass over 52,000 km² (20,000 mi²) and the latter contains many potential overflow areas. Twenty-nine reindeer were introduced to St. Matthew Island in 1944. The herd reached a peak of 6,000 in the summer of 1963 and a die-off the following winter reduced the herd to 50 animals. The St. Matthew reindeer population growth curve (Fig. 1) illustrates the similarity of initial herd growth with that of the Nelchina herd. A similar pattern of population growth and decline was reported on the Pribilof Islands by Scheffer (1951).

Assuming the Nelchina herd is typical of other herds on the Alaska mainland, the total range occupied by a herd during any given year should reflect the relative abundance of the population.

The current decline of the Nelchina herd appears inevitable and natural, but the developments of man may control the magnitude of oscillations and movements in the future.

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A PARTIAL ANALYSIS OF THE CURRENT POPULATION STATUS OF THE NELCHINA CARIBOU HERD

G. N. Bos

Alaska Department of Fish and Game
Anchorage, Alaska

ABSTRACT—Population data obtained from studies of the Nelchina caribou herd were compared for the periods before and after 1963. A census conducted in 1967 indicated a possible 28 per cent reduction in the population from the 1962 level. Evidence derived primarily from analysis of sexed and aged samples of the harvest from 1963 to 1971 suggested reduced recruitment of yearlings to the adult population. Consistently large harvests by hunters have resulted in greater adult mortality rates since 1963.

Population studies of the Nelchina herd were initiated in 1949 and gradually expanded in scope during the early 1950's. From 1955 to 1962 continuous studies and standardized techniques yielded the largest body of information available on the population. However, with expansion of caribou studies to other herds in the state, emphasis on the Nelchina caribou was sharply reduced from 1962 to 1967. Between 1967 and the present time some studies were carried on with a more active renewal of work in 1970, concurrent with a growing concern over the status of the population.

Caribou have occupied the Nelchina Basin since at least the mid-1800's (Skoog, 1968). Overlapping of ranges with 'overflow' elements of the large Steese-Fortymile and McKinley herds (see Fig. 1 in LeResche, this volume) from the north occurred in the late 1920's but the effects on the Nelchina population are unknown. There were no estimates of the population available until 1945 when 10,000 animals were estimated (Alaska Game Commission Report, cited in Skoog, 1959). From 1948 to 1954 population estimates were made periodically, ranging from 5,000 in 1948 (Nelson *et al.*, 1950) to 13,200 in 1954 (Chatelain, 1954). In February 1955 the population was estimated at 40,000 by means of a systematic aerial census (Watson and Scott, 1956). This estimate was corroborated by a similar census in 1956 which yielded a minimum estimate of 36,200 (Skoog and Scott, 1956). This work pointed out the gross underestimates made in preceding years. In February 1962 an aerial census using stratified random sampling of selected concentration areas with complete coverage of additional winter ranges resulted in an estimate of $71,000 \pm 11,867$ (Siniff and Skoog, 1964). In 1967 a direct photo count-extrapolation census technique resulted in an estimated population of 61,000 (Hemming and Glenn, 1968). Attempts to duplicate the photo census in 1968 and 1971 were unsuccessful. The present population level is unknown, but I think it is considerably reduced from the 1967 level. Postcalving studies and supporting reconnaissance flights in 1972 suggest a population of less than 10,000 caribou in the calving area.

DECLINE OF THE NELCHINA POPULATION

Until 1962 the trend in population levels was clear. Various censuses all indicated an expanding population. Calf production and survival were good, natural mortality was low and the kill by hunters was well below recruitment levels (Skoog, 1968). On the basis of

Skoog's figures, increments for the years 1955 to 1962 averaged 8.5 per cent annually.

After 1962, cursory field studies indicated adequate calf crops. In the absence of other data, the population was assumed to have remained large. The 1967 census provided the first major indication that the population had declined. To compare the estimates from 1962 and 1967 some adjustments were necessary to compensate for the seasonal differences in the timing of the counts and for differences in locations of census areas. The 1962 census estimate included an unknown contribution of animals from the Mentasta herd. If the 1964 population estimate of 5,000 Mentasta caribou (Lentfer, 1965) is subtracted from the 1962 Nelchina estimate of 71,000 and the remainder subjected to sex-specific mortality rates as suggested by Skoog (1968), the June, 1962 Nelchina herd may have numbered 64,100 caribou, excluding calves. The June 1967 estimate represented 45,700 caribou, excluding calves, or a 28 per cent reduction from the 1962 level. If the low and high ranges of the 1962 estimate are used in the calculations the corresponding range in the apparent reduction is 11 per cent to 38 per cent.

Biologists flying reconnaissance missions to determine distribution of the herd have in recent years consistently reported difficulties in locating large numbers of animals. Rough estimates of postcalving concentrations in 1971 and 1972 were progressively smaller than those made in 1967. Subjective opinions of a lowered population should be tempered by the possibility that a lack of familiarity with the Nelchina population, occasioned by rapid succession of project personnel, may have resulted in underestimations similar to those of the early 1950's. Lack of data, particularly photo-census data, precludes a determination of the current population level, but I believe a decline has occurred and may be continuing.

CAUSES OF DECLINE

Egress.—One possible reason for reduced population levels is egress of significant numbers of Nelchina caribou to other ranges. This is a plausible cause but one which has not been well documented. In the late 1950's and early 1960's the large and increasing population was exhibiting progressively more erratic and far-ranging migration movements to winter ranges. Movements of caribou beyond established ranges occurred each winter from 1961-62 to 1966-67 (Glenn, 1967; Lentfer, 1965; McGowan, 1966; Skoog, 1963a, 1963b). The 1966 movement was thought to involve large numbers of caribou which did not return (Glenn, pers. comm.).

If large numbers of caribou did move permanently from the Nelchina range, they were probably absorbed by the Fortymile herd to the north since ingress to unoccupied ranges probably would have been observed. Movement to the McKinley-Minchumina area is another, but less likely, possibility.

Lowered Recruitment.—Examination of the sex and age structure of the harvest since 1956 provides indirect evidence that the recruitment of yearlings to the population has been low since the mid-1960's. Figures 1a, b and c show that the proportion of females in the prime age category (2-5) has decreased generally since 1963 while the proportion of older females has shown a marked increase. Prior to 1963, trends in proportions are less apparent and suggest relatively stable age class sizes.

The female segment of the sample two years old or older provided the best information on past reproductive success because it was the least biased sex and age segment representing the population age structure. Disproportionately fewer calves and yearlings of either sex were taken by hunters in comparison to adults, and a bias existed in the specimen collection process, resulting in underrepresentation of calves and yearlings in the sample. Among males in the population only those three years old and older were thought to be accurately represented in the harvest. However, survival of males over five years was low and sample

sizes were not sufficient to utilize males in analysis of past recruitment.

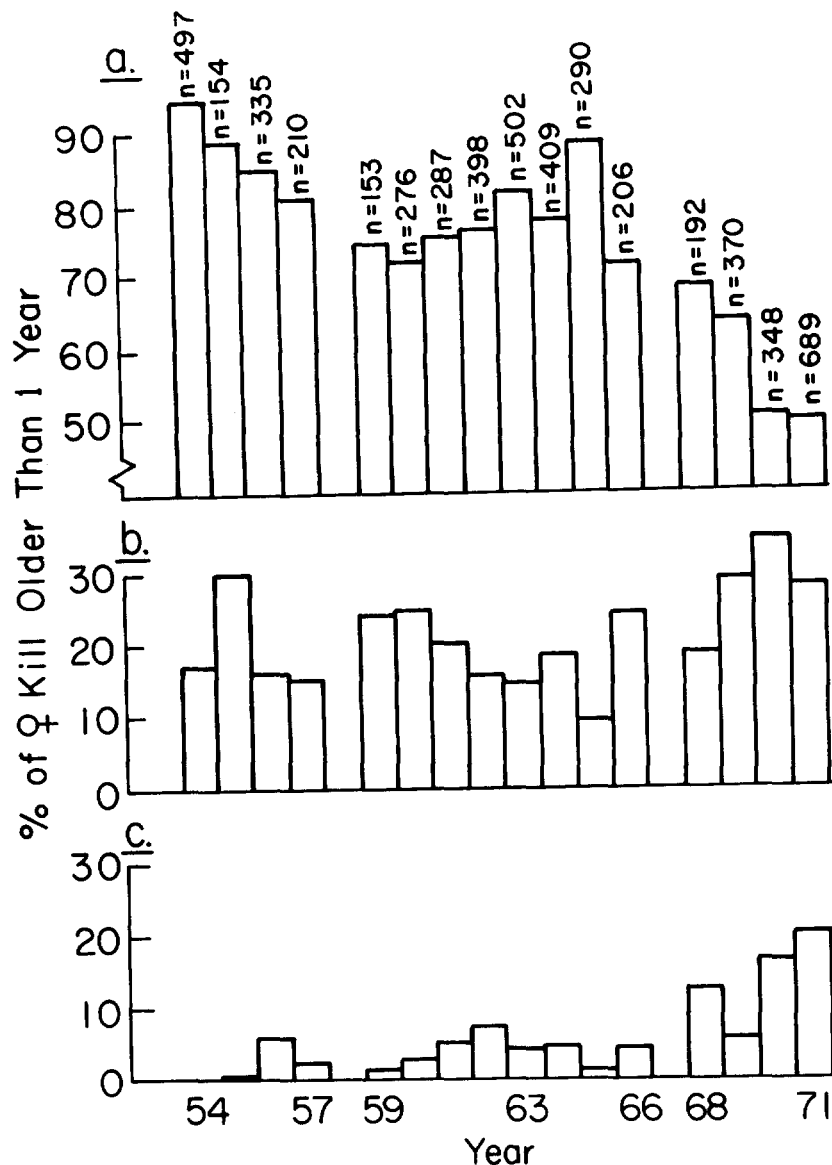


Fig. 1.—(a) Percentage of females aged 2-5 years in the kill of females older than one year. Note: insufficient data available for 1958 and 1967; data for 1957 and 1959 classified as 2-6 years; data for 1960, 1961, 1962 classified as 2-7 years. (b) Percentage of females aged 6-9 years in the kill of females older than one year. Note: insufficient data available for 1958 and 1967; data for 1957 and 1959 classified as 7-9 years; data for 1960, 1961, 1962 classified as 8-12 years. (c) Percentage of females aged older than 10 years in the kill of females older than one year. Note: insufficient data available for 1958 and 1967; data for 1960, 1961, 1962 classified as 13 years and older.

An examination of the percentage of two-year-old females in the kill is also of interest. Figure 2 presents percentages of two-year-old females in the harvest of females two years

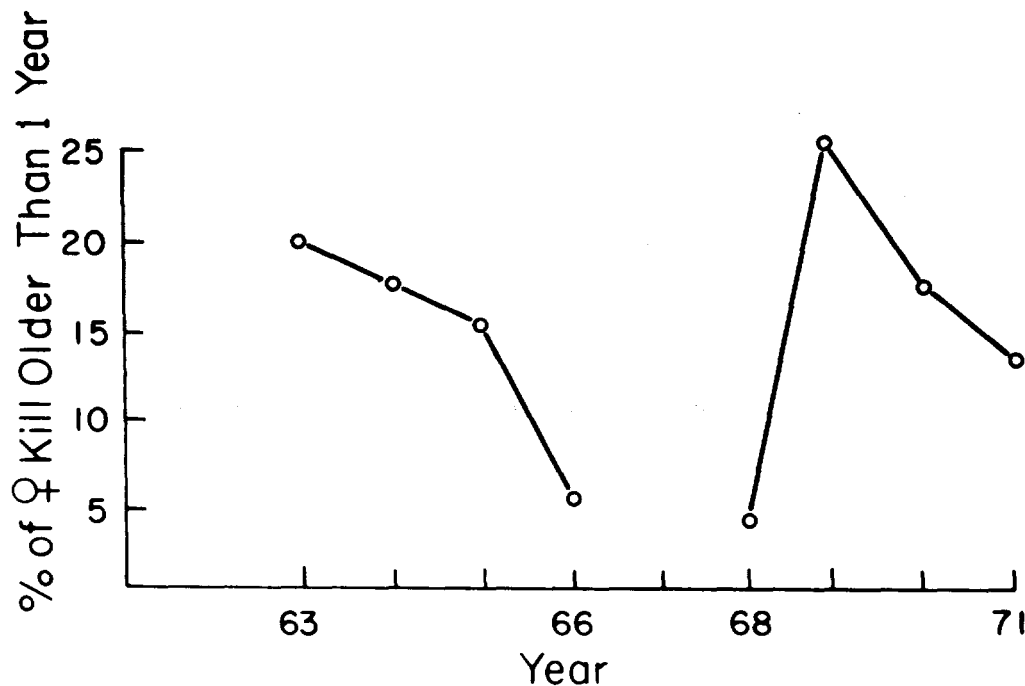


Fig. 2.—Percentage of 2-year-old females in the kill of females older than one year, 1963-1971.

old and older. The data suggest low production or survival of calves during 1964-65, 1966-67, and high values during 1967-68. Few accessory data are available. However, a spring survival count in 1967, considered by Hemming and Glenn (1968) as unrepresentative of the population, yielded only 4.7 calves:100 cows (adjusted to June base) with $n=699$ (Alaska Dept. of Fish and Game, unpubl. data). The high percentage of two-year-old females in 1969 corresponds well to the record calf:cow ratio of 57 calves:100 cows obtained during fall composition counts in 1967 (Hemming and Glenn, 1968).

Calf Production.—Natality rates have been assumed to equal fertility rates in past studies. Skoog (1968) determined that 60 per cent of all females in the fall give birth to calves in the spring. Greater proportions of older age classes of females now suggest an increased population fertility rate for females of 69 per cent. However, it is not known whether natality rates have remained high. Deterioration in the Nelchina range quality (Pegau, 1972) may affect fetal survival rates, or more likely, females stressed by nutritional deficiencies may give birth to weak calves or may fail to lactate sufficiently to meet the nutritional requirements of the neonates. During Skoog's studies prior to 1963 there was little evidence of prenatal mortality.

Calf Mortality.—Mortality of calves from all causes during the first year is estimated by taking the difference between observed calf:cow ratios in April and the assumed calf:cow ratio of 60:100 (estimated natality) of the preceding June. Skoog determined an average mortality of calves of 40 per cent (survival of 60 per cent) for the years 1955-62. Calf counts conducted in the late winters of 1970, 1971 and 1972 yielded survival estimates of 45, 52 and 24 per cent, respectively, or an average survival of 40 per cent, assuming 60 per

cent natality.

Of mortality factors operative on calves, weather and wolf predation are the most likely to have depressed recruitment of yearlings since 1963. Weather may affect calf survival in several ways. Deep long-lasting snow and inclement weather during the calving period may cause significant neonate mortality. Deep snow can delay the calving migration forcing cows to calve enroute. This was the case in 1962 and 1964 when calving along migration routes and in the northwest sector, away from traditional calving grounds was recorded (Skoog, 1963b; Lentfer, 1965). The calving movement was again disrupted in 1971 by late snow cover, and in 1972 the worst recorded winter in the history of the Nelchina Basin resulted in the latest spring migration on record. Losses of calves born under such conditions may be high due to difficult traveling conditions and dangerous river crossings. Postcalving calf counts in 1972 indicated below average calf proportions in postcalving groups of caribou — 22 per cent calves as compared to the average of 30 per cent. Inclement weather at birth may cause neonate mortality but no data are available for Nelchina caribou. Kelsall (1968) found that inclement weather during calving was an important mortality factor on newborn calves in Canada. No information is available from the Nelchina herd regarding the effects of winter severity on the survival of calves in their first winter.

Nelchina wolf populations have increased substantially over pre-1963 levels (see comments on wolf population below). Greater losses of calves to wolves are a logical consequence.

Increased Adult Mortality.—Skoog (1968) reviewed the factors contributing to mortality of adults. Hunting and wolf predation were considered the most important mortality factors. He estimated losses of adults to all other causes at 4 per cent. No new data have been acquired to qualify this estimate.

For the hunter harvest of Nelchina caribou from 1955 to 1962, Skoog (1968) determined an average kill of 8 per cent of the estimated adult population, assuming 3 per cent of the harvest was calves. This kill rate estimate may have been slightly high however, as percentages of calves in sexed and aged kill samples for these years averaged 7.4 per cent ($n=3,036$). Since 1962, 7.2 per cent of the known harvest has been calves ($n=3,677$). If calves comprised 7 per cent of the kill, the average annual loss of adults to hunting from 1955 to 1962 was 7 per cent (Table 1).

The absolute sizes of harvests have generally increased in recent years over those occurring prior to 1963. Longer hunting seasons, increased hunter pressure, increased use of off-road vehicles and the advent of snow machines are responsible for more consistently high harvests. Table 1 presents harvest information for the period 1955-1973. In the table, the estimated adult population has declined from 71,000 in 1962 to 48,000 in 1967 and to 10,000 in 1972. Thus the relative losses to the adult segment of the population increased greatly as the harvestable base presumably declined.

Emphasis needs to be placed on the relationship of recruitment to adult mortality on the female side of the population, for it is the maintenance of the breeding female population that determines population levels in a polygamous animal such as the caribou. For example, if the natality level is 60 per cent and if 45 per cent of new yearlings are females (Skoog, 1968), then a calf survival rate of 40 per cent through the first year allows for only 10.8 per cent recruitment of yearlings to the female population. Although the population presumably declined more or less steadily from 1967 to 1972, the relationship of hunting mortality on the female population to the rate of recruitment of yearling females can be illustrated by assuming that the total population held at 48,000 through 1971. The harvests of 1969 and 1971 would thus have accounted for 11.5 per cent and 12.4 per cent, respectively, of the female populations. The likelihood of a population much reduced from

TABLE 1.--Nelchina caribou harvest statistics 1955-1972.

Year	Estimated adult population ¹	Adult female (%) ²	Estimated harvest of adults ^{3,4}	Kill rate %	Adult female in kill (%) ⁴	Kill rate for female %
1955-56	40,000	22,800 (57)	3,720	9.3	1,004 (27)	4.4
1956-57	44,000	25,500 (58)	3,250	7.3	910 (28)	3.6
1957-58	48,000	28,300 (59)	2,320	4.8	580 (25)	2.0
1958-59	53,000	31,300 (59)	3,250	6.1	- -	-
1959-60	59,000	34,800 (59)	3,720	6.3	1,116 (30)	3.2
1960-61	64,000	37,800 (60)	5,110	8.0	1,737 (34)	4.6
1961-62	69,000	41,400 (60)	7,440	10.8	3,125 (42)	7.5
1962-63	71,000	43,300 (61)	3,250	4.6	1,008 (31)	2.3
1963-64			5,860		2,285 (39)	
1964-65			7,440		2,530 (34)	
1965-66			6,600		2,178 (33)	
1966-67			5,110		1,482 (29)	
1967-68	48,000	32,200 (67)	3,720	7.8	1,302 (35)	4.0
1968-69			4,650		1,860 (40)	
1969-70			7,250		3,698 (51)	
1970-71			5,950		2,202 (37)	
1971-72			7,550		4,001 (53)	
1972-73	10,000					

¹February population estimates for 1955-62 from Skoog (1968); for 1967 extrapolated from data in Hemming and Glenn (1968); for 1972 from field estimates (see text).

²Adult female percentages for 1955-62 from Skoog (1968); for 1967 and 1971 from fall composition counts.

³Harvest of adults taken as 93% of total estimated harvests based on sex and age samples of kill n=6,713.

⁴Kill estimates and sex ratios of the harvest as reported in U. S. Fish and Wildl. Serv. Fed. Aid in Wildl. Restoration Quarterly Prog. Rpts. and Job Compl. Rpts. 1955-1959, and Alaska Dept. of Fish and Game, Fed. Aid in Wildl. Restoration Project Rpts. 1960-72.

48,000 during these years and the contributing effects of natural mortality would serve to make greater losses to the female population probable. Thus it is apparent that harvest levels of recent years operating on reduced population levels could easily approach or exceed annual female recruitment levels.

Wolf predation on Nelchina caribou has long been a controversial subject and a factor difficult to assess. Skoog (1968) used observations by Burkholder to establish a predation rate of 12 caribou/wolf/year on the Nelchina range, where moose make up a substantial portion of the wolves' diet. Skoog estimated an average annual predation rate of about two per cent of the caribou population for the years 1955-1962.

Nelchina wolf populations were increasing rapidly during Skoog's studies and continued to increase after 1962. According to Rausch (1968) the wolf population increased from about 160 in 1962 to 400-450 in 1965, then declined to about 300 in 1967. Since 1967 wolf populations have remained at fairly high levels, estimated at about 300 (R. A. Rausch, pers. comm.).

The net effect of a larger wolf population and a smaller caribou population was probably a greater predation pressure on the caribou herd, despite allowance for density-dependent relationships.

SEX AND AGE STRUCTURE

Skoog (1968) determined sex ratios for neonate calves, six-month-old calves, yearlings and two-year-olds at 51, 54, 55 and 50 per cent, respectively, based on reproduction and calving ground studies, sex and age ratios obtained from field classification counts and analysis of the hunter harvest. These figures are assumed to be correct in lieu of more recent data, but the need for reassessment is recognized.

For animals three years of age and older, sexed and aged samples of the harvest provided the best data for estimating sex and age ratios. These ratios are indicated in Tables 2 and 3 as hypothetical sex and age structures for the Nelchina population in the early 1960's and early 1970's, respectively. Although the sex ratios of younger animals are assumed to have remained constant since the early 1960's, the sex ratios of older age classes and relative proportions of all age classes for each sex have shown changes in recent years from the indicated structure of the early 1960's. These changes are a result of hunting and lowered recruitment of yearlings.

EFFECTS OF HUNTING ON SEX AND AGE STRUCTURE

Sex-differential natural mortality is responsible for some imbalance in sex ratios in Alaskan caribou (Skoog, 1968). With Nelchina caribou the most apparent effect of hunting on the population has been to accentuate the natural imbalance in the sex ratio. Hunters show strong preference for adult bulls with large antlers. This strong selection for older males has effectively reduced their numbers in the population, as shown by sex ratios obtained in fall composition counts. The percentage of males of all ages in the population dropped from 42 per cent in 1962 to 30 per cent in 1971. If only animals older than yearlings are considered the disparity in sex ratios is greater. In 1962 an estimated 35 per cent of animals two years old and older were males; in 1971 only 18 per cent were males (Table 2 and 3). Despite a low relative abundance of males, sex ratios in the kill continue to reflect selection by hunters for adult males (Table 1).

The imbalance in the sex ratio has in turn affected sex ratios in the kill (Table 1). The proportion of females in the kill has grown in the past decade for two reasons. First, longer seasons and increased use of snow machines has resulted in more hunter effort during winter

TABLE 2.--Approximate sex and age structure of Nelchina herd during late autumn, early 1960's.

Age class	Both sexes	No. males	% of total males	% males in class	No. females	% of total females	% females in class
Calf	210	113	27	54	97	17	46
1 year	170	93	22	55	77	13	45
2 years	150	75	18	50	75	13	50
3-5 years	350	108	25	31	242	42	69
6-9 years	100	29	7	29	71	12	71
10+ years	20	4	1	20	16	3	80
All ages	1,000	422		42	578		58
1 year +	790	310	73	39	480	83	61
2 years +	620	216	51	35	404	70	65
3 years +	470	141	33	30	329	57	70

Note: On basis of 1,000 animals. Table from Skoog (1968).

TABLE 3.--Approximate sex and age structure of Nelchina herd during late autumn, early 1970's.

Age class	Both sexes	No. males	% of total males	% males in class	No. females	% of total females	% females in class
Calf ²	191	103	34	54	88	13	46
1 year ³	148	81	26	55	67	10	45
2 years ⁴	107	54	18	50	53	7	50
3-5 years ⁵	331	51	17	15	280	40	85
6-9 years ⁵	151	13	4	9	138	20	91
10+ years ⁵	72	3	1	4	69	10	96
All ages ¹	1,000	305		30	695		70
1 year +	809	202	66	25	607	87	75
2 years +	661	121	40	18	540	78	82
3 years +	554	67	22	12	487	70	88

¹Average of sex ratios obtained in 1971 and 1972 fall composition counts (30.5% male both years).

²Data from 1969-72, calves averaged 19.1% of total animals in fall composition counts.

³Yearling percentage from spring survival counts: average of 27.5 short yearlings per 100 cows from data 1970-72, assuming 1) 80% of noncalves are cows, 2) 45% of short yearlings are female, 3) ratio of short yearling females to adult females remains constant until fall. Thus $27.5 \times .45 = 12.4$ short yearlings:100 cows = 11.0% short yearling females. Male short yearling number determined by using 55:45 yearling sex ratio.

⁴Two-year-old female number obtained by use of female survival estimate $\hat{S} = .798$ female yearling class. Similarly, for males $\hat{S} = .663$.

⁵3-5, 6-9, 10+ age class proportions, by sex, taken from aged-kill sample from 1963 to 1971, n=2,507.

Note: Table on basis of 1,000 animals.

months when most hunters are unable to differentiate between sexes. Second, a decreasing availability of males has resulted in a compensatory increase in the take of females.

Hunting has also effected a difference in the age structure of the sexes. Among females there is selection by hunters in favor of adults over calves and yearlings, as most hunters select for the largest animals available. Age classes of females two years and older are not differentiated by hunters and are probably taken in direct proportion to their abundance in the female population. Age class proportions of females in the harvest have shown a trend to older-age animals in recent years (Fig. 1a, b, c). This suggests lower recruitment as previously discussed.

In the male segment of the kill, a different situation prevails. With relatively few older bulls and a low male to female ratio in the herd, the age structure of the males in the kill has lowered. This is because the number of male yearlings, while low in terms of the total population, has been fairly high in relation to the number of older males in the herd.

SUMMARY

The Nelchina population underwent rapid expansion between the late 1940's and the early 1960's, reaching a peak of about 70,000 in 1962 or 1963. After 1963 the herd began a decline that has continued to the present day with a current estimated level of 10,000 animals.

At the time the herd was large and increasing, large harvests under liberal seasons and bag limits were unable to offset annual increments. The initial stages of the decline were probably effected by large emigrations of caribou to other ranges. Once the population was reduced by emigration to the point that mortality exceeded recruitment the decline was established and large harvests accelerated the rate of reduction. Poor recruitment of yearlings was an important contributing factor.

The sex and age structure of the herd has shown progressive changes due to hunter selectivity and lowered yearling recruitment. There is a low bull:cow ratio in the population, especially if only breeding adults are considered. The age structure of the female segment is dominated by older animals whereas the male segment is composed of predominantly young animals. The large proportion of females in the herd endows the population with a high potential for production of young and rapid recovery of the herd. Whether this in fact occurs remains to be seen.

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AGE AND SEX STRUCTURE IN A HUNTED POPULATION OF REINDEER IN NORWAY

Egil Reimers
The Norwegian State Game Research Institute
Norway

ABSTRACT—In Rondane 96 per cent of all males harvested are three years of age or younger. No males survive their fifth year of life. Corresponding figures for females are 57 per cent three years or younger, while 4 per cent survive to their tenth year of life. The reason for these age distributions is that hunters selectively harvest animals of large body and antler size. This selective hunting leads to a distorted sex ratio of approximately one male to eight females in the reproductive group (1+ years). There are some indications that this age and sex distribution is responsible for decreased calf production in this area. Comparing the Rondane herd with other wild reindeer herds where nutritional status and sex ratio varies indicates that a distorted sex ratio combined with poor nutrition might be limiting breeding success.

Wild reindeer are confined to alpine areas in southern Norway. Presently the remaining 25,000 animals are distributed in 13 hunting areas which are more or less separated by topographical barriers or by man-made obstacles like railroads, highways and settlement. The different areas are generally small, ranging from 8,000 km² to less than 1,000 km², and even central parts of the areas are easily accessible due to a fairly dense mountain road system.

The reindeer hunt starts August 25 and ends September 25, a couple of weeks before the rutting season. Until recently there has been no restriction as to sex or age of the animals hunted, as long as bag limit has been regarded. This policy together with hunters' preferences for males has lead to a selective male hunt. The open alpine situation and the accessibility of the areas have made possible intensive male harvests which have resulted in varying degrees of distorted sex and age structures in our reindeer populations. This paper deals with an extreme such situation and speculates on consequences which might be a result from it.

STUDY AREA

Rondane reindeer area (1,500 km²) is located in the northern part of south Norway (Fig. 1). The climate is continental with low summer and winter precipitation, which allows for a well developed lichen cover throughout most of the area. There are few lakes, streams, and bog areas and spring and summer ranges are apparently poorly developed. Mammalian predators are absent from the area except for some wolverine (*Gulo gulo*) stragglers.

Data from hunting statistics and surveys (Table 1) indicates that the overwintering population of reindeer has numbered approximately 1,400 to 1,500 animals from the latter part of the 1950's until 1964. According to local authorities some 1,000 reindeer immigrated during the winter 1966-67 from the adjacent Snøhetta area where the ranges were heavily overgrazed due to overpopulation (Gaare, 1968; Reimers, 1969a, b). However, it is questionable whether these 1,000 animals remained in the Rondane area, because they

males and females in the harvest.

TABLE 1.--Population estimates and hunting statistics
for the Rondane reindeer herd.

Year	Population estimates* February-April	Harvest (Aug.-Sept.)		
		Total	Males	Females
1956		251	198	53
1957		305	244	61
1958				
1959				
1960	1,540	231	166	65
1961		311	209	102
1962	1,345	270	187	83
1963		277	210	67
1964	1,399	263		
1965		276	193	83
1966		265	174	90
1967	2,500	286	208	78
1968	2,300	262	173	89
1969	2,450	521	344	177
1970	2,360	571	282	289
1971	2,550	652	341	311
1972	1,975			

*Based on aerial and ground surveys.

RESULTS AND DISCUSSION

Males have a more rapid growth and larger body (and antler) size than females (Fig. 2). Consequently both meat and trophy hunters will select males unless hunting licenses are specific as to the sex and age to be taken. No regulation in this sense has been carried out in Rondane and more than twice as many males as females have been killed up to 1970 (Table 1). The hunting pressure is obviously hitting the mature male age classes most intensively. Figure 3 confirms this in that only 4 per cent of the males survive till an age of four years. Younger age classes are also heavily reduced. Only 21 per cent of the males survive until three years of age and 70 per cent until two years of age. The hunting pressure on calves are, for obvious reasons, light and both sexes are represented in the harvest in a 1:1 ratio.

Corresponding figures for females show that 42 per cent survive until an age of four years and approximately 4 per cent are still alive at nine years old. The reason for the more evenly distributed female age classes is to be sought in the lack of selective criteria among females three years of age and over. Females reach an ultimate body size at an age of two to three years. Dressed weights remain the same from this age and throughout life, 14-16 years of age (Reimers, 1969, 1972). For most hunters it is impossible to discriminate between age classes in the female segment 3+ years of age. The age distribution of females in this segment therefore reflects the relative number of 3+ years females in the population. Knowing the realized natality rate in the past, this information provides relevant data for sex ratios and natural mortality.

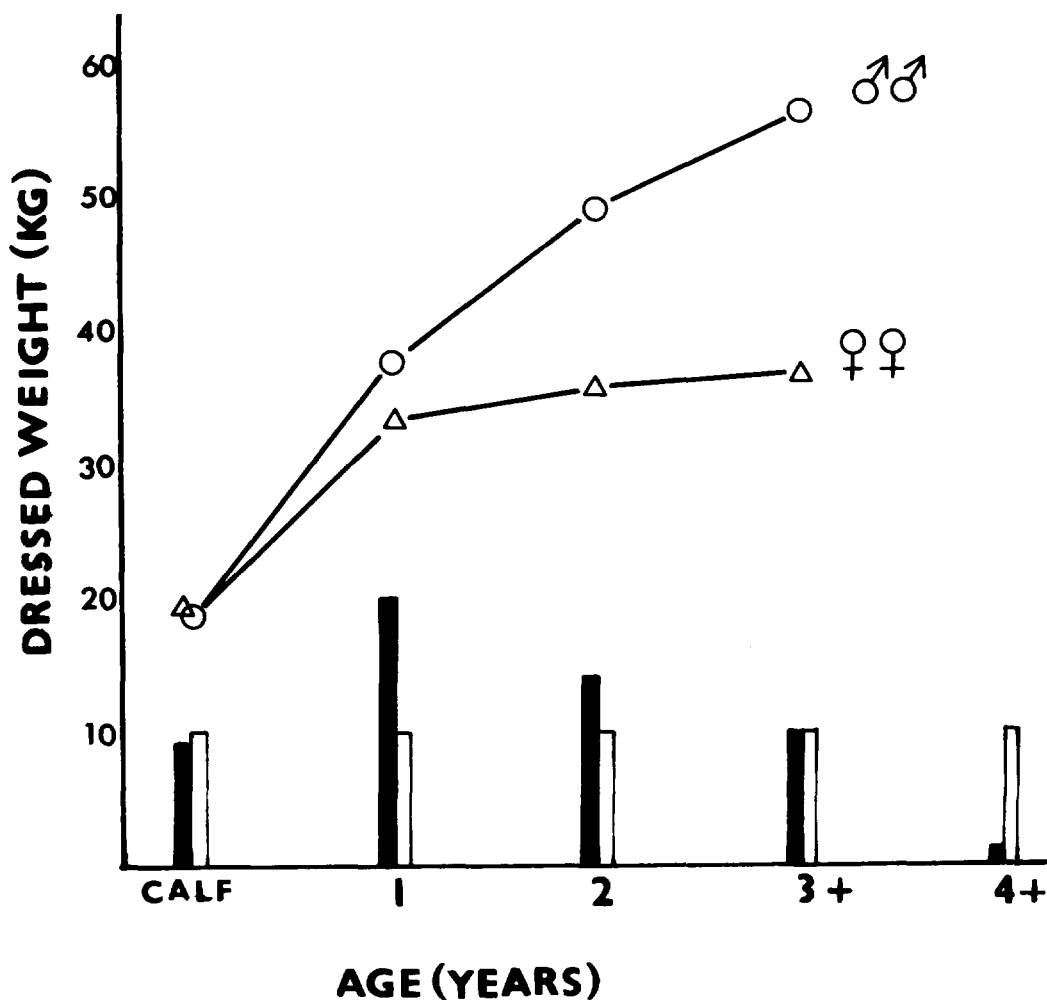


Fig. 2.—Dressed weights of male and female reindeer in Rondane. Bars (Black=males) indicate sex ratios in harvests.

One important question is how effectively will an unspecified harvest reduce the number of males and what consequences might arise from so few and such young males in the breeding population.

Figure 2 shows that among yearlings an average dressed weight difference of 4 kg in favor of males results in twice as many males being harvested as females. In areas where ranges allow for larger body size and dressed weight differences are more pronounced between sexes, such as North Ottadalen (Reimers, 1972), male and female yearlings were

harvested in a ratio 12:1.

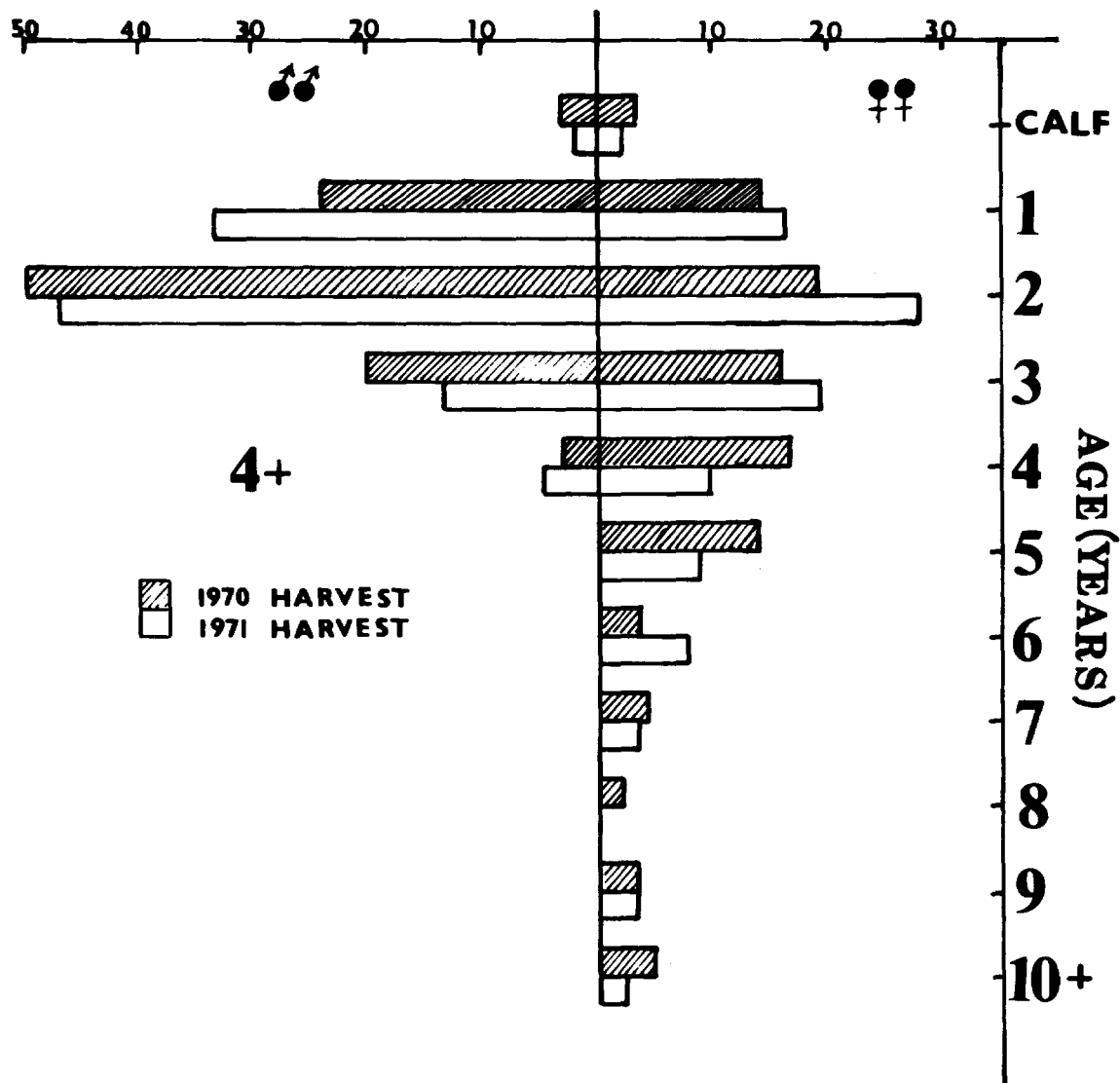


Fig. 3.—Age distribution (in per cent) of males and females in sample material from harvest.

In Rondane the sex ratio (males:females) in the harvest was 2.3:1 among two year old animals and 1:1 among three year olds. Among four year and older animals the ratio was 1:10 in favor of females. This clearly shows the impact of selective male hunt. Obviously there is limit to how distorted the sex ratio gets before hunters have to harvest females in order to get their animals. In that situation adult females will have a similar or larger body size than most of the males. This situation seems to have been reached in Rondane in 1970-71 where males and females are harvested in about equal numbers (Table 1). The sex ratio among one year and older animals in 1971, after the hunting season, was approximately 1:8 in favor of females (Table 2). If the yearling males are subtracted from the male segment the sex ratio during breeding season was 1:27 in favor of females. In a

TABLE 2.--Per cent lactating females in sample material from harvest related to nutritional status and sex ratio in the breeding population.

Area	Sampling period	Nutritional status in sampling period	Dressed weights (kg) of 1 year males	Approximate sex ratio last year of sampling period		No. of females in sample	% lactating females in sample
				Males (1yr.): Females (1yr.)	Males (2yr.): Females (1yr.)		
Snøhetta	1963-65	Poor	28(27)**	1:5.0	1:13.5	477	27
Hardangervidda	1969-70	Poor	27(48)	1:2.3	1: 4.1	559	60
Rondane	1970-71	Fair	38(62)	1:8.0	1:28.0	174	50
South Ottadalen	1967-71	Good/fair	44(23)	1:3.4	1: 7.1	76	55
North Ottadalen	1967-71	Good	53(31)	1:1.1	1: 1.7	116	62

*Females 2 years and older.

**No. of animals weighed.

polygamous species like *Rangifer* an alteration of the sex ratio towards a buildup of the female segment would increase calf production in a stable population. I have tried to simulate the population development in Rondane from 1959 up to 1972 (overlooking the population estimate in 1967 where 1,000 animals should have moved into the area). On the basis of population estimates and hunting statistics it seems that we had a calculated annual rate of increase before hunting of 10 per cent in 1959-60, increasing to 18 per cent in 1961-62 and 25 per cent in the period 1963-67. From 1968 it shows a drop to 20 per cent through 1970 and down to 3 per cent in 1971. The dramatic drop to 3 per cent is highly improbable and the population decrease from 2,550 in 1971 to 1,975 in 1972 must partly be attributed to emigration to the adjacent Knutshø area. How reliable this simulated population trend is remains questionable. However the possibility exists that there is a relationship between decreased production of calves and the extremely distorted sex and age distribution.

Table 2 relates sex ratios and nutritional status to percentage of lactating females two year and older in harvest. Table 3 indicates that the percentage of lactating females

TABLE 3.--Percentage lactating females in sample material from harvest during years of populations decrease.

Area	Year	% lactating females* in harvest	Population size (after calving)	
			Year	No. of animals
Snøhetta	1963	36	1960	15,000
	1964	23	1964	9,800
	1965	24	1968	2,500
Rondane	1970	53	1969	3,100
	1971	47	1972	2,500
Hardangervidda	1969	61	1965	33,000
	1970	57	1971	8,000

*Females 2 years and older.

decreased with increased harvest and thus population decrease. In Snøhetta the hunting licenses were not specified to sex and the decrease in percentage lactating females was highly significant ($X^2=7.7$, $P<0.01$). The male segment was heavily reduced during the period 1961-1964 (Table 2). In Rondane the increased harvest from 1969 (Table 1) apparently led to the sex-ratio found in 1971. Previous to 1969 the Rondane herd probably enjoyed a more balanced sex ratio. The decrease in percentage lactating females in the harvest could be attributed to the decline in the male segment. However, other explanations, such as high calf mortality rates on the calving grounds, are equally probable. In Hardangervidda the hunting licenses were specified sex from 1965, and harvest was more evenly distributed among males and females as indicated by the sex ratios in Table 2. The decrease in percentage lactating females was not significant ($P>0.05$) in Rondane or in Hardangervidda.

Comparing Hardangervidda and North Ottadalen (Table 2) it appears that poor nutrition alone is not responsible for a low percentage of lactating females. Both areas enjoyed high percentages. Neither does the moderately distorted sex ratio as in South Ottadalen seem to be an important reduction factor. An extremely distorted sex ratio as in

Rondane could possibly have had some effect on the number of females bred. However it seems to be a possible relationship between distorted sex ratio, poor nutrition and breeding success as indicated from the Snøhetta and Hardangervidda figures in Table 3.

How do these results correspond with data from domestic reindeer herds? Skjenneberg and Slagsvold (1968) and Druri (1955) report that in domestic herds four to six adult males to 100 females is an adequate sex-ratio, but there are examples where one adult male breeds 50 or more females. In Lødingen experimental herd nearly all breeding males are yearlings and sex ratio in the herd is approximately 1:15 in favor of females (Skjenneberg and Slagsvold, 1968). They report satisfactory calf crops. Bergerud (1971) reports an unchanging percentage of lactating females with a reduction of male segment in caribou herds. The change in sex ratio in his study was apparently far less drastic than in Rondane for example.

The breeding season appears to be a costly process for the males in terms of energy expenditure because of intense activity and at the same time decreased food intake. If the extremely concentrated calving season, which does not last longer than about 10 days in reindeer, is indicative of an equally concentrated breeding season, there is a possibility that few and young males will have to leave a greater proportion of the female segment unbred. This is in conflict with domestic reindeer practice where in some situations yearling males are used for breeding in a ratio 1:15 one year and older females and with satisfactory results. The situation might be different in a wild herd where older males will be present and just by their presence have an inhibitory effect on the young males. Unpublished data from North Ottadalen and Snøhetta tend to support this. The same seems to be true in Hardangervidda (T. Skogland, pers. comm.). If poor physical condition is added to a distorted sex ratio situation as in Snøhetta it is probable that this is a real serious threat to mating success.

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PRELIMINARY REPORT ON COMPUTER SIMULATION OF BARREN GROUND CARIBOU MANAGEMENT

F. Bunnell*, D. C. Dauphine, R. Hilborn*, D. R. Miller,
F. L. Miller, E. H. McEwan, G. R. Parker, R. Peterman*,
G. W. Scotter and C. J. Walters*

*Institute of Animal Resource Ecology
University of British Columbia
Vancouver, B. C.

ABSTRACT—A computer model was developed to look at the dynamics of a caribou population on the winter range. Represented in the model are browse and lichen production, total caribou population, winter harvest, summer harvest and calf survival. The main objective of this simulation model was to evaluate management practices. The model has proven useful as a means of testing the interaction of management interventions such as harvest rates, selective hunting, rate of forest fire burns and calf survival.

The purpose of this simulation model was to provide a framework for collating in a dynamic fashion pertinent information on barren ground caribou populations. For management purposes it is important to know if the population size of the Kaminuriak Herd is presently regulated by hunters, and how rapidly that herd would change if hunting were restricted in various ways. Secondly, we wished to evaluate the probable response of the lichen and browse food supply to changing population density in order to determine the ultimate limit of the population growth if factors other than food supply were not important. Since lichen and browse production are affected by successional conditions on forested wintering areas, we wished to assess the effects of various forest fire rates on population change and potential size.

A workshop was held at the University of British Columbia in which six biologists from the Canadian Wildlife Service collaborated with four resource model builders from the Institute of Animal Resource Ecology to develop a simulation model of the dynamics of the Kaminuriak barren ground caribou herd. General factors considered in the caribou model are shown in Figure 1. The series of indices that we considered adequate to represent a caribou herd and its winter habitat were: (1) population size by sex and age class (Miller, 1970); (2) square miles of winter habitat in various successional stages or vegetation classes (Scotter, 1964; Miller, 1970); (3) standing crop of lichens and browse per square mile in each habitat class (recalculated from data of Scotter, 1971 and Miller, 1970); (4) indices relating the severity of weather in winter (Pruitt, 1959) and during the spring calving period (Hart *et al.*, 1961); (5) reproduction, age-specific reproductive rates (Dauphine, 1970); (6) natural mortality, and harvest rates for animals of each sex-age class (Parker, 1970); (7) net production of food by habitat class; and (8) rate of food consumption by animals in each habitat class.

The model was programmed in FORTRAN IV for the IBM 360/67 system at the University of British Columbia. A detailed description of the underlying assumptions and structure of the simulation model will be published at a later date.

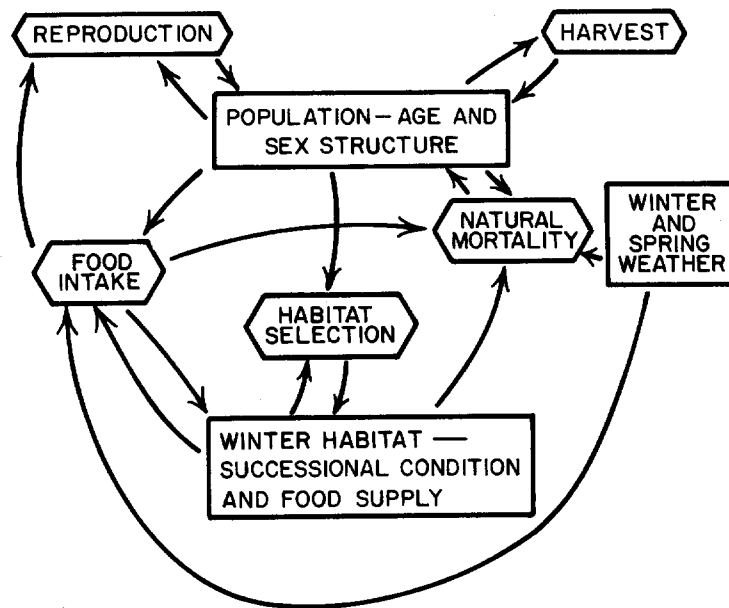


Fig. 1.—Factors considered in a simulation model of the Kaminuriak caribou herd.

RESULTS AND DISCUSSIONS

It has been speculated that the decline in the numbers of caribou from an estimated 670,000 in 1948-49 (Banfield, 1954) to 277,000 (Kelsall and Loughrey, 1955) was probably the result of two major factors: excessive hunting and range depletion by fire. Contributing factors, such as a succession of poor calving seasons and excessive kills by wolves have also been mentioned. In 1967, Thomas (1969) surveyed three mainland populations (Bluenose — 19,000, Bathurst — 144,500 and Beverly — 159,000) and arrived at an estimated 322,500 caribou. The estimated kill accounted for 12,500 animals, about 4 per cent of the entire population. Although pertinent data used to generate the simulation model were derived from the Kaminuriak population, the predicted trends should also apply to the other three mainland herds which have similar harvest rates, natural mortality and net increment values. Further, the model structure is general and can easily accommodate data for any caribou or reindeer herd.

Population trends and the response of lichen and browse supply to changing population density, as these are influenced by alternative management policies, are shown in Figure 2. At the present harvest rate (5 per cent) and calf mortality (60 per cent), the model predicts that the population of 63,000 should remain relatively stable, although gradually continue to decline. Doubling the present male harvest and reducing the female harvest by 50 per cent should result in higher long-term yields. It is interesting to note that the predicted trends of food supply and population intercept at about 220 years. If a complete ban on hunting was imposed, the model predicts a rapid increase in numbers accompanied by a decline of food supply, these two parameters intercepting at 90 years. The model predicts that the carrying capacity of the wintering area to be about 400,000 animals, 6.5 times the present population. According to the model, the food supply could support a much larger number of caribou and food is not likely to become a limiting factor in the next 50 years, regardless of what management policies are adopted. A predicted

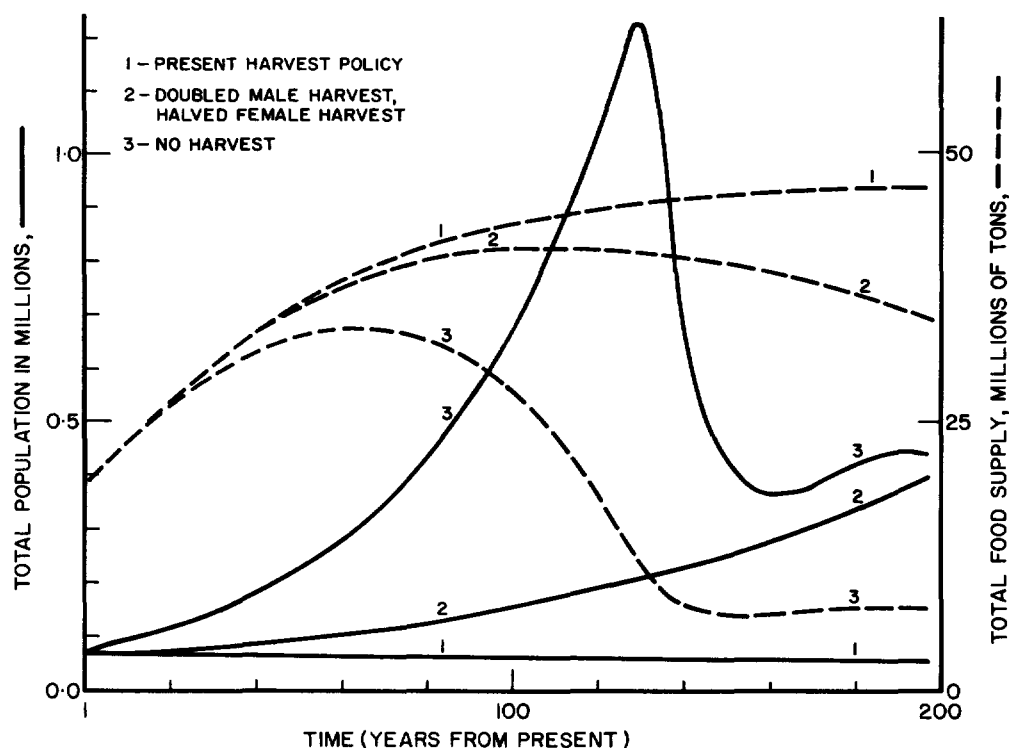


Fig. 2.—Simulated trends in the Kaminuriak Herd and its food supply under three alternative management policies.

population of about 300,000 caribou could be sustained at a 4 per cent harvest rate, while producing an annual yield of about 20,000 animals. The present management of the herd numbering about 70,000 has a sustainable yield of only 5,000 animals. However, with no harvesting, it would take about 60 years to reach the optimal level of 300,000 animals.

An attempt was made to gain an insight into the effects of increasing forest fire occurrence on the winter ranges. Among the various factors that might limit barren ground caribou populations, range destruction by fire is considered important (Scotter, 1964; Kelsall, 1968). It has been observed that caribou avoid recently-burned areas and early succession stages which are lichen-poor. Based on observations and pellet counts caribou prefer climax forests and advanced successional stages of forest growth. The model predicts that increasing the rate of burning from the normal (1 per cent) to 5 times the normal level has little effect on the population (Fig. 3). Preliminary results predict that an increase of 10 times the normal burning rate would be necessary to appreciably affect the population.

Two critical parameters in the caribou model were the calf mortality rate and the amount of food made unavailable per amount eaten due to trampling of the snow cover around feeding craters. The effect of three estimates of the annual calf mortality (50 per cent, 60 per cent and 75 per cent) on population changes were tested under the present harvest rates and good weather conditions. The average annual calf mortality rates could not be greater than 60 per cent and still generate a constant population size of the herd. Mortality rates up to 75 per cent resulted in a rapidly declining population; whereas a mortality rate of 50 per cent resulted in a rapid increase in the population size. Calf mortality, ranging from 25-80 per cent (McEwan, 1963) attributable to adverse weather has

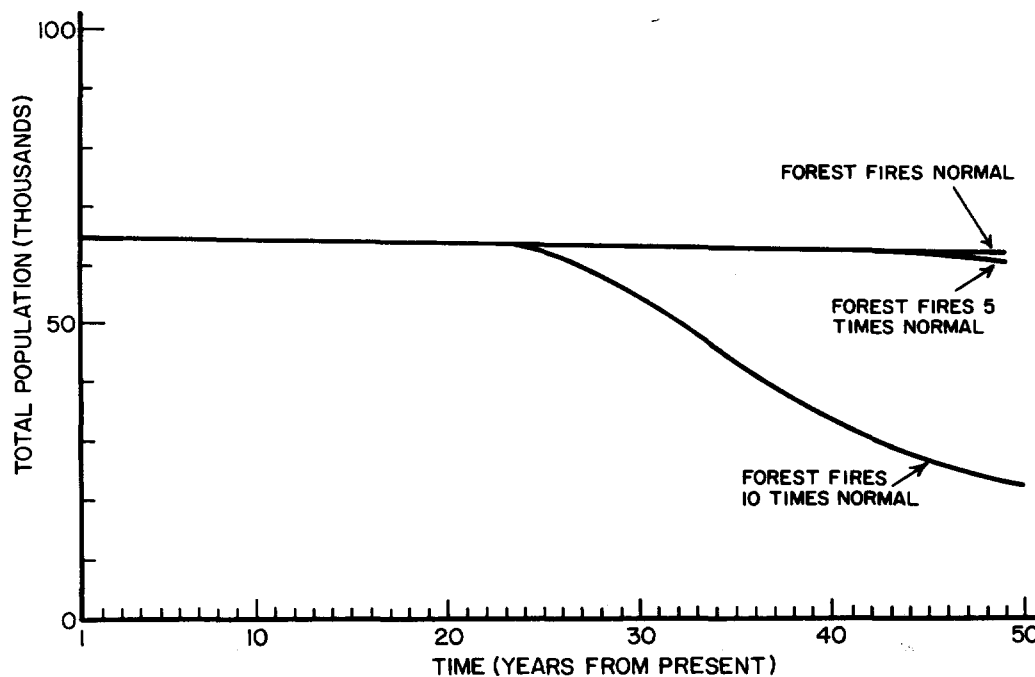


Fig. 3.—The model predicts that gross increases in forest fire rates would be necessary to appreciably affect the Kaminuriak herd.

been observed in several field locations (Kelsall, 1968) and confirmed by physiological studies (Hart *et al.*, 1962). In certain years, an entire calf crop may be lost due to severe winter and spring weather conditions. The predicted response to such a loss, assuming present harvest rates are maintained, is that the population would recover only very gradually.

Snow acts as a hindrance not only to caribou movements but also to their other activities (Pruitt, 1959). Because caribou are primarily grazers, their food supply must be excavated from beneath the snow by digging 'feeding craters'. The snow around each exposed crater is trampled and becomes frozen. Thus, for an amount of food consumed, a considerable portion of food is made unavailable. The amount made unavailable was estimated to be 10-20 times the amount eaten. If the feeding efficiencies are high (lost/eaten=2), the average population size is reduced since the overall food supply is kept at a lower level.

This first attempt to develop a simulation model of a barren ground caribou population should provide an encouraging approach to evaluate future research programmes. The real significance of the model's function is to reveal gaps in the data as well as disclose significant interactions and critical parameters. From an examination of the results it is apparent that implementation of programmes to monitor and regulate harvests is essential if the present caribou populations are to be managed efficiently.

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CALVING SEASON IN DIFFERENT POPULATIONS OF WILD REINDEER IN SOUTH NORWAY

Vidar Holthe
Directorate of Wildlife Management
Trondheim, Norway

ABSTRACT—Calving season in the three populations, North Ottadalen, South Ottadalen and Snøhetta was determined by counting the percentage of calves in relation to cows during the calving seasons, 1969-72. The latitude of the areas is 62° North. Ninety per cent of the calves were born within 10 days in each population, and the peak was found to be May 6, May 12 and May 28 respectively for the three areas. Possible reasons for the differences are discussed, and the following factors are believed to be of importance in this case: genetic differences, difference in physical condition, age of males and human disturbance.

This study deals with calving season in different populations of wild reindeer in South Norway, and includes a discussion of possible reasons for the great difference found. Great variation in breeding season among reindeer and caribou populations in the Northern Hemisphere is known (Heptner *et al.*, 1966; Lent, 1964), with rutting from September to November and calving from April to June. The difference in breeding season is believed to be mainly genetic (Hemming, pers. comm.; Lent, pers. comm.), dependent upon the latitude and the phenology in the area where the population has evolved.

The populations dealt with in this study all live at the same latitude, and since we have a lot of information about them (Braend, 1964; Reimers, 1968, 1969a, b, 1972 and unpubl. data), it should be possible to discuss the influence of other factors on the breeding season.

MATERIALS AND METHODS

From 1969 to 1972 observations were made during calving season in North Ottadalen and Snøhetta (Fig. 1), and in 1971 and 1972 in South Ottadalen. Calving season was determined by counting the number of calves in relation to females that were expected to calf, i.e. antlered females, from day to day. Pregnant female reindeer first shed their antlers after parturition (Espmark, 1971). In addition to this the age of the calves was estimated and then the approximate date of birth of the observed calves was calculated.

I have obtained information about the calving in the North Rondane population in the period 1965-72 from the local game warden, as well as a few data for 1971 on the South Rondane population. A large number of old hunters and local people have been interviewed to get information about whether there has been any change in the calving season in the last 50 years.

RESULTS

The results are shown in Table 1. The number of animals counted up during the observation period is a measure of the size of each year's material. The main calving period is the period during which 90 per cent of the calves are born, and the midpoint or peak is the date when 50 per cent of the calves are born, as suggested by Lent (1964). The earliest

TABLE 1.--Time of calving in the populations.

Population	Year	Population size	No. of animals counted during calving season	Main calving	Midpoint
North Ottadalen	1969	1,000	2,640	May 1-11	May 6
	1970	1,200	2,360	May 1-10	May 5
	1971	1,400	1,370	May 2-11	May 6
	1972	1,600	1,330	May 1-11	May 6
South Ottadalen	1971	450	125	May 8-17	May 12
	1972	450	70	May 8-17	May 12
Snøhetta	1969	1,200	1,325	May 24-June 3	May 29
	1970	1,200	536	May 24-June 1	May 28
	1971	1,250	181	May 23-June 1	May 27
	1972	1,300	155		
North Rondane	1965-72	2,400-1,800		May 20-27	May 24
South Rondane	1971	100		-most calving after May 20-	

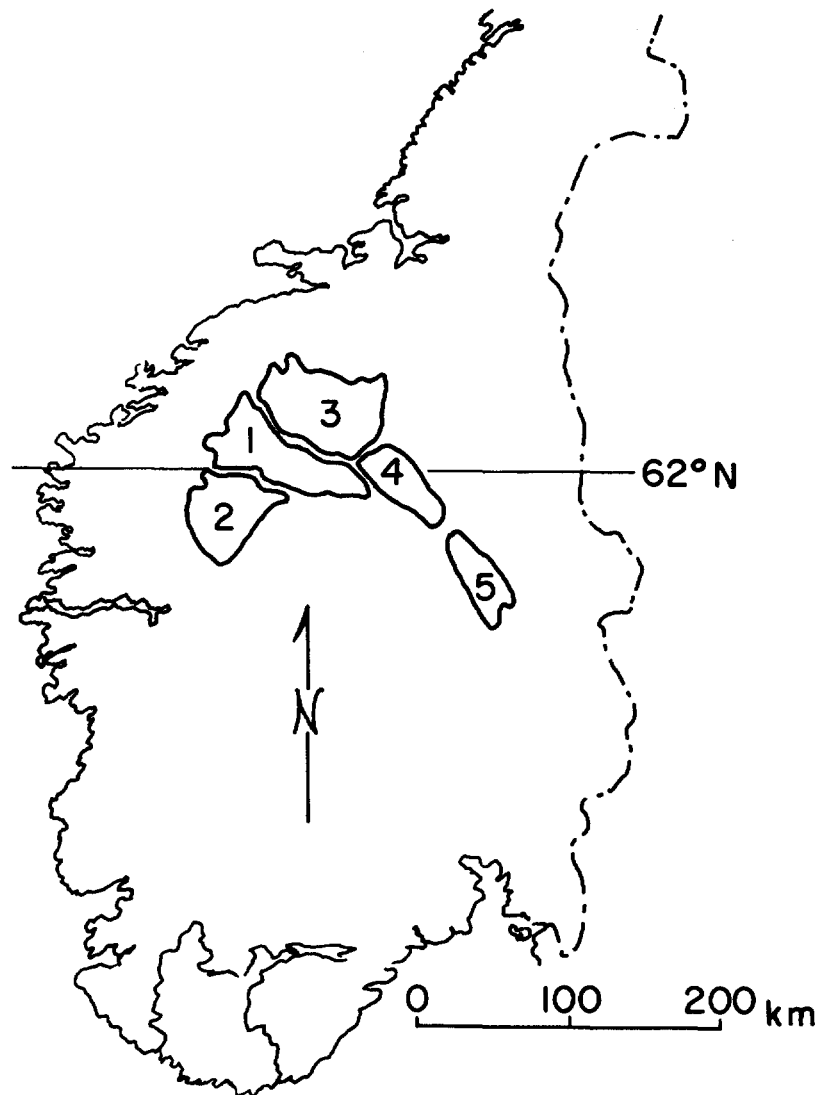


Fig. 1.—Distribution of the reindeer populations in southern Norway: (1) Ottadalen N, (2) Ottadalen S, (3) Snøhetta, (4) Rondane N and (5) Rondane S.

calving recorded in North Ottadalen is April 17, and in Snøhetta May 20. Extreme late calving also occurs, and in North Ottadalen, Snøhetta and North Rondane newborn calves have been observed in the hunting season in September. The interviews with the local people indicated a change in calving season in Snøhetta, with an earlier calving season before 1950, and an even later calving than today around 1960 (see discussion), but as very few people are in the mountains in spring and as people's memory are very bad, I am not sure how much I can rely upon this information.

DISCUSSION

Phenology

There are no phenological differences between the areas today that could cause this

difference.

Genetics

The two Ottadalen populations are genetically equal, as they both originate from the same herd of semidomestic reindeer that was released and went feral in 1964. Before the construction of the railroad across the Dovre Plateau early in this century, reindeer frequently migrated between Rondane and Snøhetta, and they still do to some extent. There is no migration between the Ottadalen populations and the Rondane/Snøhetta populations, and it is reasonable that they are genetically different (Braend, 1964).

Nutrition

Nievergelt (1966), Sadleir (1969) and Verme (1965) have shown in different species of ungulates that low nutritional level may delay the breeding season. Body size and growth rates are taken as an indicator of the level of nutrition in these populations (Reimers, 1968, 1969a, 1972 and unpubl. data). North Ottadalen has the best nutritional conditions, South Ottadalen and South Rondane second best. Snøhetta had good conditions up to 1950, but as the population increased and reached its maximum around 1960 (15,000 animals), the nutritional condition was very bad. It is slightly better today. This coincides very well with the information from the local people.

Age of Males

Sexually active males are found to induce and synchronize ovulation in female sheep, goat and other domestic ungulates (Fraser, 1968; Sadleir, 1969), and these authors say that this is also likely to be the case with other wild ungulates. Espmark (1964) and Meschaks and Nordkvist (1967) found that older reindeer males came in rut before the younger ones, and that they were more sexually active. So it is possible that the age structure of the males might influence the calving season in wild reindeer. Skjenneberg (pers. comm.), however, has not observed any change in the calving season in the research herd of semidomestic reindeer in Harstad, Norway, after they started to use only 1.5 year old males in the breeding. There is a high portion of old males in the North Ottadalen and South Rondane populations, whereas they are lacking in the other populations. There is also the possibility that the females are mated first in their second ovulation (McEwan and Whitehead, 1972) in a population with a lack of old males, but in that case at least a few females should be mated in their first ovulation, and it should result in a calving season with two peaks (Hemming and Klein, pers. comm.). That is not the case in the populations with late calving.

Human Disturbance

It is not unlikely that much human disturbance just before the rutting season may delay it. The hunting season in Norway is in September. The Ottadalen areas were first opened for hunting in 1967 and the hunting pressure has been light. The Rondane North has had a medium to heavy hunting pressure, while the South Rondane has been closed for hunting in the last years. The hunting pressure in Snøhetta is not very heavy today, but from 1960 to 1968 when the population was reduced by hunting from 15,000 to 2,000 animals, the pressure was very heavy, and Reimers (1968) found that females lost weight in September, a period when they should normally gain weight. Thomson (1971) found that the proportion of time spent trotting and running was increased by three times and the time

spent eating was very reduced in the hunting season of 1970 on Hardangervidda, when there was the same type of reduction hunt in that area. Skogland (pers. comm.) observed that the calving on Hardangervidda in 1972 occurred about 10 days earlier than the year before, after there had been no hunting in 1971.

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REINDEER SURVIVAL IN THE MACKENZIE DELTA HERD, BIRTH TO FOUR MONTHS

R. F. Nowosad, Manager
Canada Reindeer Project
Canadian Wildlife Service
Inuvik, N. W. T.
Canada

ABSTRACT—Survival of reindeer fawns was studied from 1969 to 1971 on the Mackenzie Reindeer Grazing Preserve, Northwest Territories, Canada. To permit later identification, day old fawns (3,459) were double ear tagged with colored, consecutively numbered Kurl-Lock No. 2 tags. Date of birth, weight, sex and tag numbers of each fawn were recorded. Daily collections of dead fawns were undertaken during the first two months following birth. A tally of surviving fawns was gained each August during roundup and corralling. Survival percentages during the first four months following birth varied annually, ranging from 54 per cent to 69 per cent. Up to 10 per cent of fawn deaths occurred on the fawning grounds. Differential survival between sexes was not apparent. Fawn survival appears to be directly related to date of birth, with the highest percentages occurring among those born during the peak fawning period.

Little is known concerning the survival of reindeer fawns (*Rangifer tarandus*) in North America. The majority of research has concentrated on adult animals, their survival, age, sex ratios and numbers. What information is known (Hill, 1967; Kelsall, 1968; McEwan, 1963) is scanty, thus making it impossible to draw any firm conclusions.

Although reindeer have been herded in the Mackenzie Delta area since 1935, little biological research has been undertaken. In 1968 the Canadian Wildlife Service agreed to conduct a five year research program including an examination of reindeer population dynamics. This paper deals with observations concerning reindeer fawn survival from birth to four months made during the 1969 to 1971 period.

I acknowledge the assistance given by the reindeer herders in capturing and tagging the fawns.

STUDY AREA

The studies were conducted on the Mackenzie Reindeer Grazing Reserve located east of the Mackenzie River Delta, Northwest Territories, Canada. The fawning grounds occupy the central portion of the 17,900 square mile (46,361 km²) reserve.

Northern portions of the fawning grounds are characterized by scrub tundra (willows, birches, mosses, lichens, alders). Near tree line the willows often reach heights of 5 to 7 feet (2-2.5 m) with shorter ground birch interspersed among the willow clumps. Lichens, grasses and sedges are found throughout the area. Open woodland extends over the southern portion of the fawning ground. Black spruce (*Picea mariana*), dominant in muskeg areas, and white spruce (*Picea glauca*), dominant in drier valleys and hill sides, are the most common large trees. Paper birch (*Betula resinifera*) and lesser quantities of larch (*Larix laricina*) and balsam poplar (*Populus balsamifera*) are also present. It is among the scattered trees that the

rich carpets of 'reindeer moss' (*Cladonia alpestris*, *C. arbuscula*, *C. mitis*, *C. rangiferina*) are found. These lichens and lesser quantities of willow, birch, alder, sedges and grasses comprise the winter forage of reindeer.

Foxes (*Vulpes fulva*, *Alopex lagopus*) are numerous on the fawning grounds. While wolves (*Canis lupus*), wolverine (*Gulo luscus*) and lynx (*Lynx canadensis*) are known to inhabit the area their numbers are few and the animals are seldom seen. Bears, both the black (*Ursus americanus*) and grizzly (*Ursus arctos*), occasionally follow the reindeer. Although they mainly feed on old carcasses, they have been observed killing both fawns and adult reindeer. Ravens (*Corvus corax*) abound throughout the area with flocks of up to 30 observed during the fawning period.

MATERIALS AND METHODS

Reindeer fawns are born during April and May. By this time of year the herd has been driven north from its wintering range to the edge of the tree line. Although newborn fawns can be easily caught by a man on foot, snowmobiles are used to transport the taggers among the herd. Tagging is a two man operation; one drives the snowmobile, the other catches and tags the fawns. Fawns less than a day old usually fall to the ground when chased. Older fawns attempt to avoid capture by running, but their unsteadiness over the irregular snow surface retards escape. It is almost impossible to catch fawns more than three days old even when using snowmobiles. No attempt was made to tag 'wet' fawns.

To identify individual reindeer consecutively numbered, self-piercing aluminum ear tags were attached to the upper edge of each ear near the head. Care was necessary to ensure that tags were not placed near the outer tips of the thin ears of fawns where they are easily torn loose. The two tag styles (1 3/8" x 5/16" 'Kurl-Lock No. 2' and 1 3/16" diameter round 'Visa' from Ketchum Manufacturing Sales Ltd., 396 Berkley Avenue, Ottawa, Ontario) were obtained in distinctive colors for each year enabling determination of year-classes in the field. The No. 2 tag was used exclusively in 1969 and 1970 on newborn fawns. Although it was used on most fawns in 1971, the round 'Visa' tag was used with it to a limited extent. The sex of each fawn tagged was also recorded along with the date and numbers used. During the 1970 and 1971 spring tagging operation the weight of each fawn was also recorded.

Daily collections of dead fawns were undertaken during April and May of each year. If ear tags were present, their numbers were recorded along with the animal's sex, weight and suspected cause of death. Carcasses lacking signs of predator involvement were placed in a predation-excluded category; all others were placed in a predation-involved category.

The cause of death was assigned to predation only when the actual kill was observed or a carcass had signs of predator attack. Bruises surrounding tooth marks, or blood in wounds, or frothy blood in the nares and trachea were used as indicators of predator kills. Carcasses lacking visible signs of cause of death were examined more thoroughly at the laboratory in Inuvik.

A roundup and corralling of the reindeer was undertaken each year during the first week of August. As the reindeer were put through a handling chute, the colors and numbers of the ear tags were recorded. In that way, it was possible to determine the number, sex and age of surviving reindeer. These data in turn were updated with data collected through the years and succeeding roundups.

RESULTS

During the three year study, 3,459 day-old fawns were double ear-tagged (820 in 1969, 1,209 in 1970 and 1,430 in 1971; Tables 1-3). Based on sample counts after fawning the

TABLE 1.--Fawn tagging, 1969*

Date	Males daily	Males total	Females daily	Females total	Daily total	Cumulative totals
April 2			1	1	1	1
3			1	2	1	2
6	1	1	1	3	2	4
9	1	2	2	5	3	7
10	5	7	2	7	7	14
11	3	10	2	9	5	19
12	2	12	4	13	6	25
13	8	20	7	20	15	40
14	15	35	19	39	34	74
15	14	49	18	57	32	106
16	22	71	18	75	40	146
17	28	99	26	101	54	200
18	29	128	19	120	48	248
19	32	160	31	151	63	318
20	38	198	42	193	80	391
21	25	223	30	223	55	446
22	36	259	39	262	75	521
23	60	319	42	304	102	623
24	8	327	10	314	18	641
25	36	363	42	356	78	719
26	10	373	7	363	17	736
27	21	394	30	393	51	787
29	5	399	8	401	13	800
30	5	404	4	405	9	809
May 2	2	406	1	406	3	812
5	2	408	1	407	3	815
7	2	410	1	408	3	818
9	2	412			2	820

*Fawns double ear tagged using white Kurl-Lock No. 2 tags.

Peak tagging period: April 18-28, 1969. 72% of total tagged.

Peak tagging day: April 23, 1969.

numbers of fawns tagged represented an estimated 70-75 per cent of the total fawn crop for each year. Fawn weights at tagging were recorded for the 2,639 fawns tagged in 1970 and 1971 (Tables 4-5).

Male fawns were found to be approximately one pound (0.45 kg) heavier than female fawns both in 1970 and 1971. However, fawns born in 1971 were approximately one-quarter pound (0.11 kg) lighter than fawns born in 1970. Those born later in the 1970 fawning season tended to be heavier. The reverse trend was noted among the 1971 fawns.

TABLE 2.--Fawn tagging, 1970*

Date	Males daily	Males total	Females daily	Females total	Daily total	Cumulative totals
April 10	3	3	2	2	5	5
12	5	8	0	2	5	10
13	4	12	4	6	8	18
14	20	32	27	33	47	65
15	7	39	10	43	17	82
16	25	64	25	68	50	132
17	35	99	30	98	65	197
18	43	142	37	135	80	277
19	39	181	34	169	73	350
20	24	205	26	195	50	400
21	64	269	65	260	129	529
22	70	339	57	317	127	656
23	76	415	75	392	151	807
24	54	469	39	431	93	900
25	35	504	36	467	71	971
26	20	524	31	498	51	1,022
27	13	537	13	511	26	1,048
28	11	548	5	516	16	1,064
29	20	568	11	527	31	1,095
30	14	582	13	540	27	1,122
May 1	7	589	6	546	13	1,135
2	6	595	2	548	8	1,143
3	5	600	1	549	6	1,149
4	7	607	4	553	11	1,160
6	7	614	6	559	13	1,173
7	3	617	1	560	4	1,177
9	5	622	5	565	10	1,187
10	2	624	1	566	3	1,190
13	4	628	9	575	13	1,203
14	3	631	1	576	4	1,207
15	1	632	1	577	2	1,209

*Fawns double ear tagged using green Kurl-Lock No. 2 tags.

Peak tagging period: April 18-28, 1970. 72% of total tagged.

Peak tagging day: April 23, 1970.

Survival success varied throughout the fawning period. In general, fawns born during the peak fawning period exhibited a tendency for greater survival than those born before and after the peak (Fig. 1).

Tag retention was found to exceed 90 per cent during the first four months following application (Table 6).

1969 Survival

Of the 820 fawns tagged during April-May 1969, 40 (5 per cent) were found dead on

the fawning grounds. Thirteen (33 per cent) of the deaths were in the predation-excluded category with 27 (67 per cent) assigned to the predation-involved category.

TABLE 3.--Fawn tagging, 1971*

Date	Males daily	Males total	Females daily	Females total	Daily total	Cumulative totals
April 11	2	2	0	0	2	2
12	3	5	2	2	5	7
13	6	11	1	3	7	14
14	4	15	2	5	6	20
15	3	18	4	9	7	27
16	4	22	8	17	12	39
17	9	31	5	22	14	53
18	9	40	14	36	23	76
19	16	56	19	55	35	111
20	37	93	32	87	69	180
21	31	124	34	121	65	245
22	43	167	44	165	87	332
23	54	221	36	201	90	422
24	89	310	69	270	158	580
25	65	375	76	346	141	721
26	89	464	82	428	171	892
27	63	527	54	482	117	1,009
28	21	548	14	496	35	1,044
29	49	597	36	532	85	1,129
May 1	21	640	12	569	33	1,209
2	22	662	24	593	46	1,255
3	15	677	16	609	31	1,286
4	15	692	7	616	22	1,308
5	12	704	8	624	20	1,328
6	5	709	2	626	7	1,335
7	5	714	6	632	11	1,346
8	5	719	3	635	8	1,354
9	11	730	10	645	21	1,375
10	5	735	6	651	11	1,386
11	1	736	7	658	8	1,394
12	9	745	7	665	16	1,410
13	4	749	4	669	8	1,418
14	8	757	4	673	12	1,430

An additional 8 fawns were tagged but their sex was not recorded.

*300 fawns double ear tagged with one orange Kurl-Lock No. 2 tag and one red Visa tag. All others double tagged with only Kurl-Lock No. 2 tags.

Peak tagging period: April 20-30, 1971. 75% of total tagged.

Peak tagging day: April 26, 1971.

During the 1969 August roundup, 422 (51 per cent) of the tagged fawns were counted. An additional 197 untagged fawns were also counted at that time. Through use of data

TABLE 4.--Average birth weights of reindeer fawns, April-May 1970*

Date	No.	Males		Females	
		weight in lb.		weight in lb.	
April 10-17	71	15.50 (7.03 kg)		78	15.25 (6.92 kg)
April 18-19	54	15.50 (7.03 kg)		46	14.50 (6.58 kg)
April 20-22	115	16.25 (7.37 kg)		113	15.25 (6.92 kg)
April 23	33	16.25 (7.37 kg)		42	15.50 (7.03 kg)
April 24	55	17.00 (7.71 kg)		38	16.50 (7.48 kg)
Overall	328	16.25 (7.37 kg)		317	15.25 (6.92 kg)
Peak of fawning period	203	16.50 (7.48 kg)		193	15.50 (7.03 kg)

*All fawns weighed were less than 24 hours old, weights recorded to nearest quarter pound.

TABLE 5.--Average birth weights of reindeer fawns, April-May 1971*

Date	No.	Males		Females	
		weight in lb.		weight in lb.	
April 11-19	56	15.75 (7.14 kg)		55	15.50 (7.03 kg)
April 20-21	70	16.50 (7.48 kg)		65	16.00 (7.26 kg)
April 22-23	97	16.00 (7.26 kg)		80	14.50 (6.58 kg)
April 24	89	16.00 (7.26 kg)		67	15.00 (6.80 kg)
April 25-26	154	16.50 (7.48 kg)		157	15.75 (7.14 kg)
April 27-29	135	15.50 (7.03 kg)		117	14.50 (6.58 kg)
May 1-5	73	16.00 (7.26 kg)		59	14.75 (6.69 kg)
May 5-14	65	15.25 (6.92 kg)		57	14.25 (6.46 kg)
Overall	739	16.00 (7.26 kg)		657	15.00 (6.80 kg)
Peak of fawning period	167	16.25 (7.37 kg)		143	15.50 (7.03 kg)

*All fawns weighed were less than 24 hours old, weights recorded to nearest quarter pound.

collected at the two succeeding roundups, it was determined that at least 553 (67 per cent) of the 1969 tagged fawn crop had survived the first four months. The corrected value was obtained by including 1969 fawns counted at succeeding roundups that had not originally been counted. Additional mortality, which occurred following the initial count, was believed to be approximately equal for each year's cohorts after the age of four months (author's unpubl. data). Thus, corrected values represent minimum numbers surviving. Broken down into sex classes, it was determined that 283 (69 per cent) of the males and 270 (66 per cent) of the females originally tagged during the April-May period had lived to age four months (Table 7).

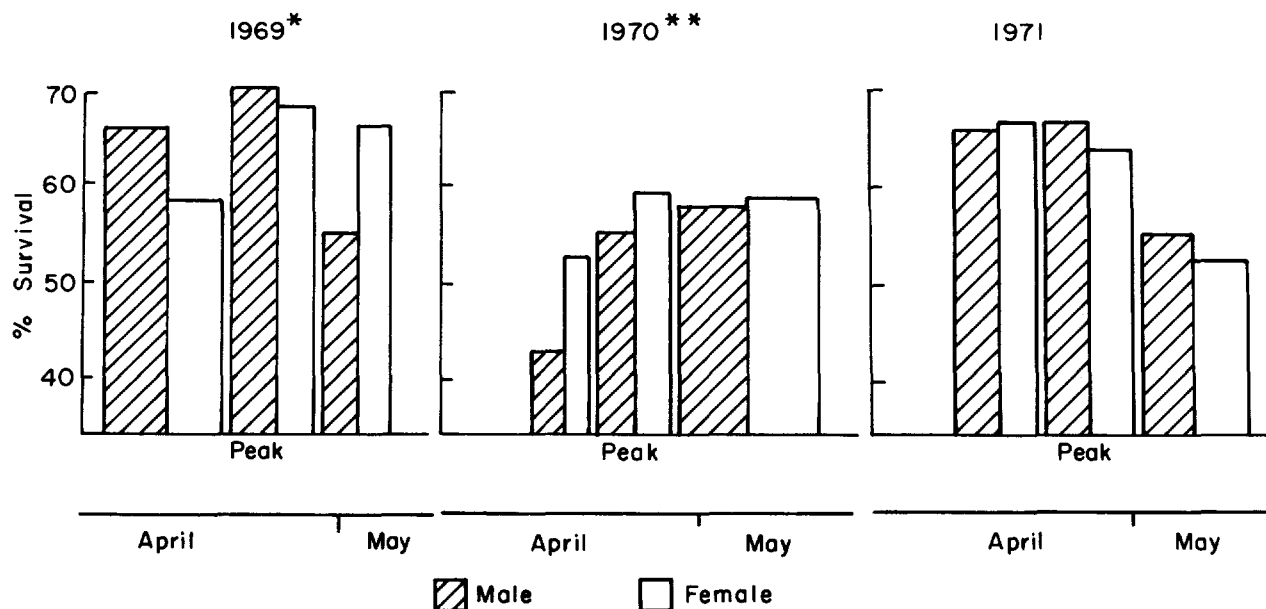


Fig. 1.—Reindeer fawn survival to age four months according to period of birth — before, during and after peak fawning period. (*Includes additional data from 1970, 1971; **includes additional data from 1971, see text.)

TABLE 6.—Ear tag retention among reindeer fawns double ear tagged as determined during August roundup, 1971.

Date tagged	Sex	Tag type	Number tagged	Sample size	No. retaining both tags	% retention
April 1971	Male	K-L No. 2	592	378	360	95
	Female	"	538	323	310	96
	Male*	K-L & Visa	165	109	104	95
	Female**	"	135	91	84	92

*Two males lost the Kurl-Lock tag and three lost the Visa tag.

**Two females lost the Kurl-Lock tag and five lost the Visa tag.

TABLE 7.—Known fawn survival — birth to four months.

Year tagged	No. tagged		% survival to age four months		
	males	females	males	females	both
1969	412	408	69*	66*	67*
1970	632	577	54**	58**	56**
1971	757	673	65	61	63

*Updated value using 1969, 1970 and 1971 data.

**Updated value using 1970 and 1971 data.

1970 Survival

A total of 61 (5 per cent) of the 1,209 fawns tagged April-May 1970 were found dead on the fawning grounds. Many of the carcasses had been eaten by predators making it impossible to determine with accuracy the exact cause of death. Eight (13 per cent) of the deaths were assigned to the predation-excluded category with 53 (87 per cent) deaths assigned to the predation-involved category. Thirty-one (51 per cent) deaths were identified as the result of predator attacks.

The August 1970 roundup sampled only a small portion of the entire reindeer herd with the result that only 354 (29 per cent) tagged fawns were counted (102 untagged fawns also counted). However, data from 1971 provided a corrected value of at least 680 (56 per cent) tagged fawns surviving. A total of 343 (54 per cent) males and 337 (58 per cent) females had survived the first four months (Table 7).

1971 Survival

One hundred and forty (10 per cent) of the 1,430 fawns tagged during April and May 1971 were found dead on the fawning grounds. Predation-excluded losses accounted for 87 (62 per cent) fawns. A total of 46 (33 per cent) of the deaths were attributed directly to predators with ravens accounting for 21 (15 per cent), foxes 20 (14 per cent) and wolves 6 (4 per cent). The cause of death of 7 (5 per cent) fawns could not be determined.

The August 1971 roundup was extremely successful with an estimated 99 per cent of the entire reindeer herd being put through the corrals. A total of 901 (63 per cent) tagged fawns were counted. That number included 488 males (65 per cent) and 413 females (61 per cent) (Table 7). An additional 277 untagged fawns were rounded up.

DISCUSSION

These findings substantiated the theory that reindeer survival was poor during the first four months of life. Investigations carried out on caribou suggested that fawn mortality was highest immediately following calving (Kelsall, 1968; Pruitt, 1961) but the data presented here do not support that suggestion. Five to 10 per cent of fawn mortality occurred on the fawning grounds (approximately two months) but 33 to 44 per cent occurred during the first four months. That indicated that fawn mortality was greatest after the fawns left the fawning grounds.

Neonatal sex ratios, as indicated by the sex and numbers of fawns tagged, favored males by a small margin (412 males:408 females; 632:577; 757:673; Tables 1-3). Survival during the first four months slightly favored males (Table 6) yet it has been shown that adult sex ratios favor females (Hill, 1967; Skuncke, 1969). Therefore, it can be assumed that differential mortality between sexes did not occur until after the reindeer were more than four months old. Sex ratios among caribou are similar to those observed among reindeer, initially equal but as adults favoring females (Bergerud, 1971; Kelsall, 1968; Lent, 1966; Thomas, 1960).

Biased mortality among fawns has also been shown for a number of North American deer. Male fawns usually demonstrate lower survival levels than females (Robinette *et al.*, 1957). Similar findings have been shown for elk, mountain goats, bighorn sheep (Cowan, 1943) and muskoxen (Tener, 1954).

McEwan (1959) reported a caribou fawn mortality of 33.5 per cent during the first three months while Skuncke (1969) gave a figure of 12 per cent mortality among reindeer fawns during the first six months. In the latter case the animals were being herded and under

constant surveillance. The present mortality findings (33 to 44 per cent during the first four months) compared favorably with those given by McEwan (1959) for barren ground caribou.

Variations in survival success during fawning had not been noted for this herd prior to the present study. The tendency for fawns born during the peak period to exhibit higher survival levels was believed to be due to a number of factors. Early in the fawning period the weather was still severe with the occasional snow storm and temperatures well below minus 15°C. Snow depths were excessive, exceeding one meter in wooded areas. Inclement weather conditions, combined with the smaller fawn size (Tables 4-5) and added stress encountered in feeding and moving about, was believed to account for the poor survival rate. During the peak fawning period the weather stabilized somewhat. Fewer storms were encountered and temperatures were about minus 5°C. By then the herd had moved slightly north of tree line to areas of shallow snow depths and sheltered valleys. On the other hand, fawns born after the peak period had to contend with snow storms, high winds and the occasional freezing rain storm. Also the herd was constantly on the move traveling 10 to 15 km daily as it migrated toward the summer range. Ground snow became soft during the day and crusty during the night presenting difficult walking conditions for the newborn fawns. Under such difficult conditions the fawns succumbed and survival rates decreased.

Other factors which may have influenced survival were the condition of the cow (McEwan and Whitehead, 1972) and the age of the cow at the time of birth (Zhigunov, 1961). As spring approaches the cow's condition deteriorates, fat levels decrease and food supplies are approaching their lowest levels. Should fawning be delayed the cow may be too run-down to support herself and a fawn.

In this herd, it was not uncommon for fawns to breed. The resultant offspring were born late in the fawning period. Survival among yearling offspring is very poor according to Zhigunov (1961) and thus the survival percentage for fawns born late in the fawning period would be reduced.

Predation usually accounts for the largest loss of fawns during the four weeks following birth. Ravens and foxes are the two most important predators. Their importance is only overshadowed by the effect of weather. In 1969 and again in 1970, predation losses far exceeded all others but in 1971, a year of extreme snow depths and windy damp weather, predation losses accounted for less than half the total loss.

McEwan (1959) and Kelsall (1960, 1968) attributed the high caribou fawn mortality observed in 1958 to inclement weather. Bergerud (1971), on the other hand, states that following 10 years of studying caribou in Newfoundland there was no evidence that fawns died from exposure. He attributes this indifference to inclement weather to the heavier birth weights of Newfoundland caribou. However, wind-chill figures tabulated for the Newfoundland study area were far below those listed by Kelsall (1960) and Hart *et al.* (1961) as causing mortality in the Northwest Territories.

Survival among the 1969 and 1971 fawns was similar while the 1970 level was somewhat lower (Table 7). The lower survival rate for 1970 was believed to result from not rounding up most of the animals until 1971.

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OBSERVATIONS OF WOLF PREDATION ON BARREN GROUND CARIBOU IN WINTER

D. R. Miller
Canadian Wildlife Service
Department of Environment
Government of Canada
Ottawa, Ontario, Canada

ABSTRACT—An aerial survey in January, 1968 produced an estimate of 258 wolves among 51,000 caribou that wintered in the Hara-Charcoal Lakes region of northeastern Saskatchewan. Ground studies of caribou were conducted at Hara Lake February 17 to 27, and again April 19 to May 7. cursory observations during February included 15 sightings of wolves and 13 of wolf-killed caribou. Systematic coverage of the 20-square-mile surface of Hara Lake during April-May provided observations of 211 wolves and 147 wolf-killed caribou. Two men with dog teams covered half the lake area daily marking the location of kills and collecting the skull, mandible and femur or tibia. Physical condition of caribou prey was determined from the lipid content of bone marrow. Condition, sex and age comparisons of the wolf-killed caribou were compared with those of a sample shot non-selectively.

Wolves killed an average of three caribou daily at Hara Lake during the April-May observations and, on the basis of old kills, two daily during March and early April. Fawns were selected prey and there was a suggestion that caribou eight years and older were also selected prey. Fawns in relatively poor physical condition appeared more vulnerable to wolf attacks than healthy fawns. Observed wolf attacks demonstrated that caribou which failed to synchronize movements with other band members were vulnerable and that caribou used their antlers for defense when brought to bay. Wolves migrated north over Hara Lake in late April, coincident with the caribou migration.

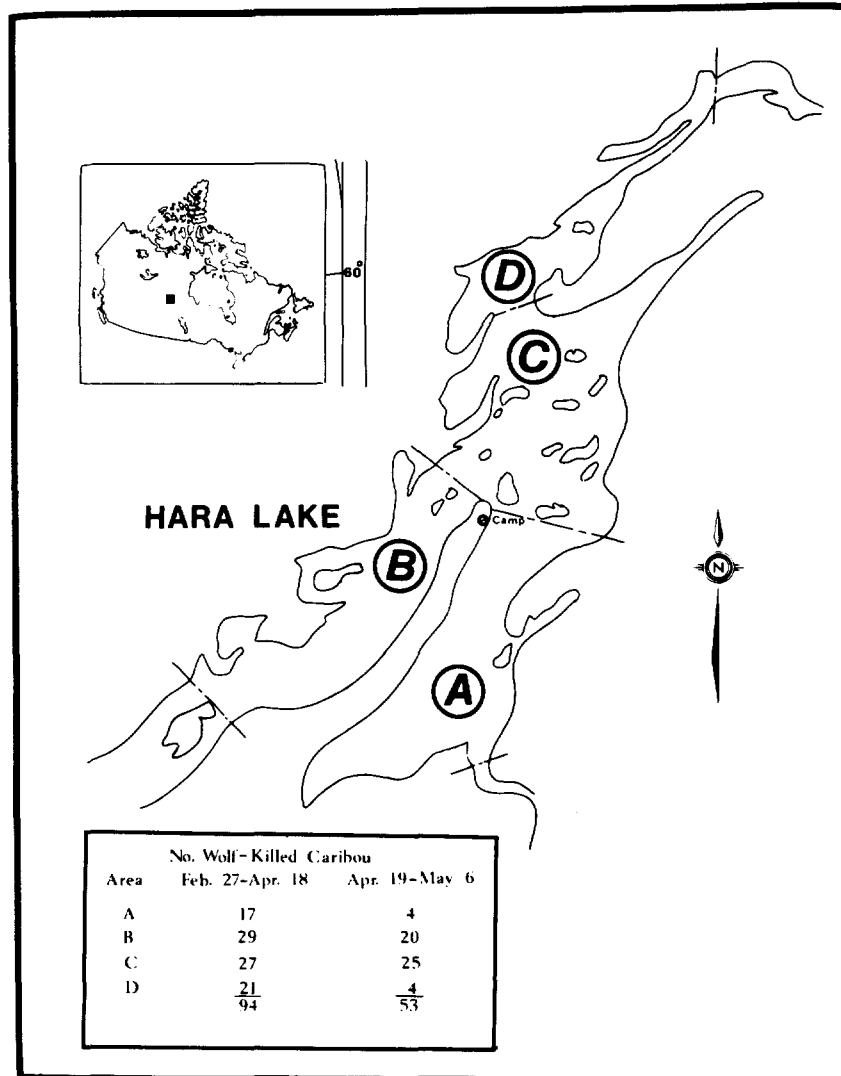
In the course of studying caribou on their taiga winter range a fortuitous situation appeared in which I had an opportunity to collect information about wolf predation that will complement more comprehensive studies. During field studies in February and April-May, 1968 wolf predation was observed on a single lake in northeastern Saskatchewan in a dense caribou concentration. This paper will report on those observations along with comparative information collected during other winters when only a few wolf observations and signs of predation were seen.

Study Area

Barren ground caribou of the population which calves in the Kaminuriak Lake area of the Keewatin District, N.W.T., regularly winter in the taiga of northwestern Manitoba and northeastern Saskatchewan north of 56° N latitude. They migrate into this area during November and leave in late April or May. Tundra wolves (*Canis lupus hudsonicus*) accompany the caribou during migration into the taiga (Kelsall, 1968) entering the territory of resident wolves (*Canis lupus griseoalbus*). Resident fauna of the taiga which may play a

role in wolf-caribou interactions include ravens (*Corvus corax*), gray jays (*Perisoreus canadensis*), red squirrels (*Tamiasciurus hudsonicus*), snowshoe hares (*Lepus americanus*), red fox (*Vulpes fulva*), wolverine (*Gulo luscus*) and moose (*Alces alces*). Moose are sparse throughout the study area.

The location of my 1968 wolf-caribou observations was at Hara Lake, Saskatchewan, at the Manitoba border, 59°05' North, 102°04' West. This taiga area consists roughly of 1/5



water, 2/5 lowland, including bogs and fens, and 2/5 upland. Black spruce (*Picea mariana*) predominates as the main tree canopy with white spruce (*P. glauca*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*) and white birch (*Betula papyrifera*) as minor components. Glacial deposits underlie the area including eskers, moraines and drumlins in a northeast-southwest orientation. The region has a history of natural wildfires which along with a complex of drainage patterns tends to break up the land area into a maze of clearings and stands in various stages of succession.

On their arrival on the taiga winter range caribou usually segregate into adult stag and doe-fawn-juvenile segments. Hara Lake was inhabited by the doe-fawn-juvenile segment during the major portion of my observations. Adult stags were not present at Hara Lake until the spring migration commenced among animals located further south.

PROCEDURES

Two field trips were taken to Hara Lake, Saskatchewan, in 1968, one from February 17 to 27 and the other April 19 to May 7. The main objective of these trips was to study caribou winter food habits and movements as related to snow depth and condition (Miller, 1973). On February 26 we searched the 51.8 km² surface of Hara Lake by dog team for wolf-killed caribou and to make specimen collections. On our return to Hara Lake in April we noted that intensive predation was occurring in the area, and it seemed that useful data on wolf predation might be obtained for a comparatively small amount of work. My two assistants, therefore, made daily dog team excursions over half the Hara Lake area in search of wolves and wolf-killed caribou carcasses. The lake surface was separated into four parts according to size and convenient landmarks for systematic coverage and location reference of observations. Notes were recorded on wolf sightings as to location, time, numbers, colors and activity. The head, mandibles and right hind leg from each carcass were tied together and transported back to camp. Wooden stakes were used to mark the location of wolf kills. I made similar observations and collections during daily snowshoe excursions in the course of collecting range data. General observations of caribou and wolf movements, distribution and behavior on Hara Lake were made from a wooden platform erected about one meter above the snow level on an open promontory 200 m from camp. We used binoculars, 7 X 35 wide angle lens, and a zoom scope, 15 to 60x mounted on a tripod for long range observations.

Sex of wolf-killed caribou, in the absence of genital organs, was determined from the presence and size of antlers (Kelsall, 1968). Age was assigned from tooth replacement and wear (Skoog, 1956). Caribou with complete permanent dentition were assigned to three broad classes: young adults (three and four year olds), prime adults (approximately five to seven year olds) and old adults. Old adults included age classes of eight years and older with lingual crests worn almost even with buccal crests and the posterior column of third molars worn down near the gum line.

Physical condition of wolf-killed caribou was determined from the fat content in marrow specimens from the femur or tibia. Bone marrow was extracted in the field, stored under cover during natural weather conditions in sealed plastic bags and fixed in 0.5 per cent solution of formalin in the laboratory at Ottawa. The lipid content was determined by Dr. Q. Laham of the University of Ottawa using ether extraction and centrifugation (Entenman, 1957).

RESULTS AND DISCUSSION

Caribou Densities and Distribution

Monthly aerial surveys by Parker (1970) showed that caribou densities around Hara Lake varied from 22 per km² (57.0 per mi²) in January to 63 per km² (162.0 per mi²) in April (Table 1). Parker estimated 51,000 caribou wintered in the Hara-Charcoal Lakes region of Saskatchewan distributed over approximately 8,300 km² in January and 1,800 km² in April. Caribou densities were consistently higher around Hara Lake than in the entire survey area. These migrant caribou densities around Hara Lake were higher than Klein (1968) reported for resident reindeer on St. Matthew Island, prior to a population crash.

TABLE 1.--Caribou and wolf densities as determined by mid-monthly aerial surveys at Hara Lake, Saskatchewan and the adjacent area inhabited by the Manitoba-Keewatin herd from January through April, 1968. Survey strip was .37 km (.23 mi) wide on either side of the plane at 152.4 m (500 ft.) altitude. Data from Parker (1970).

Area	Month	Square kilometers	Caribou estimate	Caribou per 1 km ²	Wolves per 1 km ²	Wolf estimate
Hara Lake	Jan.	259	5,700	22.0 *(57.0)	.00 *(.00)	0
	Feb.	259	10,770	41.6 (107.7)	.09 (.24)	24
	Mar.	259	7,100	27.4 (71.0)	.18 (.46)	45
	Apr.	259	16,242	62.5 (162.0)	.17 (.44)	43
Entire Area	Jan.	8,308	51,545	5.4 (14.0)	.03 (.07)	326
	Feb.	3,300	50,204	15.2 (39.4)	.05 (.13)	163
	Mar.	2,253	57,110	25.3 (65.6)	.04 (.11)	96
	Apr.	1,766	46,779	26.4 (68.5)	.03 (.09)	62

*() = number per square mile.

According to ground observations caribou migrated into the Hara Lake area in mass on February 19, 1968 (Fig. 1). The spring migration out of the Hara Lake area occurred about

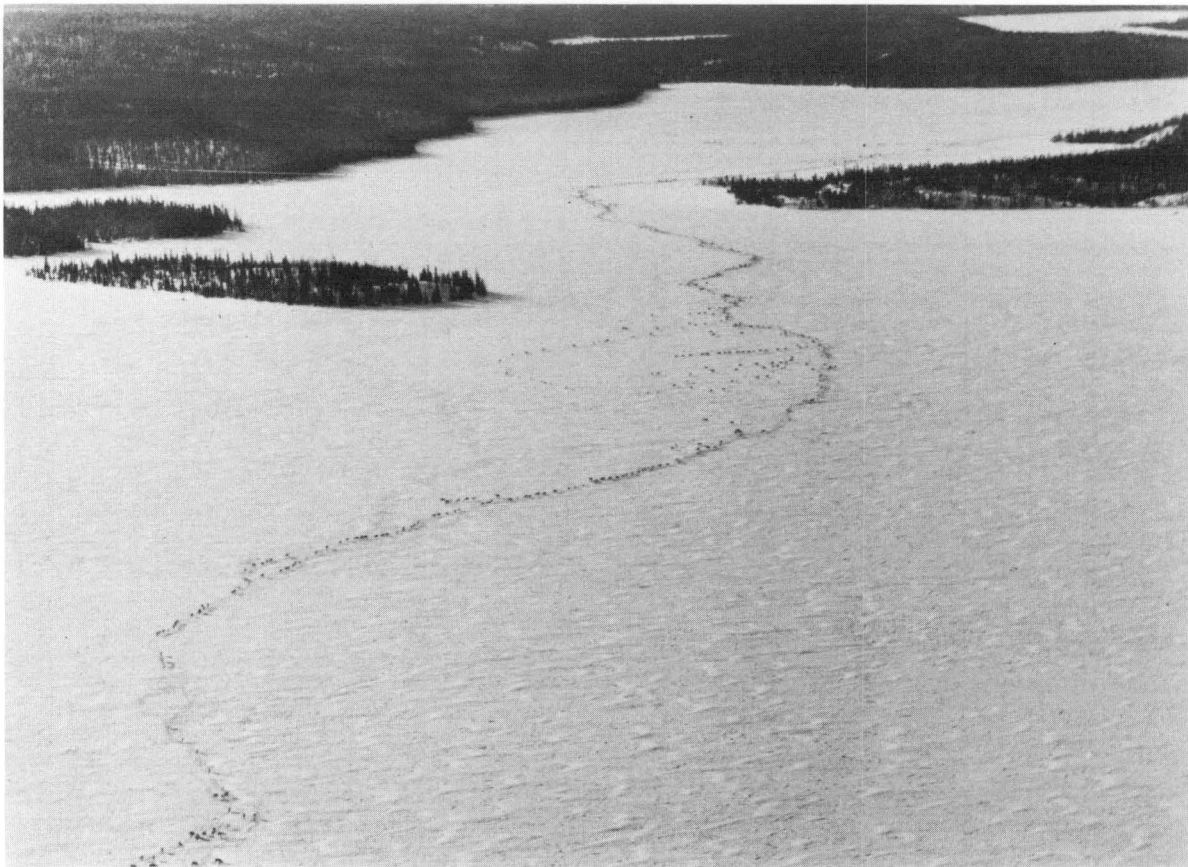


Fig. 1.—Caribou migration on south end of Hara Lake, Saskatchewan, February 19, 1968.

mid-May (Parker, pers. comm.) although animals from the south migrated north over Hara Lake as early as April 24. A total of 44 observations during April-May of 12 caribou marked with numbered collars indicated that the animals which resided at Hara Lake during the April-May study period did not move north with the migrants from the south.

Wolf Densities and Distribution

Parker (1970) made wolf counts during his 1968 monthly aerial caribou surveys. Wolf densities varied in the Hara Lake area from none observed in January to 1.7 per km² in March (Table 1). With the exception of January, Parker's aerial wolf observations show that wolf densities were greater around Hara Lake than in the entire survey area.

Cursory ground observations at Hara Lake in February yielded eight sightings of a total of 15 wolves ranging from one to five per observation. During April-May, 77 sightings of a total 211 wolves were made on the ground ranging from one to 12 per observation (Table 2). I believe eight different wolves were observed at Hara Lake in February and about 16 between April 18 and April 27.

Observations of 23, 34 and 32 wolves, respectively, moving north on Hara Lake during

TABLE 2.--Daily wolf observations made on the ground at Hara Lake, Saskatchewan
April 19 to May 6, 1968.

	April												May						Total
Date of observation	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	
No. of wolves seen	4	13	4	10	16	8	19	16	0	23	34	32	12	3	8	0	3	6	211
No. of packs seen	2	3	3	7	7	3	9	8	0	5	8	10	4	3	2	0	1	2	77
No. of wolves/pack	1-3	1-10	1-2	1-3	1-5	2-3	1-4	1-7	-	2-7	1-12	1-11	1-6	1	1-7	-	3	1-5	1-12

April 28, 29 and 30 suggested a migration of tundra wolves through the area (Table 2). Apparently the number of wolves frequenting Hara Lake after May 1 returned to the February level of about eight individuals. Color combinations of wolves within several packs revealed a difference in observations made prior to and after this three-day period. Four wolf packs were observed with more than two white or two black individuals during April 28, 29 and 30. No similar observations were made before April 28 or after April 30. The ratio of gray, white and black wolves respectively observed on Hara Lake was 35:8:13 prior to April 28, 43:19:11 on April 28 to 30, and 25:5:0 after May 30.

Wolf Hunting Methods

We observed portions of four wolf hunts on Hara Lake including a slow approach and brief attempt to gain a strategic position, an unsuccessful chase and two successful attacks. Several instances of wolves testing (Mech, 1966) caribou were observed on the lake ice. On one occasion when a caribou took a separate course from the band, the approaching wolf responded by seeking a strategic position between the lone animal and its band. Unfortunately the wolf detected our presence and departed. Apparently wolves at Hara Lake successfully employed the test and chase method to capture caribou (Murie, 1944). In forest cover the chase was employed but the approach which led to the chase in forest cover was unknown. Kelsall (1968) mentioned three methods used by wolves to capture caribou: (1) ambush, (2) relay run and (3) chase large bands and concentrate on animals that stumble, fall behind or in other ways become vulnerable. At Hara Lake the ambush method may have preceded the chase in forest cover but there was no indication of a relay run method.

Our observations at Hara Lake indicated that wolves took caribou fortuitously in forest cover, but on the snow and ice-covered lake they captured animals that fell behind or failed to synchronize their movements with other members of the band. Caribou which become separated from the band during a wolf attack were vulnerable when they attempted to rejoin the band. According to tracks in fresh snow and especially blood trails of wounded animals, wolves gained their main advantage by cutting corners on prey that made sharp turns. Wolves attempted to knock running caribou off their feet or use combined efforts of rush and retreat tactics to down caribou brought to bay or forced to stop. Caribou showed no defense when off their feet. Two caribou, when brought to bay by wolves, attempted unsuccessfully to defend themselves by using their antlers. I could find no reference in the literature of caribou using their antlers for interspecific defense. Burkholder (1959:7) states that "Caribou depend primarily upon their ability to run, having little if any defense otherwise."

April-May observations at Hara Lake showed that wolves hunted primarily at night after dusk and before dawn, although two daytime attacks and two attempted attacks were observed.

Carcass Utilization

According to 12 early morning observations on Hara Lake wolves had consumed up to 90 per cent of caribou killed during the previous night. Fawns were utilized more completely than older animals. More than 50 per cent of the caribou carcass remained at seven of the 12 kills. Tongue, neck, internal organs, fat deposits and the fetus of pregnant prey were consistently missing from partially eaten caribou. Observations of 10 caribou killed by wolves more than two days earlier showed that two carcasses were stripped of all flesh and two had more than 50 per cent flesh remaining. To what extent ravens contribute

to the use of caribou carcasses is unknown, but up to 20 ravens were observed on a single wolf kill. Ravens often found wolf-killed caribou before we did, and in one instance, two ravens were observed taking meat from a carcass a few meters from a wolf. Wolves occasionally returned to and utilized marked carcasses but they made little use of previously marked kills during April-May. To what extent our presence and collections from marked kills acted as a deterrent to subsequent use by wolves is unknown. Mech (1970) reported that wolves returned to old moose kills on Isle Royale until completely consumed, except for one kill which he had interfered with during the summer. Kolenosky (1972) reported that wolves periodically visited white-tailed deer (*Odocoileus virginianus*) kills in Ontario until the flesh had been consumed.

With three exceptions wolves had fed upon carcasses found. On two occasions we disturbed wolves immediately after a kill. Another caribou was found that had apparently escaped a wolf attack but later died from bites in the hind leg.

Large wolf packs made more efficient use of a caribou kill than small packs. On two separate occasions when two wolves were observed during early morning feeding on a fresh kill older than a fawn, less than a third of the flesh was utilized. Ravens and bald eagles (*Haliaeetus leucocephalus*), which first appeared at Hara Lake on April 29, utilized fresh carcasses during the day. Larger wolf packs left less of a fresh kill for scavengers. Burkholder (1959), Mech (1966) and Kolenosky (1972) have commented on the use of prey by large wolf packs. These data suggest that when prey are vulnerable, as caribou were at Hara Lake during April-May 1968, a pack of six wolves would kill fewer than two packs of three wolves.

Rate of Kill

At least 160 caribou are known to have been killed by wolves at Hara Lake during the winter of 1967-68 with 147 of these occurring from February 26 through May 6. Wolves killed an average of two caribou per day prior to April 17 and an average of three caribou per day between April 19 and May 7 (Table 3). There was a significant difference in the kill by wolves between the two periods ($P < 0.05$). This kill observed at Hara Lake suggested wolves had little difficulty in locating vulnerable caribou among the many animals that concentrated on and migrated over the lake.

Multiple kills by wolves during a single hunt were not observed at Hara Lake during any of my field trips in the taiga among barren ground caribou. However, wolves made fresh kills in the presence of partially eaten, frozen carcasses when vulnerable caribou were available. Pimlott *et al.* (1969) and Mech *et al.* (1971) reported similar observations with white-tailed deer in Ontario and Minnesota respectively. Therefore, the occurrence of more than one partially eaten, wolf-killed caribou or other prey at the same site is not bona fide evidence of a multiple kill. Banfield (1954) observed numerous wolf-killed caribou in the wake of a large concentration of migrating caribou. Kelsall (1968:253) observed six partially eaten, wolf-killed caribou on a single lake which probably represented a kill made over a number of days similar to what occurred at Hara Lake. There was no indication that wolves killed caribou at Hara Lake beyond their immediate needs for food.

Location of Kill

Wolves captured caribou prey primarily in the main portion of Hara Lake (Areas B & C, Fig. 1). Distribution of kills on Hara Lake between February 26 and May 7 suggest some influence from our camp site and associated daily activities after April 18 compared with the period of our absence between February 27 and April 18. Area D at the north end of

TABLE 3.--Age and sex composition of Kaminuriak caribou population as determined for free ranging animals and wolf kills at Hara Lake, Saskatchewan and scientific collections during winter of 1967-68.

Sample	Age classes (%)			Sex % (ans. 1 yr.+)		
	Sample size	Fawns	1-7 yr. old	8 yrs. (plus)	Sample size	Males Females
Free ranging						
Nov. 26-Dec. 13	933	17.3		*82.7	-	- -
Feb. 17-Feb. 27	3,284	15.8		84.2	566	14.1 85.9
April 19-May 7	3,927	11.3		88.7	298	9.7 90.3
Scientific collection						
Nov. 28-Dec. 12	105	13.3	78.1	8.6	91	47.3 52.7
April 12-May 2	103	10.7	80.6	8.7	92	59.8 40.2
Wolf kill						
Feb. 27-April 18	94	17.0	79.8	3.2	37	2.7 97.3
April 19-May 7	53	22.7	66.0	11.3	21	19.0 81.0

*Old animals could not be segregated in free-ranging caribou sample.

the lake was inhabited by two Chipewyan Indian wolf hunters after May 1 which influenced both caribou movements and wolf activities during the last week of these observations. They killed one wolf and several caribou up to May 7.

Wolf-killed caribou were not evenly distributed over Hara Lake but tended to be in groups of two to six in close proximity to each other. Large areas of the lake were devoid of any wolf kills. This suggests that certain sites provide wolves with an advantage over their prey, such as topographic features, as suggested by de Vos (1950), and/or that wolves repeat the use of routes and hunting tactics that produced results during previous hunts as suggested by Rutter and Pimlott (1968). Snow-depth and hardness, which influence caribou movements and feeding patterns (Miller, 1974), also had a bearing on where wolves captured their prey.

Age and Sex of Wolf-killed Caribou

Fawns comprised 18 per cent of the 147 caribou known to have been killed by wolves at Hara Lake between February 16 and May 7, 1968 (Table 3). This was significantly ($\chi^2 = 4.0$, $df = 1$) larger than the proportion of calves in the February and April-May segregated sample of free-ranging caribou ($n = 7,211$). According to the known wolf kill, fawns had not been selected prey prior to April 19 ($\chi^2 = .115$, $df = 1$). However, because of their smaller size and more complete consumption by wolves, our data concerning old kills found April 19 to May 7 could be biased against fawns (Pimlott *et al.*, 1969; Mech and Frenzel, 1971; Kolenosky, 1972). Our fresh wolf-killed caribou sample indicated that fawns were selected prey between April 19 and May 7 when 22.7 per cent fawns were among 53 wolf kills compared with 11.3 per cent fawns in the segregated sample of 3,927 caribou ($\chi^2 = 5.096$, $df = 1$). Mech (1966) and Shelton (1966) found wolves selecting moose calves as prey during the winter on Isle Royale while Pimlott *et al.* (1969) and Kolenosky (1972) did not find a wolf selection for white-tailed deer fawns in Ontario, and neither did Stenlund (1955) and Mech and Frenzel (1971) in Minnesota. Burkholder (1959) reported no selectivity of wolves for fawn caribou in Alaska among 22 kills although he listed two fawns among six described instances of predation and could not determine the age of six other kills. Burkholder did report that wolves selected moose calves.

Caribou eight years of age and older comprised 6.8 per cent of the total 147 wolf-killed caribou sample (Table 3). Old caribou were much more heavily represented among wolf kills after April 19 when 11.3 per cent of 53 wolf kills were old animals compared to 4.3 per cent of 94 killed prior to April 19. The overall kill of old caribou by wolves was somewhat less than the 8.9 per cent animals eight years and older in a shot-killed sample of 101 caribou taken in April, 1968 from the same population and aged by tooth sectioning (F. Miller, 1970). However, seven of nine old animals in the shot sample were eight year olds and the remaining two were nine years old. Five wolf kills were older than nine according to a visual comparison of tooth wear with F. Miller's sample. Although the sample sizes are small the apparent selection by wolves for old caribou during April and early May is consistent with findings of Crisler (1956) in Alaska. Old moose are selected prey of wolves during the winter on Isle Royale (Mech, 1966) and white-tails in Ontario (Pimlott *et al.*, 1969; Kolenosky, 1972) and in Minnesota (Mech and Frenzel, 1971). Although Burkholder (1959) does not consider that old caribou were selected by wolves during his winter observations of 22 kills in Alaska, he lists two of six kills in which age is given as 10 years or older. This would be almost 10 per cent of the 22 caribou observed of which six could not be aged.

Caribou at Hara Lake were not selectively killed by wolves according to sex. Segregated

samples of 755 free-ranging caribou during February and April-May study periods compared with 58 wolf kills showed no significant difference (chi-square = .819, df = 1).

The fat content of bone marrow from wolf kills on Hara Lake indicated that except for fawns most of the caribou prey were not suffering from malnutrition. Marrow fat content of wolf-killed caribou was compared with that of a sample shot from the same population during the same period (Dauphiné, 1970). Only in fawns did the wolf-killed animals have significantly ($P < 0.05$) lower fat content. These findings closely parallel those of Mech and Frenzel (1971) for white-tails in Minnesota. They reported that fawns that were delayed in tooth development and replacement were selected by wolves. In the case of animals older than fawns, however, the bone marrow analysis method is useful only to determine later stages of malnutrition (Riney, 1955).

Comparison of Hara Lake Observations with Other Winters

The frequency of wolf kills observed around caribou herds studied in northern Manitoba and Saskatchewan in late winters of 1966, 67 and 72 was much lower than observed at Hara Lake in 1968. Observations of caribou distribution at Hara Lake in 1968 were unique in that caribou concentrated in a higher density and remained in one area longer than observed during the other winters. Evidently these circumstances predisposed caribou to intensive predation by wolves.

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STATUS OF THE SELKIRK MOUNTAIN CARIBOU

David J. Freddy and Albert W. Erickson
Wilderness Research Center and the Department of Biology
University of Idaho
Moscow, Idaho

ABSTRACT—The Selkirk Mountain caribou (*Rangifer tarandus montanus*) are the only naturally remaining caribou in the contiguous United States, being found in the Selkirk Mountains of northern Idaho, northeastern Washington and southern British Columbia, Canada. Observations indicate there is a minimum of 35 caribou in the herd. These animals are divided into at least three small groups and occupy a somewhat discontinuous range. The animals wintered in the subalpine fir-Engelmann spruce forest in areas of moderate relief between the elevations of 1,380 m and 2,160 m. Arboreal lichens of the genus *Alectoria* comprised the main winter food. Ecological damage to already limited winter range could seriously jeopardize the size and distribution of this herd. Special land classification, logging restrictions, forest fire control and continued protected status for these animals are essential management considerations.

With the exception of occasional field work accomplished by Flinn (1959) and Bierman (1967) and the historical accounts presented by Evans (1960) and Layser (in press), this study is the first detailed investigation of the mountain caribou (*Rangifer tarandus montanus*) existing in the Selkirk Mountains of northern Idaho, northeastern Washington and southern British Columbia, Canada. The study is an international cooperative effort acknowledging that the animals are a common population interchanging between Canada and the United States. The portion of the herd inhabiting the U. S. is believed to comprise the only naturally remaining herd of caribou in the contiguous U. S.

In the late 1800's caribou were found as far south as central Idaho (Evans, 1964), but since 1900 the animals have been limited to areas near the Canadian-U. S. border, principally the Selkirk Mountains (Edwards, 1958; Evans, 1964). Reported to occur in the hundreds around 1900, the largest recorded group of caribou seen since has been 24 in 1964 (Layser, in press). Evans (1964) attributes the presumed decrease in caribou numbers to illegal hunting and to range deterioration resulting from forest fires and logging.

Although penetrated by logging and mining roads, the Selkirk area remains largely inaccessible throughout the winter, with much of the area receiving over 12 m of snow annually. The Selkirk Mountains are highly glaciated with steep narrow river valleys predominating. Elevations within the study area range from 750 m to over 2,100 m. Mature stands of cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*) and white pine (*Pinus monticola*) characterize the lower elevations and gradually give way to Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) communities dominating the high terrain. As with many forested regions, forest fires have greatly influenced the physiognomy of the area (Daubenmire and Daubenmire, 1968).

The objectives of the present study are to ascertain the abundance, composition and distribution and movements of the herd and to prepare management recommendations for perpetuating these unique animals.

METHODS

Field work for this study commenced in January, 1972 and will continue through December, 1972. The study area encompasses approximately 3,000 km² in northern Idaho, northeastern Washington and southern British Columbia (Fig. 1). The land is administered

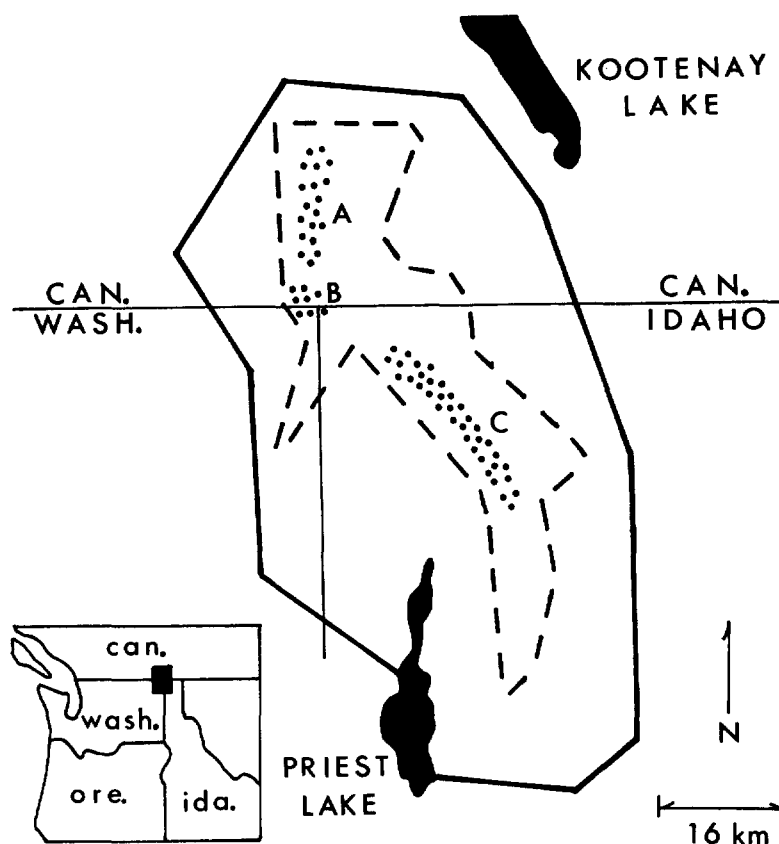


Fig. 1.—Study area (solid line), distribution of the caribou as of July, 1972 (dashed line) and areas of concentrated caribou activity (dotted areas).

by the U. S. Forest Service, the Idaho Department of Public Lands, the British Columbia Forest Service and the British Columbia Parks Branch. Management responsibility for the caribou rests with the Idaho Department of Fish and Game, the Washington Department of Game and the British Columbia Fish and Wildlife Branch.

Systematic surveys of the entire study area are being conducted to document caribou movements and activities and to estimate abundance on the basis of observed animals and track sign. To gain further insight into the distribution and movements of the herd, attempts are being made to radio-mark representative animals. Information concerning habitat use and preferences, food habits, mortality, reproductive success and population composition is being compiled from observations in the field.

With the use of U. S. and British Columbia Forest Service timber inventory maps, forest areas utilized by caribou are being described and predictions made of potential conflicts with timber management programs. To further describe habitat requirements,

sightings of caribou and of their sign are also being related to slope, aspect, elevation and forest canopy coverage. Visual estimations of the availability and abundance of arboreal lichens are also assigned to areas used by caribou and to general areas within the distributional limits of the herd.

RESULTS

Aerial and ground observations compiled to date show the Selkirk caribou to almost exclusively inhabit subalpine fir-Engelmann spruce communities from February through early July. From February through May, 67 of 72 observations (93 per cent) were in this forest type and at elevations above 1,380 m. The lowest occurrence noted was 960 m and the highest 2,160 m. From June through early July, 27 of 27 observations of caribou were at elevations above 1,380 m. The lowest recorded sighting was at 1,410 m and the highest at 2,070 m. The 1,380 m elevation approximates the beginning of the spruce-fir community in the Selkirk Mountains.

Of the total sightings to date, 7 per cent have occurred on land classified as non-forest land (tundra-like), 18 per cent in non-commercial forest (having low economic value), and 75 per cent in mature timber (having commercial value). The timber stands utilized are typically semi-open with canopies often covering less than 50 per cent of the area.

Observed movements show these caribou prefer ridges and high, moderately steep basins or small bench areas during the winter and spring. In moving between these high basins, the caribou directly transect intervening river valleys which appear to be utilized as essential travel lanes rather than feeding areas, even though the valleys frequently contain luxuriant stands of arboreal lichens. One group of five to eight caribou frequented seven specific feeding areas within an approximate 30 km² area during April and May. The animals established habitual and direct movement routes between these feeding areas, including crossings of a main TransCanada highway.

Observations in June and early July suggest little difference between the summer and winter ranges of these caribou. In the summer, the animals appear to prefer open slopes or tundra-like areas which generally occur above 1,800 m in areas adjacent to the winter ranges. Observations indicate that these caribou do not move to lower elevations in April or May as do the caribou in Wells Gray Park, British Columbia, approximately 400 km north of the study area (Edwards and Ritcey, 1959).

Feeding observations compiled throughout this winter and spring revealed that these caribou were feeding almost exclusively on the arboreal lichens, *Alectoria jubata* and *Alectoria sarmentosa*. No other foods were known to be taken through mid-June, but green forage was widely available in June and may also have been eaten. Edwards and Ritcey (1960) found the mountain caribou inhabiting Wells Gray Park to consume arboreal lichens and various forbs from May through August.

The behavior of these animals when feeding is to meander over a relatively small area casually stripping lichens from tree branches and occasionally reaching through branches towards the tree trunk where lichens are often present in greatest quantities. Lichens on recently fallen trees are also consumed. Digging feeding craters, as described by Kelsall (1968), is an impractical means for these animals to obtain food since snowpacks exceed 3 m.

The availability of arboreal lichens appears to be related to timber stand density and snowpack depths. *A. sarmentosa* occurs in the Selkirks as low as 750 m, but at this low elevation the cedar-hemlock forests are extremely dense, causing this lichen to grow high in the canopy, thus rendering it unavailable as food for caribou. Arboreal lichens generally become available to caribou between the elevations of 1,350 m and 1,440 m depending on

snowpack depths. At these elevations, the lichens are 3 to 4.5 m above the ground and are primarily composed of *A. sarmentosa*. At 1,650 m lichens grow 2.4 to 3 m above the ground, and with peak snowpacks of 3 to 3.6 m these lichens are readily available. Lichen availability improves with increases in elevation possibly due to the more favorable microclimatic conditions resulting from less dense timber stands (Edwards *et al.*, 1960; Ahti and Hepburn, 1967).

With an increase in elevation, the lichen composition also changes to the extent that *A. jubata* almost exclusively dominates above 1,650 m, especially on exposed ridges. Edwards *et al.* (1960) found similar results for the distribution of *A. jubata* in British Columbia. *A. jubata* is the dominant lichen in the high basins and benches selected as feeding areas by the Selkirk caribou.

Prior to this study, no specific attempt had been made to ascertain the numerical status of the Selkirk herd. Eleven fixed-winged survey flights conducted between March and July combined with observations on the ground indicate there is a minimum of 35 caribou in the herd. Fourteen different animals were observed. The present distribution of these caribou corresponds with the recorded historical caribou range in the Selkirk Mountains (Fig. 1).

Track sightings and known animal groups observed to date indicate three areas of concentrated activity (Fig. 1). At least three, and possibly four small groups of caribou were in these areas throughout this winter and spring. The area entirely in Canada contains a minimum of 12 caribou (area A, Fig. 1). Minimal estimates indicate four animals reside in an area on the international border (area B) and 10 animals reside in an area northeast of Priest Lake entirely within the U. S. (area C). Tracks indicated that some interchange of individuals occurs between these groups.

Mortality factors acting on the Selkirk herd and their significance are largely unknown. However, road kills and illegal hunting may be important. One road kill was recorded in 1972 and five in 1964 (Layser, in press). To what extent illegal hunting occurs is not known, but five such kills were recorded in 1964 (Layser, in press). Grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), lynxes (*Lynx canadensis*) and coyotes (*Canis latrans*) inhabit the area but there is no evidence suggesting these predators influence the status of the caribou.

Forest fire records dating to the late 1800's indicate much of the study area has been burned, especially at the lower elevations. In 24 instances during 1972, caribou were observed to visit burns that occurred at high altitudes. In 15 of these cases, tracks indicated the animals only traveled through the burned area. In nine cases some feeding occurred; and in one instance, the animals fed in small pockets of trees missed by the fire.

Since 1955, numerous roads, primarily for logging, have penetrated the major portion of the Selkirk caribou range. The completion of a TransCanada highway in the early 1960's further opened many Canadian areas to logging and also introduced highway mortalities as a herd mortality factor. Some spruce-fir timber has been harvested but logging has been concentrated in the lower cedar-hemlock forests.

In addition to caribou, substantial populations of mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) and limited populations of elk (*Cervus canadensis*), moose (*Alces alces*), mountain goat (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) reside within the study area. Small numbers of domestic cattle are also summered in areas within the caribou range. No direct association between these animals and caribou has been observed; and therefore, competition influences remain unknown.

DISCUSSION

The primary winter range of the Selkirk caribou from February through May is the subalpine fir-Engelmann spruce forest above 1,380 m. Within this zone the animals seek feeding and resting areas of moderate terrain and cross, via habitual travel routes, intervening ridges and upper river valleys. Logging in the subalpine forest has been restricted to areas of moderate relief due to road construction costs and the ecological consequences of logging on steep slopes with unstable soils. Thus, a potential conflict exists between caribou winter range and the harvesting of spruce-fir timber. However, the rotation time for the spruce-fir forest in the Selkirks appears to exceed 150 years which may reduce the commercial value of this timber. Short-term economic arguments may favor exploitation of the spruce-fir timber; but, in the long run, such forests may be better suited to watershed resources and recreation.

Although indicated to be of minimal importance to caribou at this time, the cedar-hemlock forest from approximately 1,350 m to 1,380 m may be potentially important to caribou for several reasons. First, if a downward movement occurs in the fall as reported by Edwards and Ritcey (1959), this forest type could be valuable as early winter range. Secondly, during years of abnormally high snowfall, caribou may find the upper hemlock zone suitable, or in the case of population expansion, essential. Thirdly, this forest may also serve as an important buffer zone between intensively and extensively managed forest areas. Historical records indicate that the animals used the upper hemlock forest, but the sightings were generally associated with logging operations which made sizeable amounts of lichens available and thus possibly attracted the animals to these areas.

Currently, part of the known caribou winter range is either already under or is being considered for special land management classification. However, several important segments of the winter range are currently classed as merchantable timber and should be considered for special classification. The apparent limited movements of these caribou between summer and winter ranges makes special land classification practical because it is unnecessary to protect long migration routes (Kelsall, 1968).

With the current population consisting of small bands of caribou occupying a somewhat discontinuous range, each herd segment is in a potentially precarious state. Ecological damage to the already limited wintering areas, significant mortalities, or both could seriously jeopardize the size and distribution of any one group. It seems unlikely that a diminution of one group would be compensated for by improved welfare for the remaining portions of the herd. Therefore, it seems that any effective management program must consider both the Canadian and U. S. portions of the herd and range. In his recent policy statement, the Chief of the U. S. Forest Service emphasizes giving protection to rare and endangered species of native animals and to critical wildlife habitat areas such as winter ranges, calving areas and migration routes (USDA, 1972). Such protective considerations are certainly in order for this endangered population of caribou and land management policies must consider the essential range requirements of these animals.

Considering the information obtained to date, the following management procedures are recommended:

1. Logging should be prevented in those spruce-fir forest areas known to be of importance to caribou. Special land classifications should be considered to preserve known essential winter ranges and travel lanes.
2. Consideration should be given to maintaining areas of hemlock forest above 1,350 m near or adjacent to prime winter ranges to serve as potentially needed early winter ranges and as buffer zones.
3. Controlling forest fires in, and adjacent to, prime winter ranges should be given high

priority.

4. Consideration should be given to closing roads into winter ranges.
5. The protected status of these animals should be continued with more effective law enforcement in known areas of illegal hunting.
6. To measure population trends, the agencies responsible for management of these caribou should conduct an annual aerial census in April when snow covers the entire caribou range and good weather prevails.
7. To minimize highway fatalities, consideration should be given to installing speed controls, drive fences and signs at Kootenay Pass on TransCanada Highway No. 3.
8. To prevent the introduction of brucellosis into this caribou herd, measures should be taken to allow only cattle free of brucellosis to graze within the caribou range.
9. Restrictions on hunting of other game species in the area are not proposed, but consideration should be given to minimizing the accidental killing of caribou by hunters by using education programs, signs or special permit systems.

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CHARACTERIZATION STUDIES ON RUMEN BACTERIA ISOLATED FROM ALASKAN REINDEER (*RANGIFER TARANDUS* L.)

B. A. Dehority
Department of Animal Science
Ohio Agricultural Research and Development Center
Wooster, Ohio

ABSTRACT—A total of 141 strains of rumen bacteria were isolated on a non-selective medium from semi-domestic Alaskan reindeer (*Rangifer tarandus* L.). Seventy-one strains were obtained from two animals being fed alfalfa pellets, 49 strains from an animal feeding on lichen, browse and native pasture and 21 strains from this same animal after two weeks on a ration of dried lichens. Based on general morphology, the 21 strains from this latter isolation series were divided into seven groups. Thirteen strains, at least one from each morphological group, were then reisolated to insure culture purity, and studied in detail. Three morphological types, varying considerably in physiological characteristics and fermentation end products, all appear to belong to the genus *Butyrivibrio*. Three additional morphological types have been classified as belonging to the genera *Treponema*, *Streptococcus* and *Lactobacillus*. The remaining morphological type varied from previously described species. Microscopic examination of the 49 cultures isolated from this same animal just prior to changing to the dried lichen feed revealed that the majority of organisms were morphologically similar to those described above. However, a considerably higher percentage of coccus types was observed. Using a selective cellulose medium, 21 strains of bacteria were isolated from the alfalfa pellet fed semi-domestic reindeer. Eight strains morphologically resembled organisms in the genus *Butyrivibrio* and nine the genus *Ruminococcus*. Two of the *Butyrivibrio* and all of the *Ruminococcus* type strains were extremely active in their ability to digest cellulose.

Several preliminary investigations have been made on the bacteria occurring in the rumen of reindeer; however, they have been limited to gross microscopic examination of total rumen contents. Giesecke (1970), in a paper presented in 1969 at the Third International Symposium on the Physiology of Digestion in the Ruminant, presents unpublished results obtained by Drescher-Kaden and himself on total microscopic counts of rumen bacteria for several reindeer from Lapland, Finland. Also presented are unpublished results of Hobson on Scottish reindeer, which include total microscopic counts and a listing of the morphological types of bacteria observed while the reindeer were grazing summer range. In general, the morphological types observed appeared to be representative of those observed in other ruminants.

Since so little is known about the rumen bacteria of reindeer, especially for those animals residing in the far northern or arctic environment, the present study was initiated in Alaska during the summer of 1970. Pure culture techniques were employed to isolate and subsequently characterize rumen bacteria from several semi-domestic reindeer (*Rangifer tarandus* L.).

MATERIALS AND METHODS

The anaerobic cultural techniques used in this study were similar to those described by Hungate (1950). Methods of preparation of media, dilution of rumen ingesta, characterization studies, etc., have been previously described (Dehority, 1963, 1966, 1969). Isolations were made with a non-selective medium containing glucose, cellobiose and starch as energy sources, or a selective medium containing purified cellulose as the only added substrate. When rumen fluid was available from the animal prior to the actual sampling for isolation, a 40 per cent rumen fluid basal medium similar to that described by Bryant and Burkey (1953a) was employed. In those cases where rumen fluid could not be obtained from the animal previously, a medium somewhat similar in composition to that of Caldwell and Bryant (1966) was used, to which 10 per cent reindeer rumen fluid was added.

Most isolations on non-selective medium were made from 1×10^{-7} or 1×10^{-8} g of rumen contents; however, a few isolates were obtained from 1×10^{-6} and 1×10^{-9} g. Colonies were picked after incubation at 38°C for a period ranging from 30 to 72 hours. Cellulolytic bacteria were isolated from 1×10^{-6} , 1×10^{-7} and 1×10^{-8} g of rumen contents after incubations ranging from nine to 23 days.

All of the bacterial isolation work was conducted at the Institute of Arctic Biology, University of Alaska. After isolation, the stock cultures were stored at -76°C , and subsequently transported with dry ice to the Ohio Agricultural Research and Development Center, where characterization studies were initiated.

RESULTS AND DISCUSSION

Table 1 lists the specific details and number of bacterial isolates obtained in this study. To date, the 49 isolates from the ARC series, all of which were viable, have been transferred and examined microscopically. All but one culture (ARB series) from the cellulose medium isolates were viable and these strains have been examined by phase microscopy, tested for their ability to digest cellulose broth, and end products have been determined on the different morphological types which were strongly cellulolytic. The 21 isolates from the ARD series were all viable, and the major portion of the studies to be reported will be on this series. It was believed that since the animal had been feeding on alpine tundra and browse, and then changed to a ration of dried lichen two weeks before sampling, those bacterial species still active should represent the organisms best adapted for survival under adverse arctic conditions. Although total viable counts were not made, colony numbers per roll tube of the same dilution for the ARD series were approximately 10-15 per cent of the number observed in the ARC series.

Based on morphology and motility, observed with the phase microscope, the 21 cultures in the ARD series were divided into seven morphological types. These data are shown in Table 2. Thirteen cultures, at least one from each morphological type, were then reisolated through roll tubes to insure culture purity. A second reisolation was required for two strains, ARD-10f and ARD-3a, since two morphological types were obtained in the first reisolation. As noted in Table 2, none of the 21 cultures were able to visibly digest purified cellulose in a broth medium. These results were subsequently confirmed for the 13 reisolated strains.

Tables 3 and 4 present the morphology, physiological characteristics and organic acid end products for the 13 reisolated strains. The three strains of morphological type 1 (Table 3) were quite consistent in all properties, with the exception of some variations in organic acid end products. On the basis of these criteria, the three strains can be placed in the genus *Butyrivibrio* as described by Bryant and Small (1956a). Since many characteristics of the 48

TABLE 1.--Bacterial isolations from Alaskan reindeer cows (*Rangifer tarandus* L.)

Animal number	Series number	Ration	Location	Sampling method	Number of isolates	
					Non-selective medium	Cellulose medium
16	ARA	Alfalfa pellets	I.A.B.-P ^a	Fistula	44	17
4	ARB	Alfalfa pellets	I.A.B.-EC ^a	Fistula	27	4
9	ARC	Alpine tundra and browse	Cantwell, Alaska	Stomach tube	49	1
9	ARD	Dried lichens	Cantwell, Alaska	Stomach tube	21	- ^b

^aI.A.B. - Institute of Arctic Biology, College, Alaska. P - outside pen, EC - housed in an environmental chamber.

^bNo cellulose medium isolations were made in this series due to shortage of time required for incubation.

TABLE 2.--Morphological type, motility, distribution and strains reisolated from bacterial cultures in series ARD^a

No.	Morphological type	Motility	No. of cultures	Strains reisolated
1	Small curved rods	+	9	ARD-22a, ARD-24b, ARD-36a
2	Large crescent-shaped to twisted rods	+	2	ARD-10f5, ARD-34a
3	Coccoid to oval cells	-	2	ARD-5d
4	Large straight rods, varying in length	-	1	ARD-26e
5	Spirochete	+	1	ARD-30b
6	Medium size crescent shaped rods	$\frac{-}{+}$ ^b	5	ARD-23c, ARD-27b, ARD-31a, ARD-39e
7	Medium size straight rods	$\frac{-}{+}$ ^b	1	ARD-3a3

^aNone of the cultures were able to visibly digest purified cellulose in a broth medium.

^bOccasional motile cells appeared to be present.

isolates studied by these authors varied considerably, they defined only a single species, *Butyrivibrio fibrisolvens*. Hungate (1966) later proposed a second species, *B. alactacidigens*, for those strains which do not produce lactic acid as an end product of carbohydrate fermentation. However, Shane, Gouws and Kistner (1969) in attempting to characterize 19 strains of Gram-negative curved rods isolated from sheep, which produced large amounts of butyric acid, found only one strain out of 11 which fell within the definitions for the species *B. fibrisolvens*. The remaining eight strains which produced little or no lactate, could not be identified with *B. alactacidigens*. Thus, it appears preferable to characterize the strains ARD-22a, ARD-24b and ARD-36a as belonging to the genus *Butyrivibrio*, without definite species designation. They would resemble *B. alactacidigens*, in producing little or no lactic acid, but differ primarily in their inability to hydrolyze starch.

Strains ARD-10f5 and ARD-34a, morphological type 2, are Gram-negative, twisted to spiral shaped rods, with pointed ends. The cells are extremely motile, moving through the medium in a spiral motion. Electron micrographs indicate that both strains have a single tuft of flagella, originating laterally about half way between the center and one end of the cell. The tuft appears to contain anywhere from two to eight flagella emerging from the cell in a bundle and not dividing into separate flagellum except near the end. Morphologically, the organisms resemble the species *Succinivibrio dextrinosolvens* (Bryant and Small, 1956b), but differ in being wider and possessing a tuft of flagella rather than being monotrichous. Physiological characteristics such as production of H₂S, limited fermentation of dextrin, rumen fluid requirement for strain ARD-10f5 and a high proportion of lactic acid as a fermentation product would also differ with the species description. Although the morphology of the cells does not agree with the descriptions, photomicrographs and electron micrographs for the species *Selenomonas ruminantium* (Lessel and Breed, 1954; Bryant, 1956; Kanegasaki and Takahashi, 1967; and Prins, 1971), many of the physiological characteristics are similar, and end products would fall within the extremes reported for this

TABLE 3.--Morphology, physiological characteristics and organic acid end products for bacterial strains ARD-22a, ARD-24b, ARD-36a, ARD-10f5, ARD-34a and ARD-5d, isolated from rumen contents of Alaskan reindeer (*Rangifer tarandus* L.)

Strain:	Morphological type ^a					
	1		2		3	
	ARD-22a	ARD-24b	ARD-36a	ARD-10f5	ARD-34a	ARD-5d
Cells ^b						
Dimensions (μ)						
Width	0.3-0.4	0.3-0.4	0.3-0.4	0.6-1.0	0.8-1.0	0.5
Length	1.5-2.5	1.0-2.5	1.0-3.0	1.5-4.0	2.5-7.5	0.5-0.8
Gram stain	-	-	-	-	-	+
Motility ^c	+	+	+	+	+	-
Flagella ^d	sp,m	sp,m	sp,m	1,t	1,t	-
Anaerobic	+	+	+	+	+	+ to - ^e
H ₂ S production	-	-	-	+	+	-
Final pH, glucose	5.1	5.1	5.1	4.6	5.0	4.2
Growth in trypticase-yeast extract medium	+	+	+	-	+	+
Starch hydrolysis	-	-	-	-	-	+
Acid from:						
Glucose	+	+	+	+	+	+
Cellobiose	+	+	+	+	+	+
Dextrin	+	+	+	± ^f	± ^f	+
Mannitol	--- ^g	-	-	+	-	+
Glycerol	---	-	-	-	-	-
Lactate	---	---	---	-	-	---
Organic acid end products ^h						
Total acid (meq/100 ml)	4.00	4.24	3.63	12.07	9.86	12.39
Butyric	27.0	25.5	26.4	0.2	4.7	-.2
Propionic	-1.0	-.7	-1.6	0.9	-.5	-.5
Acetic	8.8	18.2	24.0	1.6	12.0	0.4
Formic	65.2	45.0	51.2	4.1	20.9	0

Succinic	0	0	0	10.4	7.1	0
Lactic	0	12.0	0	82.8	55.9	100.3

^aSee Table 2.

^bCells from stab culture water of syneresis.

^cDetermined with phase microscope and 0.5 per cent agar medium stab test.

^dDetermined on the basis of electron micrographs. p, polar; sp, subpolar; l, lateral; m, monotrichous; t, tuft of two or more flagella.

^eAnaerobic immediately after isolation, later facultative.

^fRefers to limited growth and acid production.

^gNot determined.

^hIndividual acids reported as milliequivalent per cent of total acid produced. Values of less than 3 per cent are of doubtful significance.

TABLE 4.--Morphology, physiological characteristics and organic acid end products for bacterial strains ARD-26e, ARD-30b, ARD-23c, ARD-27b, ARD-31a, ARD-39e and ARD-3a3, isolated from rumen contents of Alaskan reindeer (*Rangifer tarandus* L.)ⁱ

Strain:	Morphological type ^a						
	4	5	6			7	
	ARD-26e	ARD-30b	ARD-23c	ARD-27b	ARD-31a	ARD-39e	ARD-3a3
Cells ^b							
Dimensions (μ)							
Width	0.6-0.75	0.5-0.6	0.5	0.5	0.5	0.5	0.4-0.5
Length	1.0-8.0	1.0-10.0	1.5-2.5	1.5-3.0	2.0-2.5	2.0-4.0	1.0-5.0
Gram stain	+ to ± ^j	-	-	-	-	-	-
Motility ^c	-	+	± ^k	±	±	±	±
Flagella ^d	-	-	sp,m	sp-1,m	sp,m	sp,m	p,m
Growth at 22° C	+	--- ^g	---	---	---	---	---
Final pH, glucose	4.4	5.0	5.1	5.4	5.4	5.7	5.1
Growth in trypticase-yeast extract medium	+	+	+	+	+	± ^f	+
Starch hydrolysis	-	± ^l	+	+	+	+	± ^l
Acid from:							
Cellobiose	+	± ^f	+	+	+	+	+
Dextrin	± ^f	+	+	+	+	+	+
Mannitol	-	+	-	-	-	-	-
Organic acid end products ^h							
Total acid (meq/100 ml)	10.48	11.79	3.72	1.46	1.45	3.11	1.88
Butyric	-.3	-.1	20.4	31.5	26.9	12.9	25.5
Propionic	-.2	-.2	-1.3	-6.8	-8.3	0.6	-3.7
Acetic	1.3	14.2	29.6	15.8	16.6	9.6	14.9
Formic	0	8.0	19.6	59.6	64.8	9.3	63.3
Succinic	0	63.3	0	0	0	0	0
Lactic	99.1	14.9	31.7	0	0	67.5	0

^{a-h}See Table 3 for legend of footnotes.

ⁱAll strains were anaerobic, did not produce H₂S, fermented glucose and did not ferment glycerol.

^jCells were primarily Gram +; however, both Gram + and Gram - granular type elements were always visible inside the cell.

^kMotility was questionable on the basis of the phase microscope and 0.5 per cent agar medium stab test. Electron micrographs indicated that less than 5 per cent of cells were flagellated.

^lPartial hydrolysis to dextrin.

species. Most strains studied to date, however, produce sizeable amounts of propionic acid. Minimum pH values for the present strains are also slightly higher than those reported for *Selenomonas*, but in the range for *Succinivibrio*. Since the two strains are Gram-negative, nonsporeforming, curved to spiral rods, with a subpolar to lateral tuft of flagella, they belong in the family *Spirillaceae* of the suborder *Pseudomonadinae* (Breed, Murray and Smith, 1957). However, on the basis of the characterization studies completed to date, they do not readily fit into any of the described genera, which includes both *Succinivibrio* and *Selenomonas*.

Strain ARD-5d is a Gram-negative, facultatively anaerobic, amylolytic, homofermentive coccus. These characteristics plus the extremely low minimum pH, readily classify this strain as belonging to the species *Streptococcus bovis* (Breed, Murray and Smith, 1957; Hungate, 1957, 1966). Strain ARD-5d appeared to be an obligate anaerobe when first isolated, but based on results of the other characterization studies it was tested again and found to be facultatively anaerobic. Hungate (1957, 1966) has reported that this species tends to become less sensitive to oxygen after continued propagation in the laboratory.

Morphology and characteristics of strain ARD-26e, Table 4, are quite similar to the +R4 group of bacteria described by Bryant *et al.* (1958c) and organism 123 of Mann and Oxford (1954). These authors both classified this group of organisms as anaerobic varieties of *Lactobacillus lactis*, as described in Bergey's Manual (Breed, Murray and Smith, 1957). The size and shape of the cells, tendency to form filaments, uneven staining with intercellular Gram-positive and Gram-negative elements, low minimum pH, homofermentative production of lactic acid, inability to hydrolyze starch and growth at 22° C all agree with classification of this organism as an anaerobic strain of *Lactobacillus lactis* (Breed, Murray and Smith, 1957).

The spirochete, strain ARD-30b, is very similar to the strain described by Bryant (1952). It differs in not requiring rumen fluid for growth, having a slightly lower minimum pH, fermentation of mannitol and dextrin and showing only a very weak fermentation of cellobiose. Organic acid end products agree quite closely. Species designations of rumen spirochetes have not been made because of the lack of sufficient information, therefore this strain cannot be classified any further than the genus *Treponema*. Rumen spirochetes were originally placed in the genus *Borellia* (Breed, Murray and Smith, 1957) however, the new edition of Bergey's Manual now in preparation has placed these species in the genus *Treponema* (R. M. Smibert, pers. comm.). The present strain differs from the described species of this genus isolated from the mouth and urogenital tract (Holdeman and Moore, 1972).

The isolates grouped in morphological type 6, strains ARD-23c, ARD-27b, ARD-31a and ARD-39e, all appear to belong to the genus *Butyrivibrio*. They differ from the strains of morphological type 1 in being somewhat larger, showing limited motility by the standard tests (less than 5 per cent of the cells were flagellated in electron micrographs), hydrolyzing starch and in all but one instance, strain ARD-23c, having a higher minimum pH. Considerable variation was observed in organic acid end products, with the main difference being that two strains produced no lactate. Margherita and Hungate (1963) and Shane, Gouws and Kistner (1969) have all placed apparently non-motile strains in this genus. It should be kept in mind that the occurrence of flagella can apparently be influenced by the growth medium, temperature, etc. (Burrows, 1949).

The last strain, ARD-3a3, also appears to belong to the genus *Butyrivibrio*. It differs in shape, location of flagellum and starch hydrolysis from morphological types 1 and 6; however, most characteristics and organic acid end products indicate classification in this genus.

Of the 21 strains isolated with cellulose medium, eight resembled organisms in the genus *Butyrivibrio*, nine in the genus *Ruminococcus* and the remaining four strains were thick rods with blunt ends. Visible loss of cellulose from a purified cellulose broth medium was observed with two of the *Butyrivibrio* type and all of the *Ruminococcus* type cultures. Of the nine *Ruminococcus* type cultures, eight were similar in that the organisms occurred as singles or diplococci, while the remaining culture contained primarily diplococci and long chains. The latter culture also produced a yellow pigment in cellulose broth. Organic acid end products were determined for two of the eight cultures and the pigment producing culture. On the basis of the data obtained, the first eight cultures could tentatively be classified as *Ruminococcus albus* (Hungate, 1957; Bryant *et al.*, 1958b), and the last culture as *Ruminococcus flavefaciens* (Bryant *et al.*, 1958b; Sijpesteijn, 1951). Both *Butyrivibrio* type cultures produced considerable amounts of butyric and formic acids, indicating their close relationship to this genus.

Phase microscope observations on the 49 isolates from the ARC series, Table 1, revealed all the same general morphological types found in the ARD series. However, a considerably higher percentage of cultures were of the coccus type.

GENERAL DISCUSSION

The occurrence of a relatively high proportion of *Butyrivibrio* species in the reindeer probably should not be surprising. This species has been observed in fairly high numbers in most domestic ruminants in various parts of the world on a wide variety of rations (Bryant and Burkey, 1953b; Bryant and Small, 1956; Hungate, 1966; Slyter and Putnam, 1967; Thorley, Sharpe and Bryant, 1968). This in part is probably explained by their ability to utilize so many of the carbohydrates in feeds as sources of energy, i.e., starch, cellulose, xylan and pectin. Studies in our laboratory on strains of *Butyrivibrio fibrisolvens* isolated from cattle with selective xylan and pectin media have indicated that these organisms can ferment a high proportion of hemicellulose and pectin from intact forages (Coen and Dehority, 1970; Gradel and Dehority, 1972).

As pointed out by Shane, Gouws and Kistner (1969), and results of the present study, the taxonomic state of the genus *Butyrivibrio* is somewhat confusing at present. Either the description of the present species, *B. fibrisolvens* and *B. alactacidigens* should be broadened to include more of the strains isolated or a thorough study of all described strains should be made to determine a better basis for division of the genus into species.

Finding the species *Streptococcus bovis* and *Lactobacillus lactis* in rumen contents from a reindeer on native pasture and browse and subsequently dried lichen was most unexpected. Both are homofermentive lactic acid producing species which are usually associated with a low rumen pH. Unfortunately, this parameter was not measured in the present study. The most obvious question in regard to these species is their substrates, since aside from the rapid digestion of starch by *S. bovis*, both species primarily ferment only simple sugars. It would appear that the maintenance of these species in the rumen of a reindeer consuming dried lichen would be very dependent upon symbiosis with the rest of the flora.

As discussed earlier, strains ARD-10f5 and ARD-34a could not be classified even to the genus level on the basis of morphology and the physiological characteristics determined. A more detailed study, possibly including several strains from the ARC series which are morphologically similar, will be required for either classification into an existing genus or describing a new genus.

The isolation of fairly high numbers of *Ruminococcus* and *Butyrivibrio* type organisms with a selective cellulose medium is similar to the results obtained by the South African

workers, who found these species to be the predominant isolates from sheep fed poor quality teff hay (Gouws and Kistner, 1965; Shane, Gouws and Kistner, 1969). As in the present study, these workers found only a very limited number of their *Butyrivibrio* species, isolated with a cellulose medium, were able to visibly digest purified cellulose in a broth medium. It is of interest that the strongly cellulolytic species, *Bacteroides succinogenes*, was not encountered in the present work. This species has been found to occur in fairly high numbers in domestic ruminants in the United States, i.e., Texas, Maryland, Washington, California and Ohio (Bryant, 1963). On the other hand, it has not been observed in New Zealand or in the comprehensive studies from South Africa (Clarke, 1964; Shane, Gouws and Kistner, 1969).

Another species not encountered in the present work, but considered to be of considerable importance in domestic ruminants, is *Bacteroides ruminicola* (Bryant *et al.*, 1958a; Bryant, 1959). Most strains actively ferment starch, xylan and pectin and can utilize the hemicellulose and pectin fraction from intact forages (Bryant *et al.*, 1958a; Dehority, 1966, 1969; Coen and Dehority, 1970; Gradel and Dehority, 1972). Clarke (1964) was unable to isolate any species in the genus *Bacteroides* from New Zealand cattle, and suggested further investigations be conducted because of its wide distribution and importance elsewhere. It will be of considerable interest to see whether any species of this genus are found among the remaining reindeer isolates listed in Table 1.

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RUMEN CILIATE PROTOZOA OF ALASKAN REINDEER
AND CARIBOU (*RANGIFER TARANDUS* L.)

B. A. Dehority
Department of Animal Science
Ohio Agricultural Research and Development Center
Wooster, Ohio

ABSTRACT—Total numbers, generic distribution and occurrence of various species of ciliate protozoa were determined for wild and semi-domestic reindeer and wild caribou living in Alaska. The fauna observed in the semi-domestic reindeer, originally obtained from a herd on the Seward Peninsula, was qualitatively similar whether the animals were fed alfalfa pellets or lichen, browse and native pasture. Total numbers were considerably higher, however, for those animals feeding on lichen, browse and native pasture. Their fauna differed quite markedly from caribou living in the same locality supposedly feeding on similar vegetation and from wild reindeer living on Umnak Island. The protozoal species observed in the wild reindeer and caribou were similar and in agreement with previous reports from Russia, Canada and Finland. In contrast, seven species of *Entodinium* were found in the semi-domestic reindeer, none of which are considered specific to reindeer. *Eudiplodinium affine*, not previously found in reindeer, and *Polyplastron multivesiculatum*, found previously in only one reindeer, were the only higher Ophryoscolecidae observed. Four species of holotrichs were found: *Isotricha intestinalis*, *I. prostoma*, *Dasytricha ruminantium* and *Bütschliella parva*. Although the fauna of the semi-domestic reindeer must be considered atypical with respect to other reports and the wild reindeer and caribou in Alaska, similarities were noted with the fauna observed in domestic sheep and goats located in the same general area.

The first observations on the rumen ciliate fauna of reindeer were reported by Eberlein in 1895. He examined rumen contents from two reindeer located at the Zoological Gardens in Berlin, and found their fauna resembled that of the other ruminant species in the zoo as well as domestic ruminants in Germany. Similar findings were reported from Finland by Kopperi (1926, 1929) for samples obtained from a single reindeer in the Helsinki Zoological Gardens and 10 free living reindeer. In contrast, Dogiel (1925) examined the rumen contents of three domestic reindeer from northern European Russia and found that their fauna differed quite markedly from that observed in other ruminants. Subsequent studies by Dogiel (1935) on rumen contents from seven additional reindeer substantiated his earlier findings. In 1958, Lubinsky (1958a, 1958b) studied the rumen ciliate fauna of 14 Palearctic reindeer. The animals, which were located at Aklavik, N.W.T., Canada, were originally introduced from Siberia. Except for several small differences, the rumen ciliate fauna of these animals was essentially the same as observed by Dogiel (1925, 1935). Lubinsky also examined rumen contents from the caribou for Courtright (1959), and observed many of the same species of ciliate protozoa as found in the reindeer.

In general, all of the above investigations were qualitative in nature, i.e., specific descriptions of the various protozoal species observed and their occurrence, with no actual reports on the quantitative composition of the fauna. The present study was undertaken to

determine total numbers, generic distribution and species distribution of the ciliate protozoa in semi-domestic and wild reindeer and wild caribou living in Alaska. After this work was initiated, Westerling (1970) reported the results of a very comprehensive study on the ciliate fauna of free living semi-domestic reindeer in Finland. He found the regular fauna in these animals to be the same as previously reported for Russian and Canadian reindeer. However, of extreme interest were his quantitative measurements on numbers and composition. These will be discussed later in comparison to the results of the present investigation.

MATERIALS AND METHODS

The semi-domestic reindeer were originally obtained from a herd on the Seward peninsula near Nome. All of the animals were transported to the Institute of Arctic Biology, University of Alaska, College, Alaska, and a part of the group was later moved to the Reindeer Research Station at Cantwell, Alaska. Reindeer cows Nos. 4, 16 and 19 were fistulated, housed at the Institute of Arctic Biology and fed alfalfa pellets. Rumen samples were obtained through the fistula. Animal No. 16 was housed alone in an outdoor concrete floor holding pen, while animals Nos. 4 and 19 were confined in metabolism crates in an environmental chamber. Reindeer cows Nos. 9 and 14 and a male No. S1 were located on pasture at the Cantwell Station. These animals were feeding on native browse and pasture which consisted primarily of dwarf birch and willow, lichen and native tundra. All samples from these reindeer were collected by means of a stomach tube inserted through the nasal passage.

Four rumen samples were obtained from wild reindeer cows located on Umnak Island. These animals were released on Umnak around 1924 and feed entirely on native pasture, since no shrubs or trees grow on the island. Rumen samples were obtained from shot animals in the spring of 1970.

Both caribou were bulls, shot in the vicinity of Soule Lake, near Cantwell. The rumens were opened, the contents mixed as much as possible and samples taken. Visual examination of the contents indicated that the caribou had been grazing the browse and pasture of that area which was similar in composition to that being consumed by the semi-domestic reindeer at Cantwell.

Additional rumen samples were obtained by stomach tube from two domestic sheep and a goat, housed at the Institute of Arctic Biology, and two domestic sheep located on Umnak Island, grazing the same pastures as the wild reindeer.

Rumen contents to be used for protozoal studies were preserved by diluting with equal parts of 50 per cent formalin. Total counts were made according to the procedure described by Purser and Moir (1959) which involves staining with Brilliant green and counting in a Sedgwick-Rafter chamber. For differential counts, acid methylene blue or acid methyl green were used to stain the nucleus. Lugol's iodine was used to stain skeletal plates. Identification of genera and species of ciliate protozoa were based on the descriptions of Dogiel (1927), Lubinsky (1958a, 1958b), Kofoid and MacLennan (1930, 1932, 1933), Sládeček (1946), Wertheim (1935) and Zielyk (1961).

RESULTS AND DISCUSSION

Table 1 presents the total numbers and per cent generic distribution of ciliate protozoa in the semi-domestic reindeer and caribou. Considering only the reindeer, total numbers of protozoa were considerably higher for those animals maintained on pasture. In general, the alfalfa pellet fed reindeer had a higher proportion of *Diplodinium* and fewer species of holotrichs. Total numbers for the caribou were similar to those for the reindeer on pasture;

TABLE 1.--Numbers and generic distribution of ciliate protozoa in the rumen contents of Alaskan reindeer and caribou (*Rangifer tarandus* L.).

	Alfalfa pellets							
	Feed:							
	Animal:	R. No. 16			R. No. 19		R. No. 4	
	Date:	7-30	8-3	8-17	7-31	8-10	7-31	8-10
Number per cc rumen contents, x 10 ⁴								
Total protozoa		0.32	6.9	9.0	13.1	13.6	5.6	3.5
Generic distribution, as % of total protozoa								
<i>Entodinium</i>		100.0	92.2	83.9	82.5	96.2	88.5	83.0
<i>Diplodinium</i>		+a	7.7	16.1	17.5	2.4	10.8	14.8
<i>Isotricha</i>		-	-	-	-	1.5	0.7	2.3
<i>Dasytricha</i>		-	-	-	+a	+a	+a	-
<i>Bütschlia</i>		-	-	-	-	-	-	-

	Lichen, native pasture and browse							
	Feed:							
	Animal:	R. No. 9		R. No. 14		R. No. SI	Caribou	
	Date:	8-13	8-14	8-13	8-14	8-14	No. 1	No. 2
Number per cc rumen contents, x 10 ⁴								
Total protozoa		120.0	163.7	85.9 ^b	232.8	372.8	224.3	205.8
Generic distribution, as % of total protozoa								
<i>Entodinium</i>		91.8	94.4	92.0	90.4	97.2	75.1	96.1
<i>Diplodinium</i>		3.0	2.2	3.4	4.5	1.5	19.3	3.9
<i>Epidinium</i>		-	-	-	-	-	5.6	-
<i>Isotricha</i>		1.7	0.9	1.1	0.8	0.2	-	-
<i>Dasytricha</i>		3.1	2.4	3.5	4.2	1.1	-	-
<i>Bütschlia</i>		0.4	-	-	0.1	0.04	-	-

^aGenera observed, but in very low numbers.

^bConsiderable difficulty was encountered in obtaining this sample and it contained an appreciable amount of saliva.

however, no holotrichs were present and caribou No. 1 had a fairly large proportion of protozoa in the genus *Epidinium*. Total numbers for the reindeer on pasture and the caribou are in close agreement with the values reported by Westerling (1970) for Finnish reindeer. In contrast, unpublished values reported by Drescher-Kaden and Giesecke, as cited by Giesecke (1970), for Finnish reindeer on a somewhat similar feeding range were considerably lower.

The species distribution of rumen ciliate protozoa in one sample from each of the semi-domestic reindeer and the two caribou are shown in Table 2. Table 3 lists the occurrence of the different species identified in the rumen contents from all the animals and samples shown in Table 1 plus those samples obtained from the wild reindeer on Umnak Island.

A very limited number of species were observed in the reindeer being fed on alfalfa pellets and housed in captivity at College, Alaska. This same fauna, plus several additional species of *Entodinium* were present in the reindeer on pasture at the Cantwell site. In contrast, the protozoal species observed in the wild reindeer and caribou were similar to

TABLE 2.--Percentage species distribution of ciliate protozoa in the rumen contents of Alaskan semi-domestic reindeer and caribou (*Rangifer tarandus* L.).

Animal:	Feed: Alfalfa pellets Native pasture and browse							
	Reindeer						Caribou	
	16	19	4	9	14	S1	1	2
<i>Entodinium</i> :								
<i>E. anteroneucleatum</i>	-	-	-	-	-	-	28.4	0.4
<i>E. bicornutum</i>	-	-	-	-	-	-	6.5	3.7
<i>E. damae</i>	-	-	-	3.8	19.8	-	10.6	-
<i>E. dilobum</i>	-	-	-	20.6	2.0	-	-	1.1
<i>E. dubardi</i>	60.2	79.5	59.4	18.0	29.3	78.6	0.5	1.2
<i>E. exiguum</i>	23.8	2.9	12.2	31.5	31.3	15.6	6.3	31.4
<i>E. longineucleatum</i>	-	-	-	-	2.8	-	2.2	5.2
<i>E. nanellum</i>	-	-	11.4	18.0	6.0	2.9	-	-
<i>E. ovinum</i>	-	-	-	-	0.8	-	-	-
<i>E. quadricuspis</i>	-	-	-	-	-	-	18.4	52.2
<i>E. simplex</i>	-	-	-	-	-	-	2.0	0.9
<i>Diplodinium</i> :								
<i>Diplodinium rangiferi</i>	-	-	-	-	-	-	0.2	0.4
<i>D. dogieli</i>	-	-	-	-	-	-	1.9	1.0
<i>Eudiplodinium affine</i>	-	3.9	-	2.7	3.3	1.2	-	-
<i>E. impalae</i>	-	-	-	-	-	-	10.2	2.5
<i>E. spectabile</i>	-	-	-	-	-	-	1.0	-
<i>Ostracodinium confluens</i>	-	-	-	-	-	-	0.6	-
<i>O. magnum</i>	-	-	-	-	-	-	0.2	-
<i>O. obtusum</i>	-	-	-	-	-	-	2.3	-
<i>Enoploplastron triloricastrum</i>	-	-	-	-	-	-	2.8	-
<i>Polyplastron multivesiculatum</i>	16.1	13.6	14.8	0.3	+ ^a	0.3	-	-
<i>Epidinium</i> :								
<i>E. ecaudatum</i>	-	-	-	-	-	-	5.6	-
<i>Isotricha</i> :								
<i>I. intestinalis</i>	-	-	2.3	1.6	0.9	0.2	-	-
<i>I. prostoma</i>	-	-	-	+ ^a	0.2	-	-	-
<i>Dasytricha</i> :								
<i>D. ruminantium</i>	-	+ ^a	-	3.1	3.5	1.1	-	-
<i>Bütschlia</i> :								
<i>B. parva</i>	-	-	-	0.4	-	+ ^a	-	-

^aObserved in low numbers. Values less than 0.1.

each other but markedly different from the semi-domestic reindeer. Only one species, *exiguum Entodinium* was observed in all animals in all locations; however, *E. dubardi* was present in all animals but one. The fauna observed in the wild reindeer from Umnak Island and the caribou is very similar to those observed in Russian, Canadian and Finnish reindeer (Dogiel, 1925, 1935; Lubinsky, 1958a, 1958b; Westerling, 1970). No new species were observed, and many of these species are considered to be specific for reindeer (Dogiel, 1927,

TABLE 3.—Occurrence of the ciliate protozoal species in rumen contents of Alaskan reindeer and caribou (*Rangifer tarandus* L.) at different locations and under different feeding conditions.

	Reindeer			Caribou
	College Alaska ^a	Cantwell Alaska ^b	Umnak Island ^c	Cantwell Alaska ^b
<i>Entodinium</i> :				
<i>E. anteroneucleatum</i>	-	-	1	2
<i>E. bicornutum</i>	-	-	4	2
<i>E. damae</i>	-	2	1	1
<i>E. dilobum</i>	-	2	-	1
<i>E. dubardi</i>	3	3	3	2
<i>E. exiguum</i>	3	3	4	2
<i>E. longineucleatum</i>	-	1	4	2
<i>E. nanellum</i>	2	3	-	-
<i>E. ovinum</i>	-	1	-	-
<i>E. quadricuspid</i>	-	-	4	2
<i>E. simplex</i>	-	-	1	2
<i>Diplodinium</i> :				
<i>Diplodinium rangiferi</i>	-	-	-	2
<i>D. dogieli</i>	-	-	3	2
<i>Enoploplastron triloricastrum</i>	-	-	-	1
<i>Eudiplodinium affine</i>	1	3	-	-
<i>E. impalae</i>	-	-	4	2
<i>E. spectabile</i>	-	-	-	2
<i>Ostracodinium confluens</i>	-	-	-	1
<i>O. magnum</i>	-	-	1	1
<i>O. obtusum</i>	-	-	-	1
<i>Polyplastron multivesiculatum</i>	3	3	-	-
<i>Epidinium</i> :				
<i>E. ecaudatum</i>	-	-	2	1
<i>E. caudatum</i>	-	-	1	-
<i>Isotricha</i> :				
<i>Isotricha intestinalis</i>	2	3	-	-
<i>I. prostoma</i>	-	2	-	-
<i>Dasytricha</i> :				
<i>D. ruminantium</i>	2	3	-	-
<i>Bütschlia</i> :				
<i>B. parva</i>	-	2	-	-
Number of animals	3	3	4	2

^aFed alfalfa pellets.

^bFeeding on lichen, native pasture and browse.

^cFeeding entirely on native pasture.

1935). However, qualitative studies by Lubinsky, as reported by Tener (1965), and unpublished results by the author have revealed that many of these same species occur in the musk-ox. *Diplodinium rangiferi* and *D. dogieli* have also been reported to occur in red

deer and fallow deer (Sládeček, 1946).

Although marked differences existed in total numbers of protozoa between the semi-domestic reindeer located at College and Cantwell, feeding on alfalfa pellets and pasture and browse, respectively, their faunas tended to be qualitatively similar (Table 3). These data might suggest that the type of feed can influence total numbers, but may be of less importance than previously thought with regard to the presence or absence of a particular species. The rather severe confinement of the animals at College may also have influenced total numbers; however, this is difficult to assess on the basis of the present data.

Eudiplodinium affine (*Diploplastron affine*, Dogiel and Fedorowa, 1925) has not been previously found in reindeer; however, it has been observed frequently in cattle, sheep and goats in Russia, China, Scotland and the United States (Dogiel, 1927; Hsiung, 1931, 1932; Eadie, 1962; Hungate, 1966; Hungate, Reichl and Prins, 1971). Sixty-five cells of *E. affine* were measured at random, and these data are shown in Table 4. Measurements for this

TABLE 4.--Dimensions of *Eudiplodinium affine* from Alaskan semi-domestic reindeer (*Rangifer tarandus* L.).

	Present Study	Dogiel and Fedorowa (1925)
Length	87.7 μ (69.3-112.7) μ	105 μ (88-120) μ
Width	60.1 μ (47.3-79.2) μ	59 μ (47-65) μ
L/W ratio	1.46 (1.24-1.74)	1.7

species, as reported by Dogiel and Fedorowa (1925), are included for comparison. In general, *E. affine* from the reindeer was shorter than those specimens measured by Dogiel and Fedorowa in domestic ruminants, which in turn lowered the mean L/W ratio.

Other than the report by Dogiel (1935) on the occurrence of *Polyplastron multivesiculatum* in one animal, this species has not been observed in reindeer fauna. Dimensions of 75 cells of *P. multivesiculatum* measured at random from the reindeer at both College and Cantwell are shown in Table 5. Also shown are Dogiel's (1935)

TABLE 5.—Dimensions of *Polyplastron multivesiculatum* from Alaskan semi-domestic reindeer (*Rangifer tarandus* L.).

	Present study	Dogiel (1935) from reindeer	Dogiel and Fedorowa (1925)
Length	156.6 μ (110.0-210.7) μ	162 μ (up to 240) μ	161 μ (120-190) μ
Width	103.8 μ (78.4-142.1) μ	122 μ (96-174) μ	95 μ (78-140) μ
L/W ratio	1.51 (1.22-1.83)	1.31	1.7

measurements for this species from reindeer and Dogiel and Fedorowa's (1925) dimensions

for this species observed in domestic cattle. As can be noted, length of the cells from all three sources was fairly similar. The mean width observed in the present study was slightly greater than reported by Dogiel and Fedorowa from cattle, but the range was almost identical. In contrast, specimens of this species were considerably wider as measured by Dogiel from reindeer. The L/W ratio of *P. multivesiculatum* in the present study thus lies midway between the other two reports.

The holotrich ciliate, *Dasytricha ruminantium*, has been found previously in Russian and Finnish reindeer (Kopperi, 1926; Dogiel, 1935; Westerling, 1970), however, since the reports by Eberlein (1895) and Kopperi (1926), holotrich ciliates in the genera *Isotricha* and *Bütschlia* have not been observed. Their occurrence in the fauna of the reindeer at Cantwell would disagree with the suggestion of Westerling (1970) that the browse-lichen diet does not provide a suitable biotype for these holotrichs.

Reindeer Nos. 9 and 14, feeding on native pasture and browse at Cantwell, were confined in a pen and switched over to a feed of dried lichens for a two-week period. The effects of this change in ration are shown in Table 6. A rather drastic drop was noted in

TABLE 6.—Effect of feeding dried lichens on numbers and generic distribution of ciliate protozoa in rumen contents of reindeer (*Rangifer tarandus* L.).

	Feed: Lichen, pasture and browse		Dried lichens	
	Animal: No. 9	No. 14	No. 9	No. 14
	Date: 8-14	8-14	8-28	8-28
Number per cc rumen contents, x 10 ⁴				
Total protozoa	163.7	232.8	21.4	31.3
Generic distribution, as % of total protozoa				
<i>Entodinium</i>	94.4	90.4	89.6	74.2
<i>Diplodinium</i>	2.2	4.5	5.2	7.9
<i>Isotricha</i>	0.9	0.8	0.8	3.1
<i>Dasytricha</i>	2.4	4.2	4.5	14.8
<i>Bütschlia</i>	-	0.1	-	+ ^a

^aGenera observed, but in very low numbers.

total numbers as well as a decrease in the per cent *Entodinium*.

Total numbers and generic distribution were determined for two domestic sheep and one goat housed at the Institute of Arctic Biology in College, Alaska (Table 7). *Eudiplodinium affine* and *Polyplastron multivesiculatum* were the only *Diplodinium* species observed, and all three genera of holotrichs were present. The possible significance of these data in relation to the fauna of the semi-domestic reindeer will be discussed later.

Rumen samples were also obtained from several domestic sheep grazing the same pastures as the wild reindeer on Umnak Island. Protozoal species observed in these samples were *Entodinium dubardi*, *nanellum* and *dilobum*, a *Eudiplodinium* species, possibly *spectabile*, *Dasytricha ruminantium* and *Epidinium ecaudatum* and *caudatum*. Comparison of these data with the fauna of the wild reindeer, shown in Table 3, indicates that only *Entodinium dubardi* and *Epidinium* species were common to both.

TABLE 7.--Numbers and generic distribution of ciliate protozoa in several domestic ruminants located in College, Alaska.

Feed	Sheep		Goat
	1	2	
	-----Brome grass hay-----		
	Number per cc rumen contents, x 10 ⁴		
Total protozoa	20.4	41.8	53.7
	Generic distribution, as % of total protozoa		
<i>Entodinium</i>	94.9	88.6	94.0
<i>Diplodinium</i>	2.4 ^a	3.0 ^a	1.3 ^b
<i>Isotricha</i>	1.8	3.0	1.5
<i>Dasytricha</i>	1.0	4.7	3.1
<i>Bütschlia</i>	-	0.8	-

^a*Eudiplodinium affine* was the only species observed.

^b*Eudiplodinium affine* and *Polyplastron multivesiculatum*.

GENERAL DISCUSSION

The fauna of the semi-domestic reindeer located at College and Cantwell, Alaska must be considered quite atypical with respect to the reports from other countries as well as the wild reindeer and caribou in Alaska. Although the total numbers were considerably higher, and a few more species were observed, the fauna of the reindeer feeding on lichen, native pasture and browse at Cantwell was quite similar to the alfalfa pellet fed animals at College. Obviously this is a result of the fact that all of these animals were originally from the same herd and were housed together at College before a part of the group was moved to Cantwell.

Several possible explanations might be advanced for the occurrence of this non-rangifer type fauna. First, the herd on Seward Peninsula, from which these animals were obtained, could have developed an atypical fauna and has subsequently remained completely isolated from other reindeer and caribou. Second, the normal rangifer type fauna was somehow lost in transit or during their stay in College, possibly as a result of a period of starvation. The animals then became atypically faunated by contact with the domestic sheep and goats also housed at the Institute. If the latter explanation was the case, then it must be assumed that the reindeer at Cantwell have not come into direct contact with the caribou living in that area.

Both of the above mentioned possibilities would require almost complete defaunation of the reindeer at some period and subsequent faunation with the non-rangifer species of ciliates. However, there is one additional means by which at least a part of this difference could have occurred. That is, the non-rangifer type fauna resulted from an antagonism between certain ciliate species. Eadie (1962, 1967) observed that in sheep, goats and calves, the large rumen Ophryoscolecids, were divided into two groups, A and B, which tended to be found together in stable populations under natural conditions. Type A organisms were *Polyplastron multivesiculatum*, *Eudiplodinium affine* and *Ophryoscolex tricornatus*, while type B organisms were *Eudiplodinium maggi*, *Epidinium* spp., *Eremoplastron* spp. and *Ostracodinium* spp. *Entodinium* and the holotrichs were common to both types. She

observed that in both sheep and goats, a type A population would readily and irreversibly remove type B organisms from the fauna. Similar observations were made in calves; however, the reverse change was also noted to occur in several cases. Subsequent experiments indicated that *Polyplastron multivesiculatum* became irreversibly dominant in a fauna by means of predation, and was observed to eliminate *Epidinium*, *Eudiplodinium maggi*, *Eremoplastron* and *Ostracodinium*. Since *Polyplastron multivesiculatum* and *Eudiplodinium affine*, both type A organisms, were the only higher Ophryoscolecids observed in the semi-domestic reindeer, the possibility of *Polyplastron* predation of the typical rangifer type B higher Ophryoscolecids cannot be overlooked. On the other hand, the absence of the *Entodinium* species supposedly specific to reindeer is unexplained.

Additional experiments in which the semi-domestic reindeer at Cantwell were inoculated with rumen contents from the caribou would be of extreme interest. Such variables as defaunation or starvation for several days prior to inoculation, which not only decreases total numbers but appears to severely limit predation in *Polyplastron*, could be included. If a rangifer type fauna became established, these animals could then be reinoculated with the non-rangifer fauna. Data of this type could answer many of the questions posed by results of the present study.

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**IN VITRO DIGESTIBILITY OF FORAGES
UTILIZED BY *RANGIFER TARANDUS***

**S. J. Person, R. G. White and J. R. Luick
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701**

ABSTRACT—Digestibilities of some forages commonly consumed by *Rangifer* were estimated using the standard Tilley-Terry *in vitro* technique. Dry matter disappearance of a representative lichen, *Cladonia alpestris*, was lower than anticipated at 6.4 per cent using rumen liquor from rumen fistulated reindeer fed commercial pellets (Purina Cattle Starter #1) and 16.2 per cent using liquor from reindeer fed mixed lichens. Dry matter digestibility of commercial pellets in the same rumen liquors were greater than expected being respectively 66.6 and 64.0 per cent. *In vivo* digestibilities of a lichen mixture and the commercial pellets were respectively 55.4 and 58.0 per cent. Rumen retention times were determined concurrently by reference to an inert particulate marker ($^{144}\text{CeCl}$). A mean retention time of 10 hours was noted for the pellet ration versus almost 5 days for the mixed lichen. Thus the commonly used incubation time of 48 hours for the first stage of *in vitro* digestion may lead to underestimation of dry matter digestibilities for lichen when incubated in liquor from reindeer consuming mainly lichens.

Determination of forage quality is an important aspect of ruminant nutrition. Historically, forage quality has been determined by proximate analysis, with results expressed in terms of crude protein (CP), crude fiber, nitrogen free extract, fat and ash as well as lignin (AOAC, 1965). More recently, the Van Soest detergent analysis (Goering and Van Soest, 1970) has gained popularity. Although results from these techniques often correlate quite well with digestibilities, the correlations are not equally applicable to all types of forage plants (Tilley and Terry, 1963). In particular, special problems have been noted when analyzing lichens, since they contain little or no cellulose, but instead, hemicellulose, lichenen and, more rarely, isolichenen are the primary structural carbohydrates (Hale, 1961).

Because the chemical components of lichen are difficult to estimate and the nutritive value of some of these compounds is unknown, *in vivo* digestibility trials would be the preferred means of determining forage quality. However, whole-animal digestibility trials are time-consuming and require large quantities of forage. It is also extremely difficult to determine the digestibility of various individual plant species within a mixed herbage. Therefore, much recent work has focused on micro-digestion techniques which involve the incubation of plant sample in either the rumen itself (in nylon bags), or in simulated rumen condition *in vitro* (Tilley and Terry, 1963; Johnson, 1966). These techniques have the inherent advantages of requiring only small amounts of forage and allowing analysis of a relatively large number of plant species.

MATERIALS AND METHODS

Animals.—Estimates of *in vivo* digestibilities were made with two mature female reindeer held in stalls under controlled temperature and photoperiod (see Cameron, 1972).

Rumen liquor for the estimation of *in vitro* digestibilities was obtained from: (a) rumen fistulated, mature female reindeer given *ad libitum* a commercial pelleted ration of 12-13 per cent CP (Purina Cattle Starter No. 1); (b) rumen fistulated, yearling reindeer (No.'s 42 and 46; see White and Gau, 1975) given a lichen diet (Holleman and Luick, 1975) of approximately 3 per cent CP; and (c) rumen fistulated Holstein-Friesian cows given a mixture of grasses and alfalfa.

Apparatus for collecting rumen liquor.—The apparatus shown in Figure 1 was used to

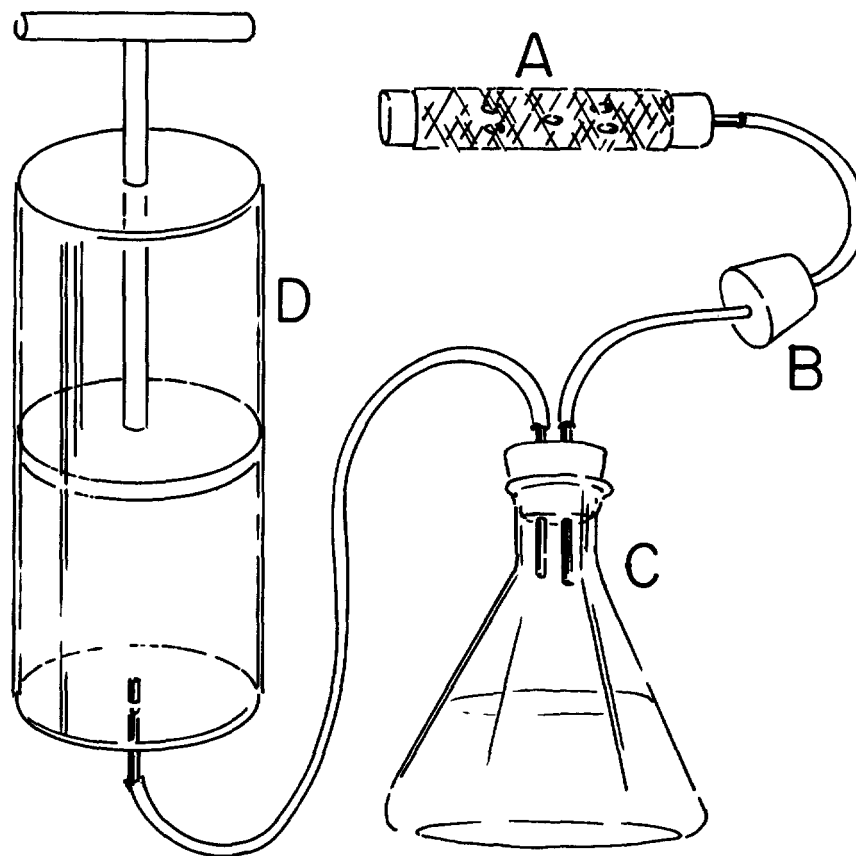


Fig. 1.—Diagrammatic representation of rumen sampling equipment. A, rumen sampling probe; 8.5 X 2.5 cm tube drilled with approximately 12 holes and covered with a fine nylon mesh (ladies nylon hose); B, rubber stopper for insertion in rumen cannula; C, erlenmeyer flask; D, vacuum source (2 l syringe or pump).

collect rumen liquor at rumen temperature under anaerobic conditions. A rigid plastic sampling tube (approximately 8.5 cm long, 2.5 cm in diameter, drilled with 12 holes of

approximately 0.5 cm diameter) and covered with fine nylon mesh (ladies nylon hose), was used to separate liquor from particulate matter *in situ*. The sampling device was connected through an erlenmeyer flask to a vacuum source consisting of a pump (Neptune Dyna-pump, Model 4K, Neptune Products, Inc., Dover, New Jersey, USA) or a large (2 l) syringe. The erlenmeyer flask was kept in a Dewar flask containing water at 39° C.

To free the erlenmeyer flask of oxygen the sampling tube was suspended in the rumen above the rumen contents and a vacuum applied. After gassing the system the sampling device was submerged in the rumen contents. Under continued vacuum, rumen liquor was collected in an anaerobic atmosphere in the erlenmeyer flask at 39° C.

In vitro micro-digestion technique.—The *in vitro* micro-digestion technique was based on that outlined by Tilley and Terry (1963). This technique involves a two stage incubation of air dried plant specimens (approximately 200 mg). The first stage incubation medium consisted of 5 ml rumen liquor and 20 ml artificial saliva (McDougall, 1949) at pH 6.9-7.0. Incubation medium was added to centrifuge tubes containing the pre-weighed forage samples, the tubes were gassed with CO₂, sealed with pressure release valves, and held at 39° C for 48 hours.

After the first stage digestion, the reactions were stopped with 1 ml of Hg Cl₂, 2 ml of Na₂CO₃ were added to improve sedimentation, the contents were centrifuged (20 minutes at 2,000 g) and the supernatant was decanted. The second stage digestion consisted of resuspending the residue at 39° C in 25 ml of a solution containing 0.1N HCl and 2 g/l pepsin. After the second stage digestion the mixture was washed and filtered through a sintered glass crucible (coarse porosity), dried (16 hours at 70° C) and weighed. Dry matter disappearance, referred to as *in vitro* digestibility, was determined after correction for necessary controls (Tilley and Terry, 1963).

Rumen-particle turnover time.—Rumen-particle turnover time was estimated in rumen fistulated reindeer given the pelleted and lichen diets using the principles for rumen liquor turnover as outlined by Weston and Hogan (1968). ¹⁴⁴Ce Cl was used as a particle marker; sampling protocol and radio-assay techniques were described earlier by White and Gau (1972). Rumen-particle turnover time is defined as the time (hours) required to replace an amount of dry matter equivalent to the rumen dry matter.

RESULTS AND DISCUSSION

Table 1 lists the effects of various sources of rumen liquor on the *in vitro* digestibility of both the pelleted ration and lichens. The mean *in vitro* digestion of lichen by rumen liquor obtained from dairy cows was 8.9 per cent. Estimates were obtained from two laboratories which have been using the Tilley-Terry *in vitro* digestion technique for routine forage analysis. Good agreement between laboratories was noted with a digestibility of 8.5 per cent from the University of Alaska Experiment Station (Palmer, Alaska) and 9.4 per cent from the Ohio Agricultural Research and Development Center (University of Ohio, Wooster, Ohio). These values compare closely with *in vitro* estimates of 6.4 per cent lichen digestibility using liquor from reindeer given the pelleted ration (Table 1). However, these estimates are only about 15-17 per cent of mean estimates for *in vivo* digestibility of lichens (Table 1) recorded by Cameron (1972). When lichen was digested in liquor obtained from reindeer given a lichen diet, the *in vitro* estimate (16.2 per cent) was more than twice that determined when liquor was obtained from reindeer given commercial livestock pellets. Although this estimate was low, being only 29 per cent of that obtained *in vivo*, it is still apparent that reindeer, adapted to the lichen diet, may have an enhanced ability to digest lichen.

The *in vitro* digestibilities of commercial livestock pellets were similar whether the

TABLE 1.—Effect of source of inoculum on the *in vitro* digestion (% dry matter disappearance) of lichen¹ and commercial pellets² in reindeer. Results are compared with whole animal estimates and *in vitro* estimates from dairy cows.

	Forage tested	
	lichen	pellets
Digestibility <i>in vivo</i> ³	55.4±1.6	58.0±2.0
Inoculum source:		
Dairy cattle	8.9	
Reindeer given pellets	6.4±4.9	66.6±4.1
Reindeer given lichen	16.2±2.9	64.0±2.3
Rumen turnover time	5 d	10 hr

¹ By weight 60% *Cladonia alpestris*, 20% *Cl. rangiferina*, 10% *Cl. arbuscula*, 5% *Cetraria islandica* and 5% was a mixture of *Cl. gracilis*, *Ce. cuculata*, *Ce. laevigata* and *Stereocaulon alpinum*.

² Purina Cattle Starter No. 1.

³ Cameron (1972).

Values are means ± standard errors.

liquor was taken from reindeer given pellets (67 per cent) or lichen (64 per cent). These estimates were approximately 14 per cent higher than the *in vivo* estimate (Table 1).

Reindeer given the lichen diet had been previously fed the pelleted livestock rations. In fact, the reindeer had been adapted to the lichen diet for only 30 days prior to the *in vitro* experiment and from the high digestibility of the pelleted ration, it is clear that microbial populations in reindeer given lichen retained their ability to digest components of the commercial pellets for at least a month. In part, this effect may be explained by the low crude fiber content (21 per cent) of the pelleted ration which should render it more readily digestible by animals adapted to a variety of diets. In agreement with this suggestion we have found that rumen liquor from field-shot caribou digest 50-63 per cent of the livestock pellets.

Based on the present findings for lichen digestion, it must be concluded that estimates of its *in vitro* digestibility by the Tilley-Terry technique is affected by the source of liquor. Hence, the technique, is unsuitable for assessing the nutritive value of lichen in its present form.

In view of the potential applicability of the *in vitro* digestibility technique to field studies involving nutrition of reindeer and caribou, an investigation of the factors affecting *in vitro* digestion of native forages was undertaken. *In vivo*, the digestion of forages appears to be related to the mean residence time of particles in rumen. For instance, food intake and digestibility have been correlated with rumen volume (Campling, 1970) and the turnover time of rumen contents tends to remain relatively constant for diets with similar 'energy concentration' to crude fiber ratios (ARC, 1965).

In the present study the turnover time associated with rumen dry matter for reindeer given pellets was 10 hours (Table 1). This value is in agreement with estimates for sheep and cattle given similar diets (Hungate, 1966). In contrast, the rumen turnover time of lichen was considerably greater (3-5 days). The longer rumen turnover time apparently resulted

from an increased rumen volume (White and Gau, 1975) and a lowered rate of dry matter outflow from the rumen. Since the rate of volatile fatty acid production in the rumen of these animals is high (White and Gau, 1975), it is suggested that an increased residence time of particles in the rumen enhances dry matter digestion.

In comparison with an *in vivo* turnover time of lichen dry matter of 3-5 days, the *in vitro* digestion technique uses a first stage residence time of only 48 hours, thus the *in vivo* conditions are apparently poorly duplicated and the estimated dry matter digestibility may be underestimated. On the other hand, the *in vitro* technique provides an accurate estimate of *in vivo* digestibility in those diets in which the rumen turnover time is substantially less than 48 hours. Optimizing rumen turnover time would lead to a maximum forage intake which may require that *in vivo* digestion of forages be maximized. Hence, incubating a forage *in vitro* for substantially longer than the mean residence time may not lead to a gross overestimation of digestibility. In future experiments, we will alter the first stage incubation period to characterize the relationship between dry matter disappearance and time for diets containing native plants and lichen.

In conclusion, it must be emphasized that the present estimates of rumen turnover time for reindeer given lichen may not be comparable with rumen turnover times of reindeer and caribou in the field. In the present study the lichen was given as the sole food source and intakes were restricted to between 1.0 and 1.6 per cent body weight (0.5-0.8 kg dry weight) per day which is considerably less than field estimates for caribou (Hanson, Whicker and Lipscomb, 1975) and reindeer (E. Gaare and T. Skogland, pers. comm.). Also, the addition of forages other than lichens to the diet stimulates ruminal fermentation (Jacobson and Skjenneberg, 1975) and decreases the mean residence time of forage dry matter (Person, White and Luick, unpublished observations) resulting in an increase in food intake.

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PLANT FRAGMENT DISCERNIBILITY IN CARIBOU RUMENS

Boyd L. Dearden and Richard M. Hansen
Range Science Department
Colorado State University
Fort Collins, Colorado 80521

Robert E. Pegau
Alaska Department of Fish and Game
Nome, Alaska 99762

ABSTRACT—A microscopic technique was used to identify and quantify plants found in 57 rumens of Alaska caribou. Thirty-two categories of plants were identified in the analyses. There were eight forage plants that individually comprised at least 1 per cent of the diets of these caribou.

Eight hand-compounded mixtures of 19 species of plants, each containing from five to twelve species, were used to observe variation between species and functional categories of plants for over or underestimation by technicians of per cent dry weights. The predictive equations, $Y = (c) X$, for the hand-compounded mixtures of the major species of plants identified in the rumens of caribou each showed a high correlation between the estimated per cent relative density (X) and the actual per cent dry weight (Y). This relationship was not strictly 1:1, but little difference in a corrected or uncorrected mean estimate of dry weight was observed for a majority of the plants. Correction factors 'c' were calculated to determine the technicians degree of over or underestimation of each plant species. It appeared that trained technicians could usually record the frequency of plant species fragments in undigested mixtures containing plants that have a distinct cellular pattern, but the dry weights of a few species are over or underestimated because they have epidermal cells that are either easy or difficult for a technician to identify.

The botanical compositions of the ingesta of herbivores grazing on native plants have been successfully accomplished by the use of various quantitative expressions such as listing of the species of each plant, the percentage frequency of each type of food, and estimates of each food mass by weight or volume. Several forms of 'point analysis' have been used to provide estimates of volume, weight, and botanical composition of food samples. The microscopic identification and quantification of plant fragments in diet samples appears to be an accurate and commonly used technique reported in the literature (Kelso, 1934; Baumgartner and Martin, 1939; Dusi, 1949; Martin, 1955; Adams, 1957; Croker, 1959; Heady and Torell, 1959; Davies, 1959; Brusven and Mulkern, 1960; Hercus, 1960; Lesperance *et al.*, 1960; Ward, 1960; Hegg, 1961; Adams *et al.*, 1962; Williams, 1962; Ward and Keith, 1962; Ridley *et al.*, 1963; Myers and Vaughan, 1965; Van Dyne and Heady, 1965; Bear and Hansen, 1966; Kiley, 1966; Stewart, 1967; Chamrod and Box, 1968; Hansen and Ueckert, 1970; Thetford *et al.*, 1971; Ueckert and Hansen, 1971; Laycock *et al.*, 1972; Malechek and Leinweber, 1972; Peden, 1972; Todd and Hansen, 1973; Flinders and Hansen, 1972; Hansen *et al.*, 1973; Hansen and Martin, 1973).

Attempts to accurately quantify the amount of each plant in a herbivore's diet by

microscopic methods have indicated that each technique has certain weaknesses (Norris, 1943; Cole, 1956; Heady and Torrell, 1959; Cole and Wilkins, 1958; Hercus, 1960; Dirschl, 1962; Dirschl, 1963; Bergerud and Russell, 1964; Van Dyne and Heady, 1965; Galt *et al.*, 1966; Grenet, 1966; Malechek, 1966; Scotter, 1967; Stewart, 1967; Hansen *et al.*, 1973).

Adams (1957) and Adams *et al.* (1962) reported a procedure to estimate the weight of food eaten by snowshoe hares from counting the number of recognized items in the feces. Valid correction factors for the differences in counts between food items can be obtained by feeding penned hares known weights of foods and then counting recognized items in the dung of the hares.

A double-sample technique has been used to obtain estimates of differences between the dry weights of forbs and grasses in hand-compounded mixtures and their estimated dryweights by a microscopic technique (Sparks and Malechek, 1968). Double sampling has recently been used to compare microscopic estimates of the abundance of plant species in pairs of esophageal and fecal samples from cattle, bison, sheep and bighorns (Free *et al.*, 1970; Hansen *et al.*, 1973; Todd and Hansen, 1973).

The objectives of this study are to describe and evaluate the variations observed in the microscopic discernibility of plant species in relation to the dry weight of plants in hand-compounded mixtures of the major species of plants identified in the rumens of Alaskan caribou.

MATERIAL AND METHODS

The major forage plants consumed by Alaskan caribou were determined by a microscopic examination of rumen samples. The rumen contents were obtained on various dates from 1969 to 1972 on typical ranges in Alaska. There were 3,800 microscope fields examined to determine the average botanical composition.

Eight mixtures of 19 kinds of caribou forages were hand-compounded to simulate the relative proportions that might occur in the diets of caribou. The plants used consisted of the aboveground parts fed upon by caribou. These hand-compounded mixtures were used to study the degree of over or underestimation of dry weight by laboratory technicians using a microscopic technique.

Microscope slides were prepared of reference plants, hand-compounded mixtures and rumen samples as described by Sparks and Malechek (1968), Ward (1970) and Flinders and Hansen (1972).

Fields were systematically located on each microscope slide and were viewed at 100 magnifications for identifiable fragments. Twenty fields were examined per microscope slide. The total number of fields examined per sample is stated in the text. Microscope slides were prepared with the number of identifiable fragments per field varying from one to five and averaging approximately three discernible fragments per microscope field.

Three microscope technicians were trained to identify all species of plants used in each hand-compounded sample. Technicians were trained to identify and quantify discerned plant fragments with the use of practice slides prepared from samples of known dry weight composition. Technicians were 'challenged' to quantify discerned fragments on microscope slides with the names and amounts of each plant species in the hand-compounded mixtures unknown to them. Each fragment in a sample was identified if its observed characteristics matched the leaf, stem, flower, seed or other plant part of the same material on a reference slide.

The relative per cent density of recognized plant fragments in each of the samples was estimated by observing fields located systematically on each of the slides. The occurrence of each recognized plant species in each field was recorded. Average per cent frequency was

computed for all plant species present in the samples. The relative per cent density, is calculated as the number of recognized fragments of a species divided by the total number of fragments of all species times 100. The relationship of per cent frequency per field to density of discerned fragments per field can be determined by the formula:

$$F = 100 (1 - e^{-D})$$

For a given per cent frequency (F), a mean density (D) of discerned particles of a species per microscope field can be determined. The density of particles per field may be converted to relative per cent density (RD) by:

$$RD = \frac{\text{Density of discerned fragments for a species}}{\sum \text{of densities of discerned fragments for all species}} \times 100$$

The RD is a better estimate of the amount of a species in a mixture than is per cent frequency. Sparks and Malechek (1968) obtained predictive equations showing a high correlation between the relative number of fragments counted and the actual per cent dry weights for forbs versus grasses in 15 hand-compounded mixtures. The relationship was approximately 1:1 and Sparks and Malechek suggested that for practical purposes it may not be necessary to use correction factors in most studies.

Sparks and Malechek (1968) reported that the RD of discerned fragments could be accurately calculated by 'counting' fragments or by 'frequency conversion'.

The relative numbers of discernible fragments of plant species in two caribou rumen samples were determined by 'counting' and by 'frequency conversion'.

Correction factors (c) were calculated for the hand-compounded mixtures. These factors can be used to determine the degree of over or underestimation of each species contained in a mixture of plants when the sample is examined by the microscopic technique. The relationship between the dry weight (Y) and the estimated (X) percentages is expressed as:

$$Y = (c) X$$

The correction factor 'c' is obtained by dividing the original per cent (Y) by the percentage which was estimated (X). An index ratio of 1.0 for a species indicates there was no over or underestimation; a value larger than 1.0 indicates a greater original percentage than the estimate; and a value less than 1.0 indicates a less original percentage than the estimate. The higher the 'c' value for a plant the lower is its discernibility, and the smaller the 'c' value the higher is its discernibility.

RESULTS

Mean RD of discerned plant fragments were calculated for 57 rumens of Alaskan caribou collected in June and December 1969, June 1971, and February 1972. The mean number of plant categories recorded per rumen of individual caribou varied between eight in December 1969 to 13 in February 1972. Thirty-two plant forages were identified in the 57 rumens of caribou. There were eight plants that individually comprised at least 1 per cent of the diets of these caribou. These eight plant species made up 95 per cent of the dry weight eaten by caribou throughout the periods of study. These are, in order of importance, cottongrass (*Eriophorum* sp.), lichen (*Cladonia* sp.), moss (unidentified), moss A

(unidentified), lichen (*Peltigera aphosa*) and an unidentified forb (Table 1). Cottongrass

TABLE 1.—Mean per cent relative density for identified fragments of plants averaged over 57 rumens from Alaskan caribou.

Plant species	Mean % of relative density
<i>Eriophorum</i> sp.	37.3
<i>Cladonia</i> sp.	30.9
Species of Moss	14.1
Unidentified Moss A	4.6
<i>Peltigera aphosa</i>	2.6
<i>Carex aquatilis</i>	2.5
Unidentified Lichen A	1.6
Unidentified Forb	1.5

and *Cladonia* comprised 68 per cent of the diets and are the dominant species on caribou ranges that are in excellent condition. Sparks and Malechek (1968) reported no differences between the estimates obtained from the 'particle count' technique and the 'frequency conversion' technique. The time required for a technician to 'count' and record discerned fragments requires more work than recording frequency per microscope field (ibid).

The relative numbers of discernible fragments of plant species in two caribou rumen samples were determined by 'counting' and by 'frequency conversion', and the number of non-identifiable fragments was counted for 400 microscope fields per sample. The purpose of these observations was to study the relationships between the numbers of discerned and unidentifiable fragments and to illustrate the similarity between RD's determined by counting discerned fragments and by estimating discerned fragments by the frequency conversion technique.

The numbers of unidentifiable fragments found in the two caribou rumen were 36 per cent and 42 per cent respectively (Tables 2 and 3). The RD's of discerned fragments of plant species determined by counting or by the frequency conversion method were not significantly different ($P = .95$). The counting technique required 16 hours of technician time, while the 'conversion technique' required only four hours. Either can be used with a similar degree of accuracy, but it is much easier and faster for the technician to determine if a species is present or absent than to count all discernible fragments.

Eight hand-compounded mixtures of 19 species of plants, each containing from five to twelve species, were used to observe variation between species and 'functional categories' of plants for over or underestimation of the per cent dry weights.

The hand-compounded mixtures were prepared with each sample containing at least one lichen, one moss, one sedge, one grass and one forb or shrub. The actual percentages of dry weight (Y) used were chosen so that the degree of over or underestimation (c) would be within a range that might be encountered in the diets of a large herbivore such as a caribou.

Each of the eight mixtures was examined by three different technicians. Regression estimates were made on 10 slide averages (200 microscope fields) of three laboratory technicians (600 fields total). The regression equations were generally better when the data was treated by species rather than by functional groups. Analyses were both by species as well as by functional groups. These analyses consisted of: (1) testing for differences between means (Y vs X) and (2) testing about the regression equation (Table 4).

The estimated (X) and actual (Y) per cents are significantly different from each other

TABLE 2.--Comparison of methods to determine relative per cent density of discerned plant fragments for caribou rumen sample #1.

ITEM	Counting method with unidentifiable fragments	Counting methods without unidentifiable fragments	Frequency conversion method
<i>Cladonia</i>	46.56	72.90	76.21
<i>Stereocaulon</i>	0.22	0.34	0.18
<i>Peltigera ophthosa</i>	2.49	3.90	2.71
Unidentified moss	9.15	14.33	12.19
Unknown moss 1	0.27	0.40	0.45
Unknown forb 1	1.39	2.18	0.91
Unknown forb 2	2.01	3.15	5.01
<i>Betula nana</i>	0.11	0.17	0.27
<i>Equisetum fluviatile</i>	0.07	0.11	0.00
<i>Vaccinium vitis-idaea</i>	0.07	0.11	0.18
<i>Salix</i>	0.22	0.34	0.45
<i>Festuca altaica</i>	0.33	0.52	0.18
<i>Hierchloe alpina</i>	0.33	0.52	0.36
<i>Pinaceae</i>	0.66	1.03	0.91
<i>Carex aquatilis</i>	0.00	0.00	0.00
Unidentifiable fragments	36.13		

TABLE 3.--Comparison of methods to determine relative per cent density of discerned plant fragments for caribou rumen sample #2.

ITEM	Counting method with unidentifiable fragments	Counting methods without unidentifiable fragments	Frequency conversion method
<i>Cladonia</i>	41.21	71.21	69.61
<i>Stereocaulon</i>	0.04	0.07	0.58
<i>Peltigera ophthosa</i>	1.91	3.31	2.36
Unidentified moss	8.81	15.22	17.02
Unknown moss 1	0.15	0.26	0.24
Unknown forb 1	0.57	0.99	1.75
Unknown forb 2	2.57	4.43	3.88
<i>Betula nana</i>	0.11	0.20	0.08
<i>Equisetum fluviatile</i>	0.00	0.00	0.08
<i>Vaccinium vitis-idaea</i>	0.00	0.00	0.00
<i>Salix</i>	0.04	0.07	0.16
<i>Festuca altaica</i>	0.84	1.46	1.75
<i>Hierchloe alpina</i>	0.15	0.26	0.58
<i>Pinaceae</i>	1.38	2.38	1.67
<i>Carex aquatilis</i>	0.08	0.13	0.24
Unidentifiable fragments	42.13		

TABLE 4.--Summary of regression analysis showing the number of observations, the regression equation, means, variances and degree of over or underestimation of plants by species and groups of species.

	n	Y = a + bX	\bar{X}	\bar{Y}	r^2	S^2_x	S^2_y	$S_{y.x}$	S_{b1}	c
<i>Calamagrostis canadensis</i>	12	Y = 4.00 + 1.12X	7.64	12.52	.85	17.98	26.13	2.04	.14	1.64
<i>Hierchloe alpina</i>	12	Y = 3.76 + .88X	9.90	12.50	.21	6.97	26.42	4.81	.55	1.26
<i>Festuca altaica</i>	6	Y = 4.47 + .82X	8.49	11.43	.55	8.00	9.78	2.35	.37	1.35
<i>Carex aquatilis</i>	12	Y = 3.29 + .66X	14.05	12.49	.92	57.95	27.04	1.55	.06	.89
<i>Carex bigelowii</i>	5	Y = 8.00 + .72X	6.63	12.80	.41	34.02	43.20	5.81	.50	1.93
<i>Eriophorum angustifolium</i>	12	Y = 3.94 + .95X	8.99	12.50	.73	21.42	26.42	2.78	.18	1.39
<i>Eriophorum brachyantherum</i>	9	Y = 9.89 + .62X	15.07	19.17	.08	14.14	65.98	8.32	.78	1.27
<i>Polytrichum juniperinum</i>	12	Y = .86 + .84X	15.97	12.51	.68	25.28	26.09	3.03	.18	.78
<i>Pleurozium schrieberi</i>	18	Y = 3.92 + .29X	31.31	12.99	.62	223.40	30.29	3.50	.06	.41
<i>Betula nana</i>	12	Y = 4.62 + .85X	9.26	12.51	.84	30.64	26.58	2.19	.12	1.35
<i>Salix pulchra</i>	6	Y = 5.39 + 1.09X	7.74	13.81	.98	50.12	60.13	1.08	.07	1.78
<i>Dryas octopetala</i>	12	Y = 4.38 + .79X	10.24	12.49	.80	34.01	26.63	2.42	.12	1.20
<i>Vaccinium vitis-idaea</i>	5	Y = 5.18 + .94X	6.04	10.86	.43	4.78	9.82	2.73	.62	1.80
<i>Epilobium angustifolium</i>	6	Y = 8.28 + .63X	9.10	14.00	.18	19.70	43.20	6.65	.67	1.54
<i>Equisetum fluviatile</i>	6	Y = 5.63 + .57X	10.17	11.44	.75	22.82	9.85	1.74	.16	1.12

<i>Cladonia</i>										
<i>rangiferina</i>	18	$Y = 2.08 + .77X$	13.01	12.15	.75	25.37	20.28	2.33	.11	.93
<i>Stereocaulon</i>										
<i>grande</i>	12	$Y = 5.71 + .76X$	8.87	12.49	.69	31.36	26.63	3.02	.16	1.41
<i>Cetraria</i>										
<i>islandica</i>	6	$Y = 1.58 + 2.02X$	7.70	14.00	.75	7.94	43.13	3.65	.58	1.83
<i>Peltigera</i>										
<i>apthosa</i>	6	$Y = 4.57 + .34X$	20.00	11.42	.58	48.30	9.75	2.26	.14	.57
Grasses	30	$Y = 4.17 + .93X$	8.71	12.29	.47	11.91	21.81	3.45	.18	1.41
Sedges	38	$Y = 6.32 + .67X$	11.72	14.11	.42	40.74	42.97	5.06	.13	1.20
Mosses	30	$Y = 6.75 + .24X$	25.18	12.80	.41	198.97	27.71	4.10	.05	.51
Shrubs	35	$Y = 5.01 + .84X$	8.88	12.49	.79	30.97	27.91	2.47	.08	1.41
Forbs	12	$Y = 7.42 + .55X$	9.63	12.72	.23	19.64	25.91	4.69	.32	1.30
Lichens	42	$Y = 7.66 + .39X$	12.07	12.41	.28	41.18	22.54	4.07	.10	1.03

for the *Calamagrostis canadensis*, *Pleurozium schrieberi*, *Vaccinium vitis-idaea*, *Cetraria islandica* and *Peltigera aphthosa* plant species (Table 5). These differences are also present in

TABLE 5.—Calculated t-values, testing for differences between actual and estimated means.

	t	Significance level
<i>Calamagrostis canadensis</i>	-2.54	.03
<i>Hierchloe alpina</i>	-1.56	.15
<i>Festuca altaica</i>	-1.71	.14
<i>Carex aquatilis</i>	0.59	.57
<i>Carex bigelowii</i>	-1.57	.18
<i>Eriophorum angustifolium</i>	-1.76	.11
<i>Eriophorum brachyantherum</i>	-1.37	.20
<i>Polytrichum juniperinum</i>	1.66	.12
<i>Pleurozium schrieberi</i>	4.88	<.01
<i>Betula nana</i>	-1.49	.16
<i>Salix pulchra</i>	-1.11	.31
<i>Dryas octopetala</i>	-1.00	.34
<i>Vaccinium vitis-idaea</i>	-2.82	.04
<i>Epilobium angustifolium</i>	-1.51	.10
<i>Equisetum fluviatile</i>	-0.54	.61
<i>Cladonia rangiferina</i>	0.54	.60
<i>Stereocaulon grande</i>	-1.65	.13
<i>Cetraria islandica</i>	-2.16	.07
<i>Peltigera aphthosa</i>	2.76	.03
Grasses	-3.38	<.01
Sedges	-1.61	.12
Mosses	4.50	<.01
Shrubs	-2.78	<.01
Forbs	-1.59	.14
Lichens	0.27	.79

the grass, moss and shrub functional groups. There can be no subjective comparisons made between the significances of the functional groups and the species in those groups. There is no difference between the means for the lichens as a group, but *Cetraria islandica* and *Peltigera aphthosa* show significant differences between means. A significant difference between means should not be used as a criterion for judgements of the respective regression equations. It is merely a statement of similarity between the means.

The c-values show underestimation of grasses, sedges, shrubs, forbs and lichens while mosses were overestimated. Underestimation of grasses, sedges, shrubs, forbs and lichens is a reflection of the high degree of overestimation of the mosses. The high degree of overestimation occurred because mosses fragmented more than did the other plants and even the tiny sized moss fragments are easy to identify.

The proportions of discerned fragments of plant species by microscopic analysis appear to depend, in part, upon the composition of plants in the mixtures.

Testing about the Regression Line

Testing the hypothesis that the slopes of the lines each equal 1, $H_0: b_1 = 1$, resulted in the t-values presented in Table 6.

TABLE 6.--Calculated t-values testing for a slope (β_1) equal to 1 by species of plants and groups of species.

	t	Significance level
<i>Calamagrostis canadensis</i>	0.79	.44
<i>Hierchloe alpina</i>	-0.21	.84
<i>Festuca altaica</i>	0.49	.64
<i>Carex aquatilis</i>	-5.66	<.01
<i>Carex bigelowii</i>	-0.55	.60
<i>Eriophorum angustifolium</i>	-0.26	.80
<i>Eriophorum brachyantherum</i>	-0.49	.64
<i>Polytrichum juniperinum</i>	-0.89	.39
<i>Pleurozium schrieberi</i>	-12.46	<.01
<i>Betula nana</i>	-1.24	.24
<i>Salix pulchra</i>	1.28	.25
<i>Dryas octopetala</i>	-1.66	.12
<i>Vaccinium vitis-idaea</i>	-0.10	.93
<i>Epilobium angustifolium</i>	-0.55	.60
<i>Equisetum fluviatile</i>	-2.63	.04
<i>Cladonia rangiferina</i>	-2.02	.06
<i>Stereocaulon grande</i>	-1.45	.17
<i>Cetraria islandica</i>	1.76	.13
<i>Peltigera apthosa</i>	-4.54	<.01
Grasses	-0.37	.72
Sedges	-2.57	.01
Mosses	-14.07	<.01
Shrubs	-2.07	.05
Forbs	-1.41	.18
Lichens	-6.12	<.01

Again no subjective comparison can be made between the significance of the functional groups and the species of the functional groups. None of the shrub species (*Betula nana*, *Salix pulchra*, *Dryas octopetala*, *Vaccinium vitis-idaea*) showed a slope significantly different from 1. Although as a whole the shrub group does show a slope significantly different from 1. The forb group as a whole displays a slope not different from 1, while *Equisetum fluviatile* does display a slope different from 1.

The species with slopes significantly different from 1 are : *Carex aquatilis*, *Pleurozium schrieberi*, *Equisetum fluviatile*, *Cladonia rangiferina* and *Peltigera apthosa*, and the functional groups with slopes significantly different from 1 are: sedges, mosses, shrubs and lichens.

The difference between the actual (Y) and estimated (X) means (Table 5) for a slope equal to 1 (Table 6) should not necessarily yield similar results when viewed simultaneously. An equation with a slope equal to 1 may in fact have independent and dependent variable

means which are significantly different from each other due to a large value for the Y-intercept. Likewise, independent and dependent variable means which are not significantly different do not insure a 45° slope.

Testing Intercepts Each Equal to 0

The resulting t-values from the testing of the hypothesis that the intercepts each equal 0, $H_0: b_0 = 0$, are listed in Table 7.

TABLE 7.--Calculated t-values testing for the y-intercept (β_0) equal to 0 by species of plants and groups of species.

	t	Significance level
<i>Calamagrostis canadensis</i>	3.18	<.01
<i>Hierchloe alpina</i>	0.67	.52
<i>Festuca altaica</i>	1.36	.22
<i>Carex aquatilis</i>	3.39	<.01
<i>Carex bigelowii</i>	1.90	.12
<i>Eriophorum angustifolium</i>	2.17	.05
<i>Eriophorum brachyantherum</i>	0.82	.44
<i>Polytrichum juniperinum</i>	-0.28	.78
<i>Pleurozium schrieberi</i>	2.00	.06
<i>Betula nana</i>	3.62	<.01
<i>Salix pulchra</i>	7.82	<.01
<i>Dryas octopetala</i>	3.00	.01
<i>Vaccinium vitis-idaea</i>	1.31	.25
<i>Epilobium angustifolium</i>	1.24	.26
<i>Equisetum fluviatile</i>	3.13	.02
<i>Cladonia rangiferina</i>	1.34	.20
<i>Stereocaulon grande</i>	3.39	<.01
<i>Cetraria islandica</i>	-0.34	.75
<i>Peltigera apthosa</i>	1.50	.19
Grasses	2.40	.02
Sedges	3.64	<.01
Mosses	4.28	<.01
Shrubs	6.31	<.01
Forbs	2.21	.05
Lichens	5.67	<.01

Simultaneous comparisons of the functional group categories with the species of the categories showed that at least one species in each category displayed an intercept significantly different from zero. Also, each category displayed an intercept significantly different from zero. The individual species which showed an intercept significantly different from zero are: *Calamagrostis canadensis*, *Carex aquatilis*, *Eriophorum angustifolium*, *Pleurozium schrieberi*, *Betula nana*, *Salix pulchra*, *Dryas octopetala*, *Equisetum fluviatile* and *Stereocaulon grande*.

The 'ideal' plant species has a 1:1 relationship between the estimated per cent (X) and the actual per cent (Y) dry weight.

The plant species for which the slopes were not different from one while the intercepts were not different from zero are: *Hierchloe alpina*, *Festuca altaica*, *Carex bigelowii*, *Eriophorum brachyantherum*, *Polytrichum juniperinum*, *Vaccinium vitis-idaea*, *Epilobium angustifolium* and *Cetraria islandica*.

This does not mean the function $Y = X$ is the proper relationship between the two variables; it is merely stating that the regression estimates of b_0 and b_1 are not significantly different from 0 and 1 respectively (Table 8).

TABLE 8.—Summary of t-tests about the means, about the slopes, and about the intercepts for species of plants and groups of species.

	Significance levels		
	Ho: $\mu_a = \mu_e$	Ho: $\beta_1 = 1$	Ho: $\beta_0 = 0$
<i>Calamagrostis canadensis</i>	.03	.44	<.01
<i>Hierchloe alpina</i>	.15	.84	.52
<i>Festuca altaica</i>	.14	.64	.22
<i>Carex aquatilis</i>	.57	<.01	<.01
<i>Carex bigelowii</i>	.18	.60	.12
<i>Eriophorum angustifolium</i>	.11	.80	.05
<i>Eriophorum brachyantherum</i>	.20	.64	.44
<i>Polytrichum juniperinum</i>	.12	.39	.78
<i>Pleurozium schrieberi</i>	<.01	<.01	.06
<i>Betula nana</i>	.16	.24	<.01
<i>Salix pulchra</i>	.31	.25	<.01
<i>Dryas octopetala</i>	.34	.12	.01
<i>Vaccinium vitis-idaea</i>	.04	.93	.25
<i>Epilobium angustifolium</i>	.10	.60	.26
<i>Equisetum fluviatile</i>	.61	.04	.02
<i>Cladonia rangiferina</i>	.60	.06	.20
<i>Stereocaulon grande</i>	.13	.17	<.01
<i>Cetraria islandica</i>	.07	.13	.75
<i>Peltigera aphosa</i>	.03	<.01	.19
Grasses	<.01	.72	.02
Sedges	.12	.01	<.01
Mosses	<.01	<.01	<.01
Shrubs	<.01	.05	<.01
Forbs	.14	.18	.05
Lichens	.79	<.01	<.01

Six of the eight species previously mentioned, having slopes not different from one and intercepts not different from zero, also, have actual (Y) and estimated per cent (X) means not significantly different from each other. They are: *Hierchloe alpina*, *Festuca altaica*, *Carex bigelowii*, *Eriophorum brachyantherum*, *Polytrichum juniperinum* and *Epilobium angustifolium*. Graphs of the original data points (10 slide means) and the regression lines are shown in Figures 1 through 6.

This relationship, however, is not strictly 1:1 as indicated by the t-tests about the slopes and intercepts. One would observe little difference in a corrected or uncorrected mean estimate of dry weight. Individual examination of the graphs provides a subjective

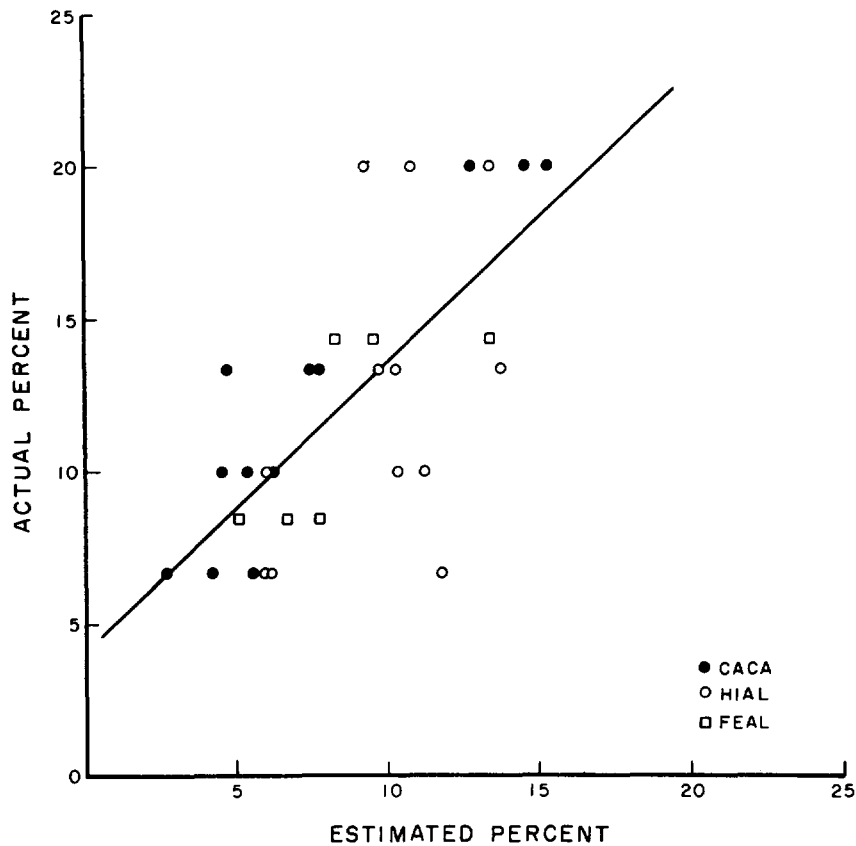


Fig. 1.—The estimated dry weight and actual dry weight of *Calamagrostis canadensis* (CACA), *Heirochloe alpina* (HIAL) and *Festuca altaica* (FEAL) in mixtures of plants examined by a microscopic technique for the discerned plant fragments on microscope slides.

view of the 'scatter' present or absent in the predications.

It appears that trained technicians can accurately discern the frequency of fragments in undigested mixtures containing plants that have distinct cellular patterns.

The microscopic technique used in estimating per cent composition (X) of hand-compounded mixtures of non-digested plants is both a valid and accurate means of determining the actual dry weight composition (Y).

DISCUSSION

Evidence from other studies on the dry weight quantification for botanical composition in diets using recognizable plant fragments in the digestive tracts of livestock and wild herbivores has been consistently questioned. The identification of all species found in the ingesta and feces to indirectly estimate per cent dry weight of species eaten depends upon relative discernibility as influenced by the distinctiveness of each plant species as well as relative changes in the identifiable characteristics of each plant species as altered by digestion. Martin (1955) was able to recognize, in the feces and stomachs of sheep (*Ovis*

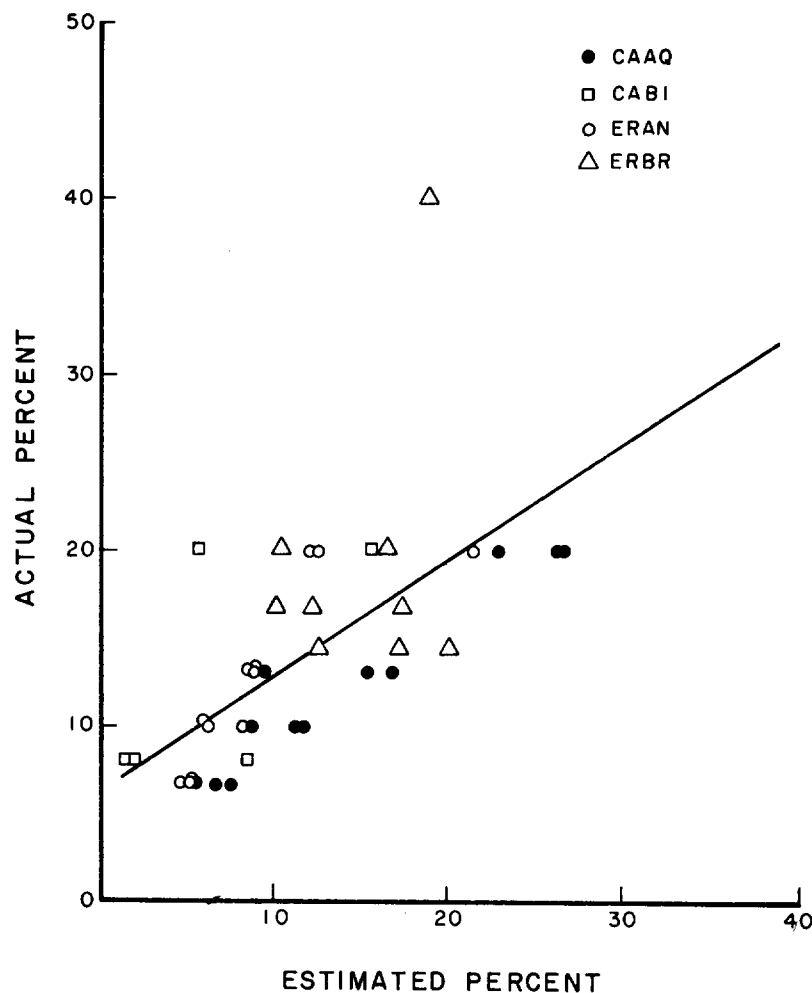


Fig. 2.—The estimated dry weight and actual dry weight of *Carex aquatilis* (CAAQ), *Carex bigelowii* (CABI), *Eriophorum angustifolium* (ERAN) and *Eriophorum brachyantherum* (ERBR) in mixtures of plants examined by a microscopic technique for the discerned plant fragments on microscope slides.

aries), only 16 of the 40 species which were present in the pasture and which he suspected were all being ingested. Without proof, he concluded that many species were completely digested or reduced to such small fragments as to be unidentifiable. No evidence was presented to show that the sheep whose feces he sampled had recently ingested any of the unrecorded species for fragments to be present in the feces. Croker (1959) could not identify in sheep feces one of about 25 grass species which were present in the pasture. The species she could not find had a thin cuticle which disintegrated *in vitro* and she suspected it had been completely digested. It was not certain that the grass concerned had, in fact, been ingested recently. In a study by Hercus (1960), it was found that for every herbage species ingested some recognizable cuticle or epidermis was found in the feces of sheep, and it was concluded that feces analysis can be used to investigate the botanical composition of the diet of any herbivorous animal. Storr (1961) states that in annual plants only the cuticle, which bears an outline of epidermal cells and is identifiable, survives maceration *in vitro* and

digestion. The entire epidermis survives since cutin is deposited in all of the cell walls in perennials. He found that all of the limited number of dicotyledons ingested were recognizable in the feces. Todd and Hansen (1973) could find no significant differences between the plant fragments found in the rumens and those in the colons of individual bighorn sheep (*Ovis canadensis canadensis*). They concluded that the relative number of plant fragments of each kind of plant in their sample remained similar while passing through the digestive process. They suggested that digestion reduces the mean weight of fragments rather than eliminating the whole fragment. Using paired fistula and fecal samples of cows, bison and sheep, Hansen *et al.* (1973) determined that the degree of dietary overlap between herbivores, areas, seasons and grazing intensity is approximately the same for discerned plant fragments in the feces as it is in the paired esophageal samples. Plants having a low frequency are less likely to be discovered when subsampling and these are the components which are frequently not discerned by microscopic analyses and are underestimated when rumen or fecal sampling has been done by the microscopic technique.

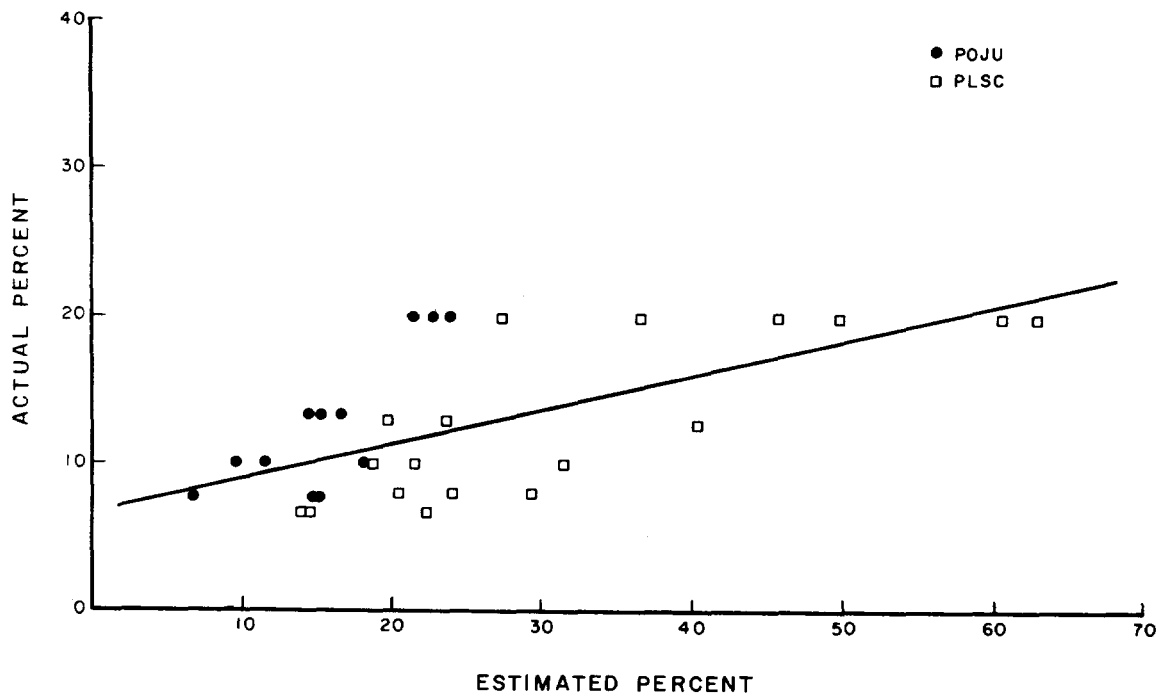


Fig. 3.—The estimated dry weight and actual dry weight of *Polytrichum juniperinum* (POJU) and *Pleurozium schrieberi* (PLSC) in mixtures of plants examined by a microscopic technique for the discerned plant fragments on microscope slides.

In this study, the major food plants were as easily identified in the rumens as they were in the hand-compounded mixtures. Examination of ruminal contents provided estimates of the major foods ingested by the caribou and indicated the general proportions in which these food items were ingested. This study also showed that technicians can identify some species of plants easier and more frequently than others and this causes some fragments of plants to be over or underestimated when percentages are used to describe a diet.

Since certain plants are assumed to be digested more thoroughly than others it has been assumed that highly digestible plants are more likely to lose their identifiable

characteristics than are less digestible plants. Some of our observations (unpublished) suggest that the per cent relative densities are influenced more by technician variability and technique than by digestion. This hypothesis is currently being tested and evaluated for foods fed to reindeer.

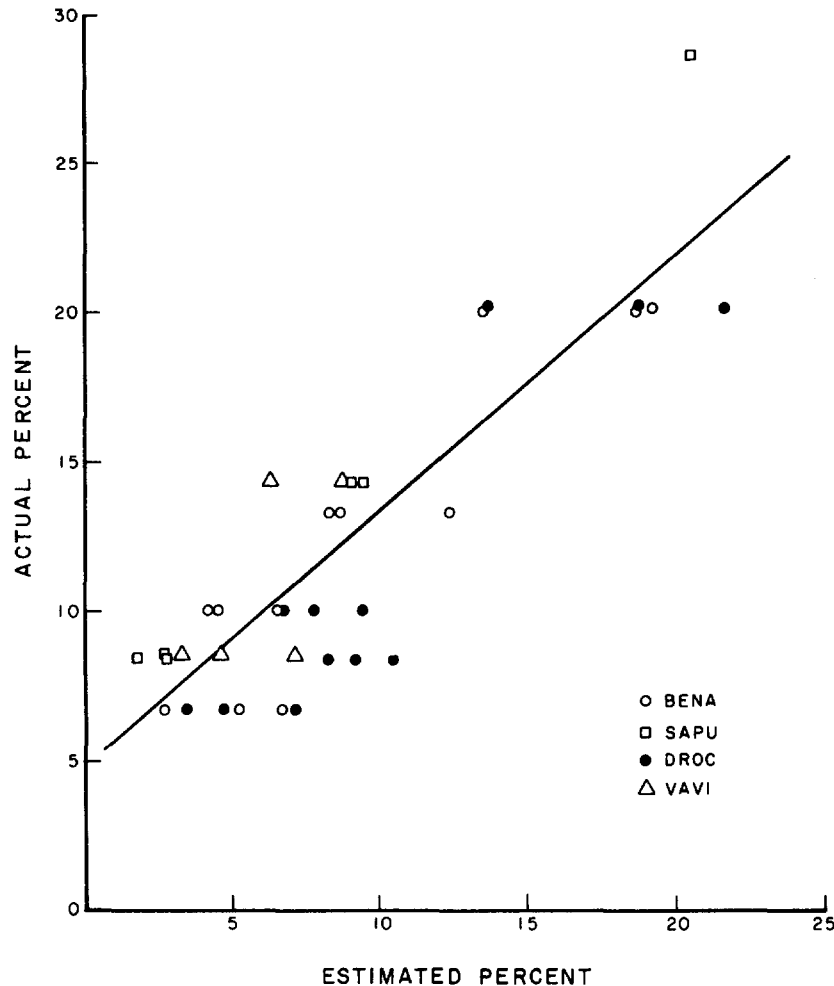


Fig. 4.—The estimated dry weight and actual dry weight of *Betula nana* (BENA), *Salix pulchra* (SAPU), *Dryas octopetala* (DROC) and *Vaccinium vitis-idaea* (VAVI) in mixtures of plants examined by a microscopic technique for the discerned plant fragments on microscope slides.

The overestimation of moss occurred because most mosses fragmented more than other plants and even the tiny sized moss fragments are easy to identify. Perhaps mosses should be ignored when reporting botanical composition because of their high degree of overestimation. Our unpublished observations suggest that they are not digestible in reindeer, cattle or bison.

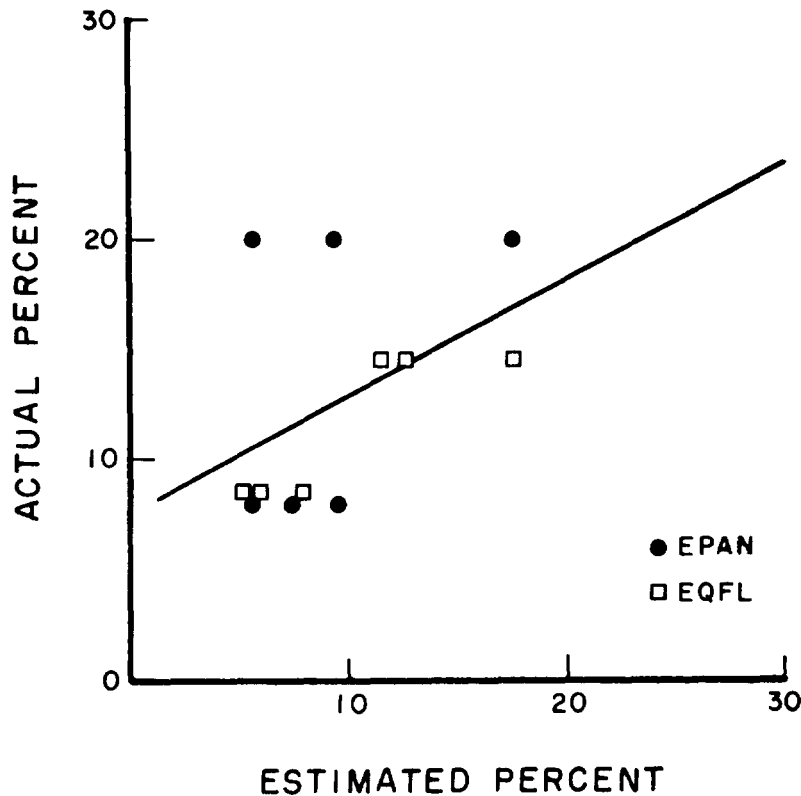


Fig. 5.—The estimated dry weight and actual dry weight of *Epilobium angustifolium* (EPAN) and *Equisetum fluviatile* (EQFL) in mixtures of plants examined by a microscopic technique for the discerned plant fragments on microscope slides.

CONCLUSIONS

The method of quantification used in this study was by converting percentage of identified plant fragments to percentage relative density. Per cent relative density was used to determine the dietary composition of 57 rumens of caribou for various parts of Alaska and to compare the estimated proportions (X) with the hand-compounded proportions (Y) of plants commonly found on caribou rangelands.

The accuracy of the estimation of the proportions (RD's) of food items ingested is influenced directly by many complex and interrelated factors. The relationship between the ingesta (Y) and the estimated (X) is expressed as: $Y = (c) X$. Emphasis must be placed on the determination of the correction term (c) if estimated proportions (X) are to accurately relate to ingesta (Y). Estimates of the correction term have generally been limited in scope and intensity. Current investigators should attempt to obtain more precise estimates of (c) and then use the estimator (X) as comparable to the ingesta (Y).

This study has attempted to establish only correction terms for technician over or underestimation (c_1). Other correction terms are needed for such parameters as:

1. Differential digestion (c_2)
2. Seasonal and phenological stages of plants (c_3)
3. Physiological state of the animal (c_4)

4. Species of digester (c_5)
5. Specifics such as stress, changing environmental conditions, fluctuating food availability, animal competition, population pressure, etc. (c_n).

These associations, which make up the differences between the estimated consumption (X) and the ingesta (Y), have only begun to be understood. Once these parameters have been defined, the correction term 'c' will have the most meaning when calculated as:

$$c = \frac{c_1 + c_2 + c_3 + c_4 + c_5 \dots + c_n}{n}$$

This suggests a method for obtaining correction values for the proportions of food plants ingested by wild herbivores. Plants could be hand plucked or clipped to provide duplication of vegetation foraged by wild animals, then ground to uniform size and microdigested in ruminal fistulated animals.

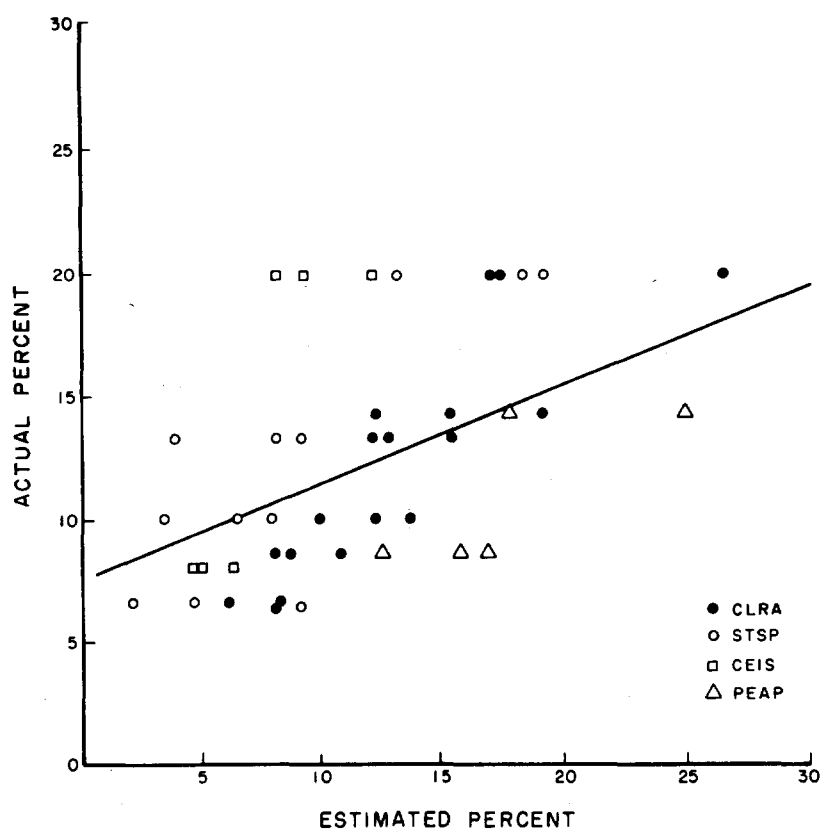


Fig. 6.—The estimated dry weight and actual dry weight of *Cladonia rangeriferina* (CLRA), *Stereocaulon grande* (STSP), *Cetraria islandica* (CEIS) and *Peltigera apthosa* (PEAP) in mixtures of plants examined by a microscopic technique for the discerned plant fragments on microscope slides.

Since the dry weights (Y) of each food item placed in the nylon bags for microdigestion are known and the estimated proportions (X) of each plant species after

microdigestion are known, as well as the proportions estimated by counts of epidermal fragments in the feces of the wild herbivore, correction terms may be calculated to estimate from the RD's of feces the estimated dry weights ingested by the foraging wild herbivore.

Greater depth of interpretation and a more critical examination of relationships can improve the value of this technique, which has both historic and current applications.

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EFFECT OF CHANGES IN DIET ON THE REINDEER RUMEN MUCOSA

Bengt Westerling
College of Veterinary Medicine
Department of Anatomy and Embryology
Helsinki, Finland

ABSTRACT—The structure of the rumen mucosa of free living reindeer in September, December and February and that of pellet- and hay-fed animals was studied microscopically by various staining methods. From fall to winter the ruminal papillae became more folded longitudinally and the thickness of folds decreased. The relative thickness of the *stratum spinosum* decreased due to a decrease in the number of cell layers and flattening of cells. A thickening of the *stratum corneum* towards winter was also observed. Extended feeding of commercial reindeer-pellets and hay induced an opposite development. No significant changes in the degree of keratinization was recorded by staining for -SH and -S-S- groups. It is concluded that the reindeer rumen mucosa undergoes a structural adaptation between pasture seasons and that considerable adaptation is required when the deer begin feeding on commercial pellets and roughages.

A number of workers have studied the effect of diet on the structural development of the rumen mucosa in domestic ruminants and the question has been reviewed by McGilliard *et al.* (1965). Also in adult sheep and cattle, structural alterations in the mucosa have been observed to follow changes in physical properties and energy content of the ration (Brownlee, 1956; Nockels *et al.*, 1966).

The diet of the free living reindeer is quite different in winter as compared to summer. Consequently it seemed worth while to study the structure of the rumen mucosa of reindeer in order to detect the possible differences between summer and winter and also the possible effects of pen feeding.

The rumen mucosa has been referred to as a parakeratotic, psoriatic epithelium (Lavker *et al.*, 1969) and the histological nomenclature mostly applied to the forestomach mucosa was proposed by Henriksson and Habel (1961). According to these, the rumen epithelium is divided, starting from the basal lamina outward, in the following layers: *stratum basale*, *stratum spinosum*, *stratum transitionale* and *stratum corneum*, and the *stratum granulosum* when present is included in the *stratum transitionale*.

MATERIALS AND METHODS

Sections (2 x 2 cm) of dorsal and ventral rumen walls from non-fasting semi-domestic reindeer of various ages in good condition were collected in connection with routine slaughter and fixed in 4 per cent formol. The samples were taken less than 20 minutes after the animals were killed. Sample group number, time and ecological site of sampling are shown in Table 1. Groups 1-5 represent free living animals given no additional feed prior to slaughtering. Group 6 had been pen fed for six weeks with a commercial pelleted feed consisting mainly of ground grass and grain, dried beet pulp and hay ad lib. The animal comprising Group 7 had been pen fed for 13 weeks with the said pellets plus hay and that of Group 8, pen fed for 12 weeks on the same pellets plus lichen.

TABLE 1.—Thickness ratio *stratum corneum/stratum germinativum* + *stratum transitionale*. Differences between means marked x and xx were proved significant at the 99% level.

Group No.	Date of sampling	Site	N*	Thickness ratio		S.D.
				Mean	Range	
1	28. 9.70	taiga zone	5	1:4.02 ^x	2-8	0.42
2	23. 9.71	birch belt	5	1:5.32 ^x	3-10	1.15
3	15.12.70	birch belt	5	1:2.60 ^{xx}	1-6	0.50
4	12. 2.71	taiga zone	5	1:2.24 ^{xx}	1-5	0.36
5	12. 2.72	birch belt	5	1:2.74 ^{xx}	1-5	0.33
6	16.12.69	pen fed	5	1:7.24 ^x	3-14	1.10
7	14. 3.69	pen fed	1	1:11.97	6-16	-
8	23. 6.70	pen fed	1	1:4.30	3-9	-

*N = number of animals.

The tissue samples were embedded in paraffin and cut into 10 μ sections at a right angle to the long axis of the ruminal papillae. The sections were stained with HE and van Gieson connective tissue stain. For the study of keratinization of the epithelium, the PAAB method for -S-S groups according to Adams and Sloper and the DDD method for -SH groups according to Barnett and Seligman were applied (ref. Pearse, 1968).

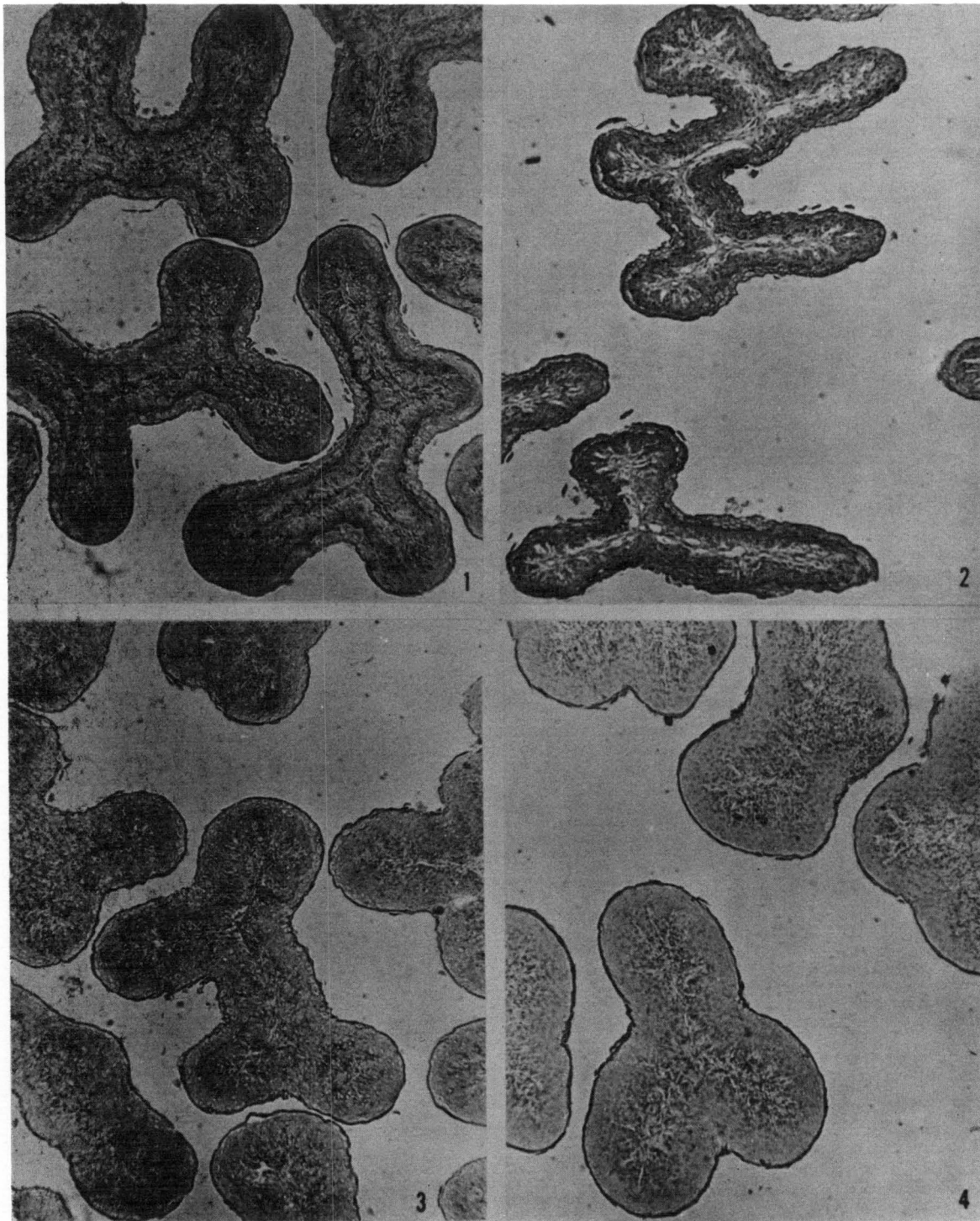
The thickness ratio *stratum corneum/stratum transitionale* + *stratum germinativum* was found to be the best way to objectively express the histological differences. Necessary measurements were taken with the aid of an ocular micrometer on sections cut from the widest distal part of the papillae. From each animal, measurements from 25 dorsal and 25 ventral papillae were taken. The measuring sites were chosen at random and measurements were taken from 10 sites per papilla section. The statistical treatment was based on the mean ratio calculated per animal.

RESULTS

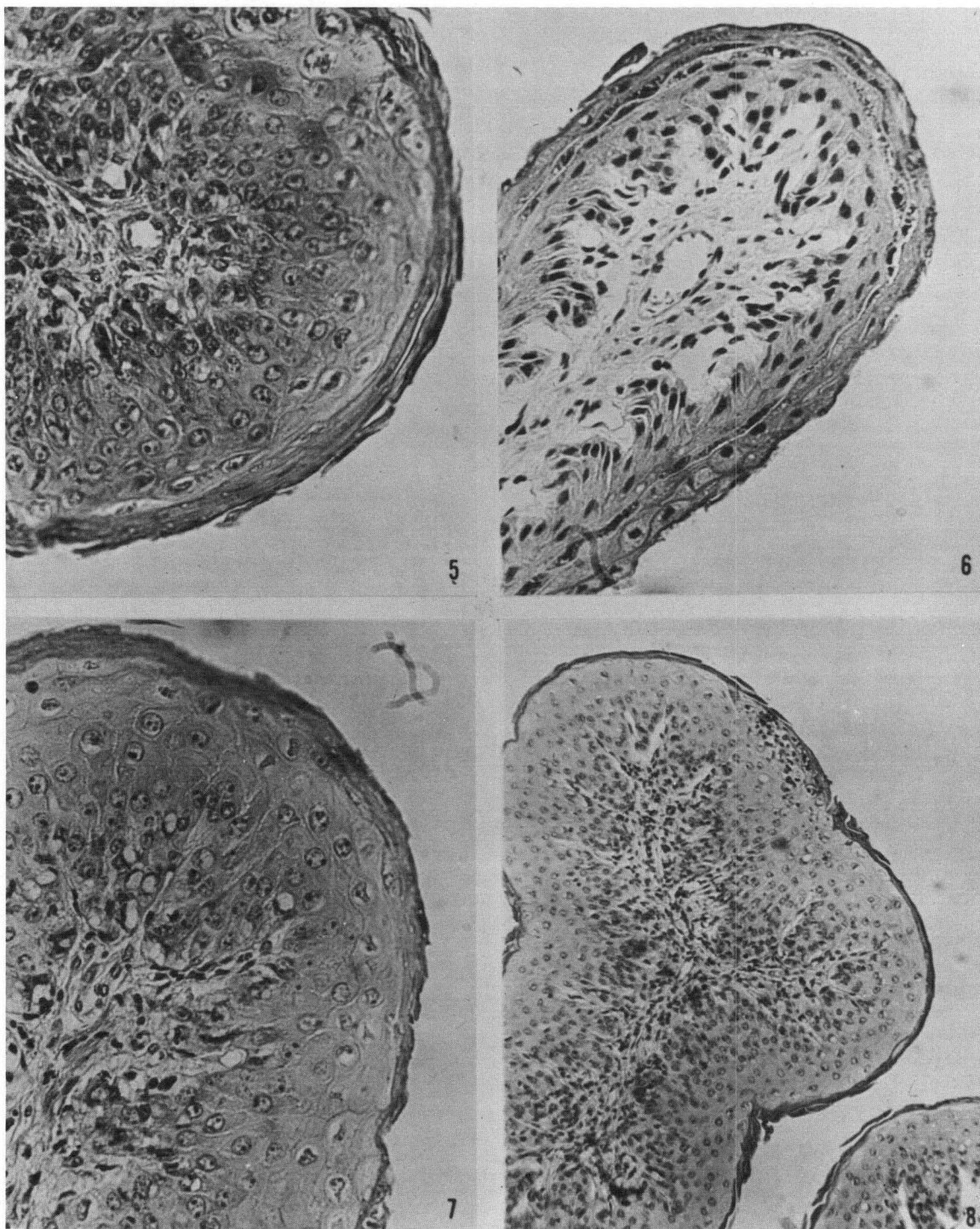
In Table 1, the mean epithelial ratios are calculated and their ranges and standard deviations presented. Differences of statistical significance are indicated. According to these figures, the ratio was significantly lower in animals on winter pastures than in animals grazing green plants or on pen feeding.

On section, the papillae of the free living reindeer were considerably bulkier in September than in December and February (Plates 1 and 2). In the winter the papillae appeared thinner and more folded longitudinally. In this respect the papillae of the pen fed deer (Plate 3) resembled those of the September samples. In animal No. 7 however, the papillae were swollen to such an extent that the folds were almost lacking (Plate 4).

The main reason for these differences, as well as for the differences in epithelial ratio, seems to be the difference in thickness of the *stratum spinosum*, which in winter was found considerably thinner, because of fewer cell layers and smaller and more flattened cells in this stratum (Plates 5 and 6). In the animals which were pen fed for six weeks, the thickness of the *stratum spinosum* resembled that of the September samples (Plate 7). In winter the *stratum corneum* was thicker, which depended partly on the presence of more cell layers and partly on thicker appearance of the cells in this stratum. The thickness and structure of



Plates 1-4.—Section profiles of papillae from ventral rumen of reindeer. 1 and 2: free living deer in September and February, 3: pen fed for six weeks and 4: pen fed for 13 weeks. (x 160) HE stain.



Plates 5-8.—Sections illustrating epithelial structure. 5 and 6: free living deer in September and February, 7: pen fed for six weeks (x 630) and 8: granulocytic focus in the epithelium, pen fed for 13 weeks (x 370). HE stain.

the *stratum transitionale* varied considerably without detectable reference to diet.

Even if the cornified layer was found thicker and more parakeratotic in the free living animals during winter than in the other reindeer, no difference in the staining intensity given by the PAAB and DDD methods could be observed. In the winter the *stratum corneum* was looser than in September, which was manifested by the fact that sectioning and processing of the sections required more care to prevent the surface layers from tearing off.

No differences were detected, referable to age or sample origin from ventral and dorsal rumen, where the epithelial ratio is concerned.

Judging subjectively, no difference in papillary height referable to the time of year was observed, but animal No. 7 seemed to possess shorter and more swollen papillae than any other animal sampled. In all the pen fed animals excepting No. 8, the mucosa was considerably paler than in the free living animals. In all the pen fed animals, small foci of granulocytic infiltration were found in the *stratum transitionale* and *stratum corneum* (Plate 8). No such foci were found in the free living animals.

DISCUSSION

The findings indicate that the reindeer's rumen mucosa undergoes structural adaptation between pasture seasons, and that adaptation is also noted when the deer begin feeding on pelleted feed and roughages. The firmer structure of the *stratum corneum* in September when the feed is coarser than in winter indicate an adaptation of bearing more mechanical tear. The granulocytic infiltrations regularly found in the pen fed deer could indicate mechanical lesions caused by coarse components in the ration.

The fact that the *stratum spinosum* was thinner in the winter than in September seems to indicate that the rumen mucosa is less active when the animals graze on lichen than when feeding on green plants. It seems illogical however, that an animal which bases its energy supply mainly on volatile fatty acid (VFA) should have a less active rumen mucosa in the time of year when its requirements for energy would be at its highest. The breaking down of the main carbohydrates of lichen, i.e., lichenin and iso-lichenin, does not necessarily require fermentation the way cellulose does. Lichenin has shown to be utilized up to 60 per cent by rats and iso-lichenin is hydrolyzed by diastase to maltose (Whistler and Smart, 1953). It would be of interest to know whether nutritionally significant amounts of lichen particles pass into the abomasum with the liquid pool of the rumen contents and escape rumen fermentation. If this would be the case, intestinal hydrolysis and cecal fermentation could be of greater significance in the lichen grazing reindeer than in other ruminants studied. Intestinal hydrolysis of lichen carbohydrates could possibly provide an explanation for the remarkably high plasma glucose levels generally found in reindeer (Kossila, 1970; Luick *et al.*, 1973). Also the very low VFA content in rumens from grazing reindeer in December reported by Cameron and Gau (1970) could indicate that in the grazing reindeer rumen fermentation is relatively unimportant as a means of utilizing lichen carbohydrates. This line of reasoning could provide an explanation for the less active appearance of the rumen mucosa in winter.

The time period required to account for structural reorganization of the rumen mucosa is not known. Neither is it known whether this reorganization, which in winter should demand a building up of new tissue, constitutes a significant obstacle to adaptation to the body following emergency feed offered by man to starving deer. Results of the present study suggest that adaptation is required not only on the part of the rumen flora, but also on the part of the rumen wall.

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VOLATILE FATTY ACID (VFA) PRODUCTION IN THE RUMEN AND CECUM OF REINDEER

R. G. White and A. M. Gau
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

ABSTRACT—The *in vitro* VFA production rate technique was used to compare rumen and cecal fermentation patterns of reindeer given either lichen (ca 3 per cent CP) or a pelleted ration (Purina Cattle Starter #1 ca 12 per cent CP). Ruminal VFA production rates estimated on samples obtained from rumen fistulated reindeer given the pelleted ration were between 12 and 17 mM/l.hr for VFA concentrations of 60 to 73 mM/l. Ruminal VFA production rates for reindeer given lichen were similar to results for the pelleted diet (14 to 37 mM/l.hr) for a range in VFA concentration of 56 to 105 mM/l. In comparison, cecal production rates for the lichen diet were generally higher (23-84 mM/l.hr) than the ruminal rates. On both the pelleted and lichen diets total VFA produced by the cecum amounted to approximately 20 per cent of that produced by the rumen. Over 65 per cent (range 65-80 per cent) of ruminal VFA was absorbed from the rumen. Whole animal rates of VFA production in the rumen and cecum were related to the VFA pool size.

As much as 57 per cent of the digested energy (DE) and 60-80 per cent of ingested metabolizable energy (ME) of the sheep passes through the ruminal pool of VFA (see review by Annison and Armstrong, 1970). Also, for each 100 g organic matter digested in the rumen, approximately 0.85 mole of VFA are produced (Weston and Hogan, 1968).

Thus the VFA pool constitutes an important intermediate in digestion of organic matter in the ruminant. The pool is relatively easily sampled and the rate of production of VFA can be estimated by *in vitro* (Hungate, 1966) and *in vivo* (Leng, 1970) techniques. If the stoichiometry of the above-mentioned conversion of organic matter to VFA remains constant, and provided the organic matter digestibility is known, measurement of VFA production rate could be used to estimate organic matter intake.

The limitations involved in using this principal as a technique for estimating food intake by reindeer and caribou are (a) it is not known if the reactions in the rumen of this genus is equivalent to sheep and (b) it is conceivable that the stoichiometry of the above reactions may be dependent on the type of forage ingested. The diets of reindeer and caribou vary from a high protein-high soluble carbohydrate in early summer, to medium protein-high fiber in early winter to finally a low protein-medium to high carbohydrate (lichen) in winter. This range in dietary change should give ample latitude for testing the stoichiometry between organic matter digestion and VFA production.

The present report is of preliminary studies being made to determine the importance of VFA's in the digestion of herbage by reindeer. Ruminal VFA production rates have been measured by the zero-time *in vitro* technique of Hungate (1966). To date, reindeer have been given *ad libitum* commercial pellets (12 per cent CP) or a fixed ration of lichen (3 per cent CP). Also, comparison has been made of the fermentation role of the cecum relative to the rumen.

MATERIALS AND METHODS

Four rumen fistulated female reindeer were used for ruminal VFA production rates. Reindeer No. 10 and 12 were given the commercial pelleted diet while the other two animals (No. 42 and 46) were changed from the commercial pelleted ration (Purina Cattle Starter No. 1) to a lichen diet and were slaughtered at the end of the experiment (see Holleman and Luick, 1975). *In vitro* ruminal and cecal VFA production rates were estimated on these latter cows and with two additional cows (no. 20 and 21) used in the same slaughter study. Cecal and ruminal VFA production rates were also determined on one cow (No. 47) given *ad libitum* commercial pellets.

The pelleted ration given animals No. 10 and 12 contained 12-13 per cent crude protein, 2 per cent crude fat and 4.1 kcal/g dry matter of energy. In comparison the lichen diet consisted of only 3 per cent crude protein but had an almost identical fat and caloric content (Cameron, 1972). The lichen diet contained *Cladonia alpestris* and *Cladonia rangiferina* as the principal lichen components (see Holleman and Luick, 1975).

Rumen liquor was obtained by squeezing mixed contents through four layers of muslin. The liquor was acidified with 9N phosphoric acid (1 ml liquor + 0.1 ml acid) and stored at -16° C.

VFA concentration was estimated after steam distillation by titration with NaOH using Brom Thymol Blue as an indicator. Molar proportions of VFA's were estimated by gas-liquid chromatography using a 6 ft X 0.25 in (OD) glass column packed with chromasorb (A/W, 80-100 mesh) coated with 10 per cent FFAP. Acidified rumen liquor (0.5-1 μ l) could also be injected onto this column for the direct determination of individual VFA concentrations and molar proportions.

Rumen liquor, water and dry matter contents were estimated *in vivo* with mixed injections of ^{51}Cr -EDTA and ^{144}Ce and were also determined on samples taken at slaughter. For the *in vivo* determination of rumen water and dry matter, 0.7 mCi of ^{51}Cr -EDTA and 0.3 μCi ^{144}Ce Cl were injected into the rumen through a rumen fistula. Samples of mixed rumen contents were taken at intervals of 2, 4, 6, 8 hours and 1, 2 and 3 days. A known weight of mixed contents was assayed simultaneously for ^{51}Cr and ^{144}Ce using a RIDL Gamma Ray Spectrometer. Results for the assay of ^{51}Cr were expressed as $\mu\text{Ci/ml}$ of rumen water and for the ^{144}Ce were expressed as $\mu\text{Ci/g}$ dry matter. A known volume of rumen liquor was assayed for ^{51}Cr and results were expressed as $\mu\text{Ci/ml}$ liquor. The volumes of distribution and turnover times of the rumen parameters were calculated as described by Weston and Hogan (1968).

VFA pool size was calculated as the product of VFA concentration (mM/l liquor or mM/g dry matter) and the respective liquor volume or dry matter weight.

RESULTS AND DISCUSSION

Rumen liquor and dry matter contents of reindeer given lichen was in excess of those given pellets (Table 1). This difference was even more marked for rumen turnover time and the implications of this finding in relation to digestion of lichen is discussed elsewhere in this volume (Person *et al.*, 1975).

VFA concentrations and production rates are shown in Table 2. The range of ruminal VFA concentrations for the pelleted ration (45-73 mM/l) were slightly less than that for lichen (56-105 mM/l), however, the production rates per unit rumen dry matter ($\mu\text{M/g}\cdot\text{hr}$) were similar. This similarity was clearer when results were expressed as a function of rumen liquor (i.e., mM/l \cdot hr), however, this latter basis did not allow comparisons to be made between ruminal and cecal rates of VFA production. In general, rates of VFA production

TABLE 1.--Rumen volume of reindeer given commercial pellets (P) or lichen (L).

Animal No.	Diet	Body weight (kg)	Rumen dry matter (%)	Rumen liquor (l)	Dry weight of rumen contents (kg)
<i>In vivo estimates</i>					
10	P + straw	108	14.2	16.2	--
12	P + lichen	102	13.7	15.3	--
42	P (<i>ad lib</i>)	57	15.1	8.6	--
44	P (<i>ad lib</i>)	46	17.0	6.9	--
42	P (<i>ad lib</i>)	59	16.0	8.2	1.97
46	P (<i>ad lib</i>)	48	17.0	7.8	1.16
<i>Estimates at slaughter</i>					
47	P (<i>ad lib</i>)	53	13.7	5.1	0.95
42	L (0.8 kg/d)	45	15.5	7.6	1.29
46	L (0.5 kg/d)	40	14.7	7.2	1.46
21	L (1.1 kg/d)	67	15.5	6.9	2.15
20	L (1.0 kg/d)	83	13.9	11.0	1.52

per unit dry matter were greater in cecal than ruminal contents. After these rates were corrected for the total weight of contents a reversal in this trend was noted. That is, cecal VFA production for the lichen diet were between 14 and 86 per cent of the ruminal rate. In animal No. 21 the very high rate, relative to that for the rumen, may have been due to the time since feeding. This animal had been fed 36 hours previously; in contrast cow No. 20 was fed less than 20 hours previously and cows No. 42, 46 and 47 were without feed for approximately 3 hours.

No significant relationship was noted between VFA concentration and production rate. However, a significant relationship was noted between VFA production rate and pool size (Fig. 1). The slope of the regression line was similar for both rumen and cecal contents, showing that for each mM increase in the pool size, 805 $\mu\text{M/hr}$ of VFA is produced. This slope is also similar to that for sheep (Weston and Hogan, 1968) but the elevation of the lines are different. Also shown in Figure 1 are observations for two animals which were given approximately two-thirds *ad libitum* intake of the commercial pellet ration once per day. Two observations were made just prior to feeding and two others, four hours post feeding. Although the VFA production rate had more than doubled after feeding, VFA concentrations were similar to the pre-feeding estimates. These latter data give some impression of the likely variation which may be expected in animals which eat intermittently.

From the rates of turnover of rumen liquor and dry matter it was calculated that for the *ad libitum* pelleted ration, 72 to 82 per cent (4 estimates) of the ruminal VFA were absorbed from the rumen. For the lichen ration, between 63 and 80 per cent were absorbed from the rumen of reindeer No. 42 and 46 respectively. These values are similar to that of 76 per cent for sheep given chopped perennial ryegrass or forage oats (Weston and Hogan, 1968).

The four animals given lichen consumed approximately 11 and 25 g/hr of digestible

TABLE 2.--VFA production rate in the rumen and cecum of reindeer.

Animal No.	Diet	Total VFA concentration (mM/l)	Pool size (mM)	VFA production rate:		
				per unit dry matter (μ M/gDM·hr)	whole animal (mM/hr) (mM/kgBW·hr)	
Rumen fistulated reindeer						
10	P + straw	47	761	(23)*	367	3.4
12	P + lichen	45	688	(23)*	345	3.4
42	P <i>ad lib</i>	60	516	(12)*	125	1.8
46	P <i>ad lib</i>	61	476	(13)*	87	1.9
42	P <i>ad lib</i>	63	518	72	141	2.4
46	P <i>ad lib</i>	73	567	112	130	2.7
Estimates at slaughter -- ruminal						
47	P <i>ad lib</i>	102	524	131	125	2.4
42	Lichen	105	834	219	282	6.3
46	Lichen	63	472	54	60	2.5
20	Lichen	87	640	79	170	1.4
21	Lichen	56	622	63	96	2.0
Estimates at slaughter -- cecal						
47	P <i>ad lib</i>	74	40	339	27	0.51
42	Lichen	104	103	558	83	1.85
46	Lichen	62	42	79	8	0.20
20	Lichen	57	95	220	53	0.64
21	Lichen	55	128	216	83	1.25

*Expressed as mM/l liquor·hr.

P, Purina Cattle Starter No. 1.

organic matter. Since the hourly rate of consumption was not estimated accurately (and reindeer No. 21 was fasting) the relationship between VFA production per 100 g organic matter digested could not be estimated. This aspect of the work will be investigated in the future.

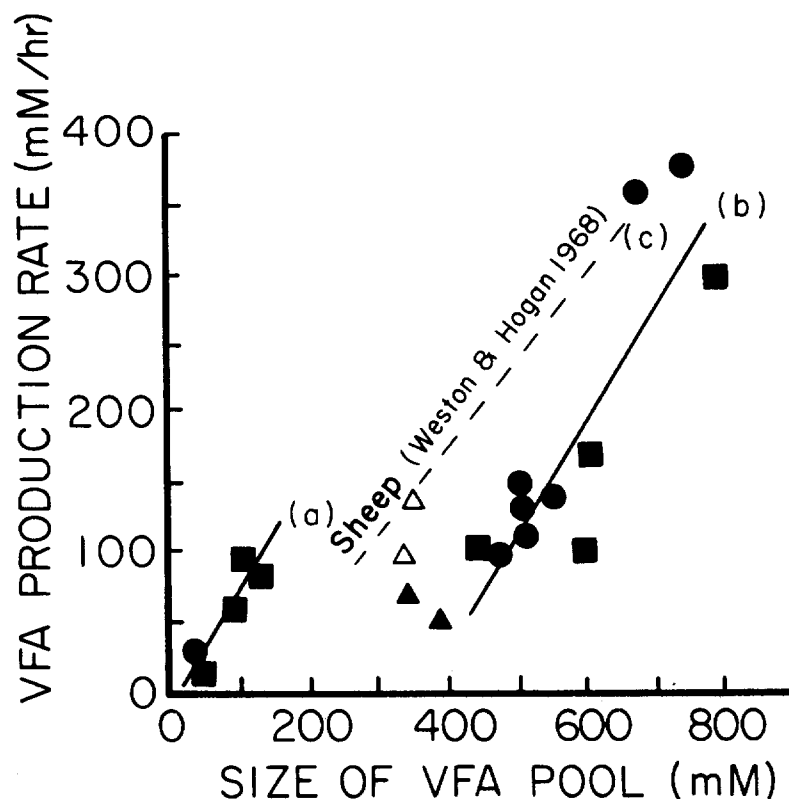


Fig. 1.—Relationship between VFA production rate (R) and pool size (P) in reindeer given a commercial pellet ration (●) or lichen (■). Regression lines for the cecum (a) and rumen (b) are given by: $R_a = 0.807 P_a - 14.9$ $r = 0.940$ $P < 0.05$ and $R_b = 0.804 P_b - 297$ $r = 0.866$ $P < 0.01$. ▲, △, immediate pre- and 4 hour post-feeding estimates for the pellet ration (2/3 *ad lib*) offered once daily. C, regression line for sheep given perennial ryegrass or forage oats (Weston and Hogan, 1968).

Thus, it has been shown that reindeer are capable of fermenting lichen; the results suggest that the relatively high apparent digestibilities of lichen dry matter (55.4 ± 1.6 per cent) and organic matter (58.1 ± 1.5 per cent) (Cameron, 1972) involves both ruminal and cecal fermentation as well as normal gastric digestion and absorption from the small intestine.

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COMPARATIVE STUDY IN REINDEER AND WHITE-TAILED
DEER OF FINLAND ON RUMEN METABOLISM
AND FATTY ACIDS OF ADIPOSE TISSUES

J. Brüggemann, Ute Drescher-Kaden, Renate Schubert
H. Erbersdobler and D. Giesecke
Institute für Tierphysiologie und Ernährungsphysiologie
Universität München
Munich, Germany

ABSTRACT—During a field study in September-October 1968 a total of 10 reindeer fed in groups mainly on poor range, oats or commercial grassmeal-based pellets, and of nine white-tailed deer on good range were examined by *in vitro* rumen fermentation and various analytical techniques. Apart from nutritional and individual differences reindeer showed relatively high rumen populations of protozoa and an acetate-butyrate-type fermentation. In rumen fermentation rates, total volatile fatty acids, and total bacteria reindeer were exceeded by white-tailed deer which were virtually free of protozoa and had an acetate-propionate-type fermentation. Further differences within and between species in the rates of cellulose and starch breakdown as well as in certain physiological and anatomical criteria were mostly related to nutrition and rumen microbial activities.

With regard to adipose tissues the perinephric and omental fats of reindeer showed higher levels of fatty acids C 18:1 and lower levels of C 18:0 and were thus less saturated than those of white-tailed deer. In addition some dietary effects appeared to exist. In comparison, the main characteristics of reindeer differed markedly not only from white-tailed deer but also from six other wild ruminant species of Europe so far studied.

When ruminants adapt to marginal habitats or to a new nutritional environment because of climatical changes and/or migration, the microorganisms in the rumen play a very important role. Not until the recent decade studies on deer species in North America (Klein, 1962, 1965) and in Europe (Brüggemann *et al.*, 1963, 1967a) have promoted the understanding of microbial functions in the nutrition of wild ruminants as reviewed elsewhere (Giesecke, 1970). In 1968 our group was offered the opportunity to carry through some investigations on reindeer and white-tailed deer in Finland during October which is the period of transition to winter feeding conditions. Even though time and animal numbers available for our investigations were rather limited we made use of this chance in order to obtain (a) data on rumen and fat metabolism in species from the north of Europe under physiological conditions similar to the onset of winter in the Alps where most of our current research is performed; (b) information on species of wild ruminants which are of general and scientific interest both in North America and Europe; and (c) some indication of the effect of supplementary feeding of reindeer on rumen and fat metabolism as a basis for practical advise.

MATERIALS AND METHODS

A total of 10 reindeer were sampled in Lapland north of the Arctic Circle near to Rovaniemi just after the first snowfall. Four of the animals were on natural range, four received mainly oats and two a pelleted diet with grassmeal and dried beet pulp as main constituents. The range was a mixed forest of birch, spruce and pine with dwarf willows and junipers, heather, lichens and grasses.

Nine white-tailed deer were sampled in Middle Finland near to Viaala in an area of mixed leaf and needle woods with some grassland.

Reindeer were sampled within a few minutes after slaughter, white-tailed deer within one-half to two hours after shooting. The criteria and methods are based on our earlier discussion on methodology (Bruggemann *et al.*, 1968). Rumen microbial counts were made on weighed samples of rumen contents after three extractions with physiological saline containing formalin (10 per cent v/v). Estimates of fermentation rates were measured as gas production, corrected to normal temperature and pressure (NTP), of whole rumen contents in bicarbonate buffer. Pure substrates were used for measurement of cellulolytic and amylolytic rates. Samples of perinephric and omental fat were stored in the deepfreeze, and gaschromatography was used for the analyses of methylated long chain fatty acids (Schubert, 1969) as well as for volatile fatty acids (VFA) (Giesecke, 1967). Values are given as means \pm standard errors.

RESULTS AND DISCUSSION

Data on rumen microorganisms and fermentation activities are summarized in Table 1; reindeer had relative low counts of rumen bacteria; this may be due in part to low plain of energy nutrition and to the high numbers of ciliate protozoa which used to feed on bacteria. The bacterial population consisted mainly of gram-negative cocci and rods, and the latter as well as *selenomonads*, *Quin's Ovals* and *Oscillospiras* were more abundant in animals fed oats or pellets. In the microfauna, *entodinia* predominated (about 90 per cent) over *epidinia* (4 per cent) and *diplo-dinia* (3 per cent) and some holotrichs were observed in reindeer fed oats. In white-tailed deer the complete absence of protozoa was obviously compensated for by an increase of bacterial density. A striking abundance of protozoa in reindeer was noted by Hobson (1969) in Scotland mainly during winter, and Dehority (this volume) has reported similar high protozoa counts for animals on range but not on alfalfa or dried lichens.

Rumen microbial activities of reindeer on range were markedly lower than those of white-tailed deer except for cellulose breakdown, however, feeding of oats or pellets improved fermentation rates and starch breakdown considerably. It would thus appear that rumen fermentation in reindeer was mainly limited by the availability of easily digestible carbohydrates.

Results of Table 2 may support this view. Reindeer were characterized by a relative high proportion of fibre in the rumen, low levels of VFA and much lower rumen acidity (pH 7) than white-tailed deer (pH 6.1). The proportions of individual VFA differed significantly, and the acetic/propionic ratio in reindeer averaged 7:1 as compared to 2.4:1 in white-tailed deer. Even in animals fed oats most of the starch was apparently converted into butyric acid by rumen protozoa (which do not produce propionate). In contrast to these results Luick and colleagues (Luick *et al.*, 1970) have found high propionate and very low butyrate levels in reindeer fed on lichens either by grazing or in pens. As rumen VFA have special functions in animal metabolism, propionate being glucogenic but acetate and butyrate lipo- and ketogenic, dietary effects on rumen fermentation products deserve particular attention.

TABLE 1.--Rumen microorganisms and *in vitro* fermentation activities of reindeer on different diets and of white-tailed deer.

Observations	Reindeer fed on range (4) ^a	oats (4)	pellets (2)	Reindeer mean (10)		White-tailed deer (9)
Total bacteria x 10 ⁹ /g RC ^b	7.8±2.1	7.2±2.0	11.7±5.8	8.4±2.9	y	21.0±8.2
Total protozoa x 10 ⁴ /g RC	46.1±9.1	231.0±64.7	138.4±68.7			0.0
Fermentation rate ml gas _{NTP} /g DM/h ^c	1.9±1.2	5.1±1.6	2.6±1.9	3.3±2.0	x	6.9±3.3
Cellulolytic rate g cellulose/l SRL/h ^d	0.46±0.14	0.40±0.21	0.46±0.42			0.33±0.13
Amylolytic rate g starch/l SRL/h	0.70±0.42	1.87±0.81	1.97±0.45			1.28±0.55

^a() = number of animals.

^bRC = rumen contents.

^cDM = rumen dry matter.

^dSRL = strained rumen liquid.

^x_p<0.05.

^y_p<0.01.

TABLE 2.--Characteristics of rumen dry matter and fermentation products of reindeer on different diets and of white-tailed deer.

Observations	range (4) ^a	Reindeer fed on		White-tailed deer (8)
		oats (4)	pellets (2)	
Crude protein gN x 6.25/100 g DM ^b	16.6	17.5	20.4	28.5
Crude fibre g/100 g DM	32.0	27.6	28.4	23.5
Ammonia-N mg/100 ml SRL ^c	9.1±2.0	21.6±2.2	12.2±0.4	14.2±3.5
Volatile fatty acids total μ moles/g RC ^d	30.2±5.1	64.6±20.4	44.3±17.5	89.6±27.3
Acetate molar %	76.0	72.9	75.7	62.1
Propionate molar %	12.6	8.4	11.5	26.1
Butyrate molar %	8.3	17.3	10.4	9.7
Valerate molar %	3.0	1.7	3.3	1.7

^a() = number of animals.

^bDM = rumen dry matter.

^cSRL = strained rumen liquid.

^dRC = rumen contents.

TABLE 3.--Main differences of adipose tissue fatty acids in reindeer fed on different diets and in white-tailed deer.

Fatty acids in % of total	range (2) ^a	Reindeer fed on		Reindeer total (11)		White-tailed deer (9)
		oats (7)	pellets (2)			
C-16:0	20.7±1.9	27.0±2.23	27.6±3.95	26.0±3.44	y	22.2±1.89
C-18:0	33.5±0.28	27.1±4.27	28.0±2.54	28.4±4.23	z	37.4±2.88
C-18:1	27.7±0.49	27.0±2.78	32.6±3.18	28.2±3.24	z	21.5±3.56
Ratio of saturated:unsaturated acids	61.0:39.0	60.7:39.3	59.5:40.5	60.9:39.1		68.0:32.0

^a() = number of samples.

^y_p<0.01.

^z_p<0.001.

Rumen metabolism may definitely influence adipose tissue fatty acids by microbial biohydrogenation of unsaturated dietary lipids. Our data in Table 3 show a higher degree of unsaturation for fat samples of reindeer as compared to white-tailed deer. The main differences were confined to the C 16:0, C 18:0 and C 18:1 acids which comprised more than 80 per cent of the total. The low level of C 18:0 in reindeer is unusual for adult wild ruminants in Europe (Schubert, 1969). Garton and Duncan (1971) have explained similar observations on reindeer in Scotland by the very low content of fatty acids in lichens; however, two of the three animals examined were sampled in summer when reindeer in this biotope feed mainly on grass (up to 80 per cent) and heather (up to 20 per cent) according to Hobson (1969). Thus, in summer, reindeer would be expected to consume sufficient C 18:3 lipids for biohydrogenation to C 18:0, but there were no obvious differences of fatty acid patterns of animals sampled in summer or in winter. Unfortunately, our results refer only to October. However, even when reindeer are fed a lichen-free diet of oats of approximately 4 per cent crude fat, the proportion of C 18:0 was surprisingly low. Certainly, dietary effects are also suggested by our data but we would suppose that additional factors may govern the fatty acid composition of adipose tissues.

On a comparative basis the two species of ruminants can be attributed to different feeding types, reindeer resembling a roughage feeder like red deer, though possibly less efficient, and white-tailed deer a selective feeder like roe deer. Both differ distinctly in rumen fibre and protein, acetic/propionic ratio and diversity of ciliate protozoa. In addition, the difference of capacity for digesting bulky fibrous food is clearly demonstrated by the relative size of the rumen-reticulum (e.g., the weight of the filled organ per 100 kg of body weight was 13.1 kg for reindeer and 5.7 kg for white-tailed deer).

Considering the various limitations of this study, we feel reluctant to generalize our conclusions. Under the particular conditions examined, however, the energy nutrition of reindeer was rather poor as compared to red deer or to chamois in the Alps at the beginning of winter (Brüggemann *et al.*, 1967b). If supplementary feeding is used in order to overcome reindeer losses during winter, the pelleted diet would appear superior to oats in providing more balanced conditions of rumen nutrients (fibre, protein, NH_3) and microorganisms as well as of VFA for utilization by animal tissues. The relatively high levels of rumen butyrate to propionate obtained with oats feeding in reindeer could be a potential source of ketosis during late pregnancy and early lactation.

Apart from these more practical questions two problems would, in our opinion, appear most challenging: one is the physiology of nitrogen recycling and rumen turnover, and the second is the metabolism of fatty acids and adipose tissues.

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UREA RECYCLING IN CARIBOU, CATTLE AND SHEEP

R. A. Wales and L. P. Milligan
Department of Animal Science
University of Alberta
Edmonton, Alberta

E. H. McEwan
Canadian Wildlife Service
University of British Columbia
Vancouver, British Columbia

ABSTRACT—The tracer technique developed by Ford (1969) was employed to estimate the proportion and quantity of the urea pool labelled by intravenous administration of ^{14}C -urea that was transferred to the digestive tracts of caribou and beef bulls fed low protein diets. Caribou trials were conducted during both the summer growth and winter dormancy phases of the growth cycle. The results were compared with data from similar experiments conducted on sheep by Ford (1969).

Summer caribou, beef bulls and sheep all recycled about 45 per cent of the injected label to the digestive tract, and the quantity of urea recycled appeared to be dependent upon the plasma urea concentration. The winter caribou recycled a greater quantity of urea per unit metabolic body size, without any significant increase in the plasma urea concentration from summer levels. Rather, the proportion of label recycled increased to 58 per cent, which was considered indicative of a shift in the disposition of plasma urea.

Factors including the cyclical growth pattern and, particularly, changes in the composition of the diet which might be involved in the enhancement of urea recycling noted in *Rangifer tarandus* during the winter dormancy period are discussed.

It is now well established that urea recycled from the blood to the rumen, both directly across the rumen wall and via saliva, can contribute significantly to the nitrogen economy of ruminant animals (Cocimano and Leng, 1967; Varady *et al.*, 1967; Houpt and Houpt, 1968; Vercoe, 1968; Waldo, 1968; Ford and Milligan, 1970; Thornton, 1970). In trials conducted on sheep (Ford, 1969), it was estimated that recycled urea provided nearly one-third as much nitrogen to the digestive tract as was available from the ration. The ability to recycle urea to enhance rumen microbial protein synthesis may well constitute the margin of survival for free-ranging ruminants living in areas of unfavorable nutritional conditions.

The present studies were undertaken to compare the extent of urea recycling in captive *Rangifer tarandus* (*Rangifer tarandus* refers to both reindeer and caribou, although subspecific names are seen occasionally), beef bulls and sheep. It was desired to ascertain if real, quantitative differences in recycling of plasma urea can exist in different species of ruminants or within an individual animal at different points in time.

METHODS

A ^{14}C -urea tracer technique (Ford, 1969; Ford and Milligan, 1970) was employed to estimate the proportion and quantity of plasma urea transferred to the digestive tracts of cattle and captive caribou. Two mature bulls of the species *Rangifer tarandus* were used in both summer and winter trials: reindeer R4 was studied in six trials and caribou X4 was studied in three trials. A complete, pelleted ration of 12 per cent crude protein content (no. 36-69c) was provided. In addition, dried lichen was fed along with a reduced amount of 36-69c during the winter trials. Total daily feed was offered in eight portions at three hour intervals. Water was available *ad libitum* and intake was measured. Use of a metabolism crate facilitated collection of urine separate from feces. Trials were conducted at the Zoology Vivarium, University of British Columbia, in a roofed, partially enclosed shed.

In trials at the University of Alberta, two crossbred yearling beef bulls were used; one successful trial was conducted on each of bulls #324 and #328. Chopped oat hay of 8 per cent crude protein content was fed in portions at three hour intervals. Water intake was measured. The bulls were closely confined in individual stanchions at room temperature with continuous lighting.

Metabolic steady state was approached using the above arrangements, as evidenced by a relative constancy of blood urea concentration through each trial. The body urea pool was labelled with a single intravenous injection of approximately 100 μC of ^{14}C -urea (Radiochemical Center, Amersham, England). Total urine collection was achieved utilizing an ice-cooled urine storage system designed to avoid ureolytic activity (Wales, 1972). Transfer of excreted urine to the storage vessel from the animal involved use of a male urine collection harness (Ford, 1969) for the beef bulls and sloped metal V-trough for the caribou (Wales, 1972). The minimum trial period was 48 hours, but trials were continued until the ^{14}C content of the urine was negligible. Venous blood samples were collected intermittently throughout each trial using heparinized vacutainers (Beckton, Dickinson and Co., Canada, Ltd., Clarkson, Ontario). The mean plasma urea concentration during each trial is reported.

Plasma and urine urea concentrations were determined by the method of Fawcett and Scott (1960). The ^{14}C in urine was measured by adding 0.20 ml urine to 15 ml of the scintillation mixture of Jeffay and Alvarez (1961) and counting in a Nuclear Chicago Mark I liquid scintillation system using the channels - ratios method of quench correction (Bruno and Christian, 1961). Investigations revealed that, following ^{14}C -urea administration, the portion of ^{14}C present as carbonate, or bicarbonate, in the urine of caribou and beef bulls was negligible. At least 95 per cent of the label present in urine proved to be acid volatile following incubation with urease. One trial on beef bull #328 is not reported because urine collection was incomplete.

Statistical procedures used to assist in interpretation of the data are described by Steel and Torrie (1960).

RESULTS

The protein and energy contents of ration no. 36-69c and of the lichen are presented in Table 1. Table 2 provides a summary of animals and trial treatments. On a metabolic body size basis, nitrogen intakes of the caribou were reduced by at least one-third in winter versus summer trials. Nitrogen intakes of the beef bulls per unit of metabolic body size were similar to those of the winter caribou. Figure 1 indicates the range of variation in plasma urea concentrations over the course of three typical trials that exemplify each treatment group. Plasma urea concentrations of the beef bulls, which averaged 8.5 mg/100 ml, were low compared to those of the caribou bulls. Plasma urea concentrations of the caribou bulls

tended to be slightly higher in winter than in summer trials, despite the lowered nitrogen intake in winter.

TABLE 1.--Energy, nitrogen and crude protein contents per unit dry matter and moisture content of ration no. 36-69c and lichen.

Component	No. 36-69c	Lichen
Moisture, %	9	10
Gross energy, kJ/g	18.8	17.6
Apparent digestible energy, kJ/g	13.8	11.7
Nitrogen, mg/g	19.2	3.2
Crude protein, %	12.0	2.0

The experimental results relating to urea kinetics are summarized in Table 3. The constancy of daily urea excretion and relative uniformity of plasma urea concentrations for trials within any one treatment series suggest that standardization of treatments was attained. Tables 4 and 5 present the treatments and data from similar experiments conducted on sheep by Ford (1969) and Ford and Milligan (1970) and are considered appropriate for comparison with the present results. Nitrogen intakes per unit of metabolic body size of the sheep used in the study by Ford (1969) were similar to the nitrogen intakes of the winter caribou and beef bulls (Table 3).

The proportion and quantity of urea recycled in individual trials (Tables 3 and 5) are summarized on a group average basis in Table 6. The winter caribou and the sheep recycled significantly ($P<0.05$) greater quantities of plasma urea per unit of metabolic body size than did either the beef bulls or the summer caribou. Further comparisons between group averages indicate that cattle, sheep and summer caribou all recycled a similar proportion of the plasma urea (Table 7). The winter caribou recycled a significantly greater proportion of the plasma urea than did any other group.

DISCUSSION

The technique used in the present study provides an estimate of the proportion and amount of the urea pool labelled by intravenous injection of ^{14}C -urea that is recycled to the digestive tract at any particular plasma urea concentration; factors which influence or determine the plasma urea concentration were not specifically studied. Subsequent discussion of the data will generally allude to direct transfer of plasma urea across the wall of the digestive tract, since salivary transfer probably accounts for less than 20 per cent of total urea recycling to the rumen (Waldo, 1968). In actual fact, the data presented represents the total of both modes of urea transfer to the digestive tract.

The data indicate that beef bulls, sheep and summer caribou all recycled about 45 per cent of the injected label. Summer caribou group averages are presented both with and without the inclusion of Trial III, as it is suspected that the initial injection of label into the bloodstream was incomplete in Trial III. This would have resulted in a low urinary recovery of label relative to the amount thought to have been injected and a high estimate of recycling.

Previous research on sheep (Cocimano and Leng, 1967; Ford and Milligan, 1970) has indicated that, within physiological limits, the quantity of urea recycled is proportional to the plasma urea concentration. On a group average basis, the trials on beef bulls and summer

TABLE 2.--Animals and nutritional treatments for urea recycling experiments.

Trial no.	Animal	Body weight (kg)	Ration	Ration intake (g/d)	Nitrogen intake (g/d)	Water intake (l/d)	N intake (g/kg ^{0.75} /d)
I.	R4	204	36-69c	4000	77	11.7	1.4
II.	R4	205	36-69c	4000	77	13.7	1.4
III.	R4	207	36-69c	4000	77	15.6	1.4
IV.	X4	151	36-69c	4000	77	15.6	1.7
V.	R4	130	36-69c	1615	36	12.2	0.94
			lichen	1465			
VI.	R4	130	36-69c	1615	36	8.3	0.94
			lichen	1490			
VII.	X4	130	36-69c	1615	34	11.3	0.88
			lichen	920			
IX.	R4	130	36-69c	1615	36	10.1	0.94
			lichen	1590			
X.	X4	130	36-69c	1865	38	7.7	0.99
			lichen	720			
XII.	324	300	oat hay	5500	70	22.0	0.97
XIV.	328	300	oat hay	5500	70	18.2	0.97

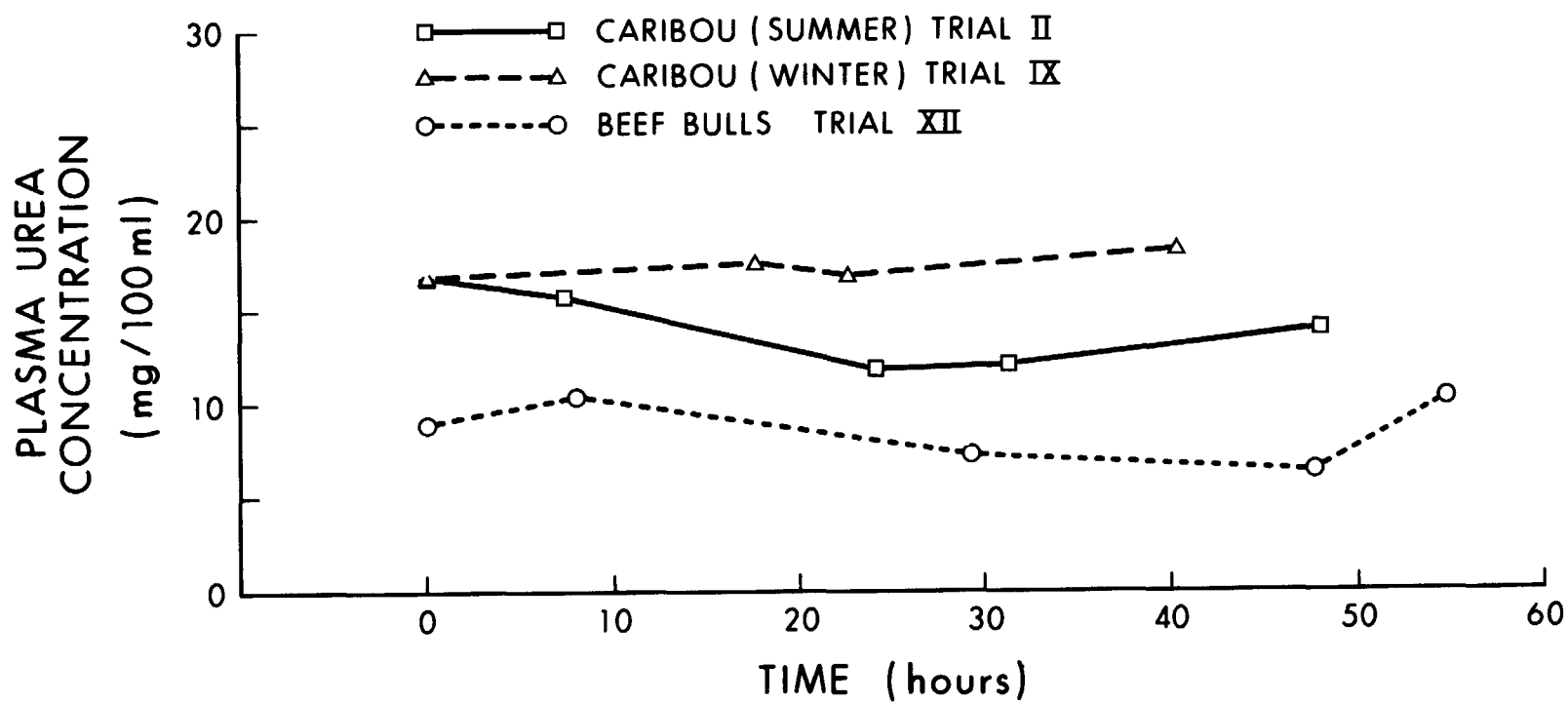


Fig. 1.—Variations in plasma urea concentrations during typical trials.

TABLE 3.--Summary of effects of nitrogen intake on parameters of urea synthesis and recycling in caribou and beef bulls.

		¹⁴ C						
	Trial no.	Plasma urea (mg/100 ml)	recovered in urine (%)	¹⁴ C recycled ¹ (%)	Urea excretion (g/d)	Urea recycled ² (g/d)	Urea flux ³ (g/d)	Urea recycled (g/kg ^{0.75} /d)
Caribou summer	I.	15.8	52.4	47.6	23.5	21.4	44.9	0.40
	II.	14.2	51.1	48.9	20.5	19.6	40.1	0.36
	III.	15.9	38.3	61.7	22.2	35.7	57.9	0.66
	IV.	17.1	55.1	44.9	22.6	18.4	41.0	0.34
Caribou winter	V.	18.0	36.9	63.1	17.9	30.6	48.5	0.79
	VI.	18.1	42.2	57.8	18.5	25.3	43.8	0.65
	VII.	20.9	43.0	57.0	17.7	23.5	41.2	0.61
	IX.	17.4	40.3	59.7	17.4	25.7	43.1	0.66
	X.	19.2	47.9	52.1	18.5	20.1	38.6	0.52
Beef bulls	XII.	8.6	56.2	43.8	25.0	19.5	44.5	0.27
	XIV.	8.5	48.2	51.8	25.1	26.9	52.0	0.37

¹100% - % of ¹⁴C recovered in urine.

²Urea excretion rate X $\frac{\% \text{ } ^{14}\text{C recycled}}{\% \text{ } ^{14}\text{C recovered in urine}}$

³Urea excretion + urea recycled.

TABLE 4.--Nutritional treatments for urea recycling experiments on sheep (adapted from Ford, 1969; Ford and Milligan, 1970).

Trial no.	Sheep ¹	Ration	Ration intake (g/d)	Water infused (ml/d)	N intake (g/kg ^{0.75} /d)
10,12,13	ewe	hay	725	1570	0.78
16	ram	hay	920	1570	0.85
17,19,20	ram	hay	1000	1570	0.92
32	ram	hay	1000	3100	0.92
33,34	ram	barley	500	1570	0.54

¹The body weight of the ewe was maintained at 34 kg, while that of the ram was maintained at 42 kg.

caribou also suggest a relationship between these two parameters. Therefore, although the proportion of the urea flux recycled was similar in all three groups, the quantity of urea recycled per unit of metabolic body size, from greatest to least, was in the order of sheep, summer caribou and beef bulls (Table 6) which was also the order of plasma urea concentrations.

There is some evidence that the limit to the transfer of urea from the blood to the rumen occurs at lower plasma urea concentrations and at slightly lower concentrations of ammonia in the rumen of cattle than of sheep (Vercoe, 1968; Thornton, 1970). The present results further suggest that, when fed low protein diets supplying similar amounts of nitrogen per unit metabolic body size, cattle maintain a lower plasma urea concentration than do either sheep or caribou.

Caribou fed a simulated winter diet appeared to have some advantage over both sheep and cattle and their own summer performance in all aspects of urea recycling. The proportion of label recycled increased significantly to 58 per cent from 47 per cent in the summer (Trial III excluded, Table 6) while the quantity of urea recycled daily was 0.65 g per unit of metabolic size as contrasted to an average summer value of 0.37 g urea recycled per unit of metabolic body size.

During the winter trials, the weights of animals R4 and X4 were 63 and 86 per cent of their weights during the summer trials and this would infer that their body compositions were rather different during the two periods of study. It could be argued that the most valid means of comparison between the summer and winter estimates of urea recycling may not be on the basis of metabolic body size. However, even in absolute terms, there were differences; in the winter trials the caribou recycled an average of 25.0 g of urea per day, while in the summer an average of 19.9 g of urea was recycled per day (excluding Trial III). During the winter the average urea flux was 43.0 g per day, while in the summer trials (excluding Trial III) it was 42.0 g per day. Thus, a trend was noted toward a greater proportion of the plasma urea being recycled even though the urea flux and plasma urea concentration during the winter and summer caribou trials were essentially equivalent.

It seems justifiable to suggest that caribou may have a greater potential to recycle urea than do typical domestic species of ruminants: the full expression of this potential may be realized only during the winter. Regulation of urea recycling could be associated with reproductive processes and the cyclical nature of the growth pattern, or regulation may at least partially be dependent upon the differing nutrient characteristics of winter versus

TABLE 5.--Urea synthesis and recycling in sheep (data were adapted from Ford, 1969;
Ford and Milligan, 1970).

Trial no.	Plasma urea (mg/100 ml)	Urea excretion (g/d)	¹⁴ C recovered in urine (%)	¹⁴ C recycled ¹ (%)	Urea recycled ² (g/d)	Urea flux ³ (g/d)	Urea recycled (g/kg ^{0.75} /d)
10	21.6	9.27	56.7	43.3	7.07	16.3	0.50
12	18.6	11.2	49.9	50.1	11.3	22.5	0.80
13	18.3	9.04	58.6	41.4	6.41	15.4	0.45
16	33.6	14.2	52.4	47.6	12.9	27.1	0.78
17	30.9	11.8	56.9	43.1	8.91	20.7	0.54
19	33.7	10.1	48.4	51.6	10.8	20.9	0.65
20	25.3	13.5	58.3	41.7	9.66	23.2	0.59
32	15.8	11.2	57.2	42.8	8.33	19.5	0.50
33	21.7	10.7	65.3	34.7	5.70	16.4	0.34
34	21.8	15.6	71.6	28.4	6.19	21.8	0.38
Average				42.5		Average	0.55

¹100% - % of ¹⁴C recovered in urine.

²Urea excretion rate X $\frac{\% \text{ } ^{14}\text{C recycled}}{\% \text{ } ^{14}\text{C recovered in urine.}}$

³Urea excretion + urea recycled.

TABLE 6.--Comparison of proportion and quantity of urea recycled in caribou, beef bulls and sheep.

Treatment group	Group averages	
	Urea recycled %	Urea recycled g/kg ^{0.75} /d
Caribou (summer) ¹	48.8	0.41a,b
Caribou (summer-Trial III excluded)	46.6	0.37a
Caribou (winter)	57.9	0.65c
Beef bulls	47.8	0.32a
Sheep ²	42.5	0.55b,c

a,b,c Averages for quantity of urea recycled followed by different superscripts are significantly different ($P < 0.05$, t-test).

¹ Values for this group were weighted for the unequal numbers of observations on the animals.

² From Ford (1969); Ford and Milligan (1970).

TABLE 7.--Statistical analysis of per cent urea recycling in caribou, beef cattle and sheep. Differences between treatment averages¹ (unpaired observations, equal variances) were compared by the t-test.

Comparison between	Difference between averages	Calculated "t"	Significance
Caribou (winter) and caribou (summer)	9.1	2.56	*
Same as above (Trial III omitted)	11.3	4.37	**
Caribou (summer) and beef bulls	1.0	0.16	-
Caribou (winter) and beef bulls	10.1	2.74	*
Caribou (summer) and sheep	6.3	1.80	-
Caribou (winter) and sheep	15.4	5.37	**
Sheep and beef bulls	5.3	1.14	-

¹ Averages for caribou (summer) were weighted for the unequal numbers of observations on the animals.

*Differences significant ($P < 0.10$).

**Differences significant ($P < 0.01$).

summer forage. A key factor involved may be physiological adaptation of reindeer and caribou such that they can utilize forage of very low protein content more efficiently than can cattle or sheep (Nordfeldt *et al.*, 1961).

The mechanism of transfer of plasma urea to the digestive tract is still controversial, but one hypothesis (Varady *et al.*, 1967) suggests that limitation of urea recycling occurs as a result of accumulation of rumen ammonia. The intake of diets of high digestible energy content promotes rapid microbial assimilation of ammonia (Thornton, 1970), thus serving to maintain lower rumen ammonia concentrations and, perhaps, to enhance urea transfer from plasma to the rumen. Lichen constitutes a major portion of the winter forage of free-ranging caribou and the energy to protein ratio of lichen is high (Scotter, 1965; McEwan, 1968) both in absolute terms and relative to the summer diet. Therefore, the proportion of plasma urea recycled may be increased during the winter, partially because the high energy to protein ratio in the diet results in lower rumen ammonia concentrations than occur when summer forage is consumed. Thus, a greater quantity of urea would be recycled to the rumen at any given plasma urea concentration during the winter than during the summer. There could also be efficient incorporation of the nitrogen from urea into microbial protein as a result of the ready availability of energy from the winter diet.

Although the nitrogen intake of the winter caribou was reduced significantly from summer levels, it is perhaps questionable if free-ranging *Rangifer tarandus* in winter have access to the amount of crude protein given the experimental animals. Lichen accounted for 35-45 per cent of the simulated ration by weight, but this proportion and the other constituents of the diet may not be comparable to the material consumed by caribou under natural winter conditions.

It is recognized that the use of mature caribou bulls may not provide the most informative data concerning urea recycling. Significant differences in urea recycling may appear when animals of varying sex and age characteristics are considered. Further comparative trials on young growing animals, breeding females and lactating females are considered important to a thorough investigation of urea recycling in *Rangifer tarandus*.

ACKNOWLEDGMENTS

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RANGE ECOLOGY OF THE DOMESTICATED REINDEER IN THE FINNISH CONIFEROUS FOREST AREA

Seppo Sulkava and Timo Helle
Department of Zoology, University of Oulu
Finland

ABSTRACT—Most of the 200,000 reindeer of Finland are living in the coniferous forests. The management areas are small, on the average 2100 km², and the reindeer are bound to these throughout the entire year.

The winter food in the Oulanka area includes three main components: *Cladonia*-lichens, *Alectoria*-beard-lichens and green *Deschampsia*-grass. The average amount of *Cladonia* sp. in dry pine forest was only 126 kg/hectare (dry weight). In the adjacent border-zone (no reindeer) it was 1500 kg. That of grass on some clearings was in autumn 420 kg/hectare, and that of *Alectoria* sp. within the reindeer's reach (210 cm) in dense young pine forest 27 kg, in old pine forest 3 kg and in spruce forest 15 kg/hectare.

The distribution of the grazing in forests and on clearings was studied 1971/72 by line-surveys. Snow came in October, and the reindeer were digging both in forests and clearings. In November the snow became very hard (10-20 cm, 800-1500 g/cm²). The digging in forests ended in November; on clearings not until in February. During the rest of the winter, about three months, the reindeer were feeding only on beard-lichens. The nutritive values of food-plants are analyzed.

Reindeer raising is practiced over the northern one-third of Finland; an area of about 120,000 km². The southern boundary of this area runs mainly along the Kiiminki River near 65° N, a little north of the town of Oulu. The area is chiefly covered by coniferous forests, two-thirds of which is dominated by pine (*Pinus silvestris*) and one-third by spruce (*Picea abies*). Peatlands occupy 10-30 per cent of the land in the northern parts of the area and 30-60 per cent in the southern parts. In the far north about 5 per cent of the whole reindeer rearing area lies above the timber-line and about 10 per cent in the subalpine birch (*Betula tortuosa*) forest zone.

The total stock of reindeer is about 200,000 head of animals more than a year old in the autumn, plus about 100,000 calves yearly. The average density of adult reindeer is thus 1.7/km² and 51,500 head of reindeer (26 per cent) are situated in those districts which are at least partly above the timber-line or in the birch forest zone. The majority live in the coniferous forest zone.

There were 6,795 individual owners of reindeer (approximately 3,000 families) in 1970. Each owner in the northern part of the area had an average of 55 reindeer at least one year old, while in the southern part the figure was only 20. For most of them reindeer husbandry supplies only a part of their livelihood.

Reindeer herding is organized in districts (57 such 'grazing associations' existed in 1970). The districts are rather small, averaging 2100 km², and never wider than 125 km. The reindeer are gathered twice a year; in the middle of the summer for marking the calves and in the autumn for counting and slaughtering. At other seasons the reindeer wander in the forest area mostly in smaller groups. They are not herded continuously.

During some severe winters some of the reindeer have been artificially fed, mainly with dry hay in the forests or in enclosures. Near the eastern border of Finland the herdsmen sometimes spend a great deal of time hunting wolverine, wolf or bear which prey on the reindeer, though traffic accidents kill more reindeer than predatory animals (e.g., loss to predators 688 and to traffic 1,297 in 1970).

ORIGIN OF THE FINNISH DOMESTICATED REINDEER

The Finnish domesticated reindeer originate, according to Siivonen (1975), from the Scandinavian mountain reindeer, *Rangifer tarandus tarandus*, which typically spend at least the winter in treeless mountain areas (Steen, 1966; Gaare, 1968). A small population of Finnish wild forest reindeer, *R. t. fennicus*, is found to the south-east of the reindeer-rearing area.

Mainly due to their origin the ecology associated with the Finnish reindeer presents some special features:

1. The Finnish reindeer are mountain reindeer which have been moved to the forests of northern Finland only during the last two or three centuries and have been forced to live all the year-round in the area of coniferous forests.
2. The small, often centralized herding districts accentuate the restriction of the reindeer to the forests. Herding districts in the most important reindeer-rearing areas in other countries are much more extensive and usually include some tundra or treeless mountains.
3. The Finnish reindeer do not migrate seasonally as they do in almost all other areas. Their only movements are towards the damp forests and peatlands in the summer. The mountain reindeer has thus had to abandon its migratory habits.
4. During the summer insects probably cause the reindeer more discomfort in the forests than they would on tundra or in the mountains.

For these reasons very wide-ranging ecological investigations into reindeer rearing are necessary in Finland in order to examine the ability of the mountain reindeer to adapt to the forest conditions.

PAST AND PRESENT INVESTIGATIONS

Several studies have already been made on the Finnish reindeer, but there are only a few published works devoted to their ecology. These include a summary of the capacity of the pastures (Helle, 1966), studies on lichen consumption (Pojärvi, 1945) and on the growth of lichens (Kärenlampi, 1971). Basic information about reindeer biology, diet, food resources, grazing pressures, etc. is still lacking.

In order to study the ecological background for reindeer husbandry under the special conditions prevailing in Finland, a far-reaching ecologically oriented research program was prepared in 1970. The study included three principal aspects: food, pastures and artificial feeding. The ecological work is led by Dr. S. Sulkava (Department of Zoology, University of Oulu), the physiological part by Dr. B. Westerling (College of Veterinary Medicine, Helsinki) and the feeding aspect by Lic. R. Heikkilä (Agricultural Research Station, Rovaniemi). Overall supervision is by Professor L. Siivonen (Department of Zoology, University of Oulu).

Food studies include the composition of the diet in different seasons, the nutritive values of the food plants in different areas and at different seasons, grazing pressures in different vegetation types and on various food plants, and the effects of snow cover on grazing. Studies on artificial feeding include experiments using various feeds, and

investigations into the digestion and physiology of starving reindeer.

This program has received a grant of Fmk 40,000 per annum for three years from the SITRA-foundation. The ecological work is concentrated on the herding district around the Oulanka Biological Station. This report is mainly based on the plans for the ecological work and the preliminary results obtained. The material was gathered and examined by T. Helle. The work is still going on and some essential material is not yet available.

THE OULANKA AREA AND THE PROGRAM FOR 1970-73

In the Oulanka area half of the forest is dominated by pine and half by spruce, with peatlands occupying 30-40 per cent of the surface area. Settlement is very sparse and cultivated fields take up only 2 per cent of the land. Only 5-10 per cent of the forests are dry pine forest, where an average of 35 per cent of the ground layer is covered by reindeer lichens (*Cladonia*). Forest clearing has been extensive, with roughly one-third of the forest cut during the last 15-20 years. The area is snow-covered for about seven months of the year and the maximum snow depth in March averages 70 cm.

Only one man (T. Helle) has been working at Oulanka in 1971/72, chiefly studying the winter food resources and the effects of snow cover on the distribution of grazing.

In this area the winter food of the reindeer has three main components typical of different biotypes: reindeer lichens (*Cladonia*) in dry pine forests, green grass (mainly *Deschampsia flexuosa*) under snow on clearings and tree lichens (mainly *Alectoria* beard lichens) most often in spruce forests.

METHODS OF STUDYING FOOD RESOURCES

The biomass of *Cladonia* and *Stereocaulon* lichens was studied in six separate dry pine forests. A total of 188 squares, each 50 x 50 cm, was taken by random sampling (Greig-Smith, 1964). The living parts of the lichens were cut off, dried at +105° C and weighed. The sampling took place in spring, and the figures presented here are corrected for the beginning of the next winter by multiplying by the average growth rate of 30 per cent (after Kärenlampi, 1971).

The beard lichens (almost all are *Alectoria* spp., mainly *A. jubata* and in smaller quantities *A. fremontii*, *implexa* and *sarmentosa*) were sampled in three forest types: dense 30 to 60 year-old pine forest (6,000 trees/hectare), old pine forest (900 trees/hectare) and old spruce forest (300 trees/hectare). Sixteen young and 27 old pines were chosen from three pine forests by random sampling. Only 10 spruces were analysed. The beard lichens were picked in zones 30 cm high up to 240 cm. Reindeer may reach to a height of about 210 cm above the ground in winter, and the browse-line is often very clear.

The biomass of *Deschampsia* grass on clearings was measured in September 1971. The percentage coverage of the grass was estimated in 179 squares of 1 m² along a line 1,800 m long in a wide clearing (8 km²). The same was done for 20 squares of 9 m², chosen by random sampling, in a small clearing (4 hectares). The biomass of the grass was measured in 16 squares (50 x 50 cm); the grass being cut off, dried at +105° C and weighed. The coverage of the grass was estimated and the results are given for 10 per cent coverage. The results in two clearings were 5.0 and 4.7 g/0.25 m²/10 per cent coverage. The mean (4.9 ± 0.29 g) was used for the calculation of the grass biomass on the basis of percentage coverage.

FOOD RESOURCES PER HECTARE

The biomass of *Cladonia* lichens in the dry pine forests around Oulanka averages, because of the heavy grazing, only 126 kg/hectare (dry weight), varying between 70 kg and 150 kg. In the boundary zone near the Soviet border, which has been without reindeer for 30 years, the corresponding figure was 1,500 kg/hectare. The average coverage of lichens was 35 per cent in the grazed areas and 45 per cent in the border zone, and their mean lengths 25 to 58 mm respectively.

In the grazed areas the biomass of the lichens may be divided among the different lichen species as follows (a mean of 95 squares):

	<u>%</u>	<u>Mean g/0.25 m²</u>	<u>Standard error</u>
<i>Cladonia rangiferina</i>	40.7	0.81	0.06
<i>Cl. mitis</i> (+ <i>silvatica</i>)	28.7	0.57	0.06
<i>Cl. uncialis</i>	13.5	0.27	0.06
<i>Cl. alpestris</i>	0.3	0.006	0.002
<i>Cladonia</i> sp. (tubes)	14.1	0.35	0.09
<i>Stereocaulon</i> sp.	2.7	0.05	0.02

The biomass of beard lichens within reach of the reindeer (210 cm) is very variable. In dense pine forests it averaged 27 kg/hectare, but in old pine forests only 2.7 kg/hectare, and in spruce forests 15 kg/hectare. In the border zone it was measured only in old pine forest, giving 5.9 kg/hectare, more than twice as much as in the grazed area.

In addition to the sources of food mentioned above the reindeer are able to eat beard lichens in spring when the melting snow breaks off dry branches with their lichens from the trees. The same effect is sometimes caused by storms. In winter 1971/72 the biomass of lichens brought down by two storms (in February and March) was estimated by picking the beard lichens from 60 randomly chosen squares (4 or 9 m²). These storms released a total of 15 kg of beard lichens per hectare in old pine forests. The majority of the reindeer in the area were feeding on this lichen as their principal food during March and April, and they would sometimes even dig for it under snow (at least 5 cm).

The biomass of *Deschampsia flexuosa* grass in clearings is naturally very variable. The average for an extensive 10-15 year old clearing (mostly spruce forest) in September was 420 kg/hectare and for a small clearing 770 kg/hectare. The coverage of the grass in these clearings averaged 21 and 39 per cent respectively.

DISTRIBUTION OF GRAZING AMONG DIFFERENT BIOTOPES

The distribution of grazing was estimated in winter 1971/72 in the Oulanka area by the line survey method. The lengths of the lines were 15 km in pine forests, 5 km in spruce forests and 5.6 km in clearings. The lines were skied monthly about five days after a snowfall. The numbers of fresh crosswise tracks, the amount of fresh digging (m² on a 4 m broad strip) and the numbers of trees and fallen branches from which reindeer had been feeding on beard lichen were counted for 200 m sections along these lines.

In early winter (October) 1971/72 the reindeer were digging for both lichens in forests and grass in clearings. In November the soft snow cover (depth 10-20 cm) hardened to a very hard layer (10-15 cm thick with a hardness of 800-1,500 g/cm², measured after Klein *et al.*, 1950). This layer remained in the lower strata of the snow cover all winter both in the forests and in open places.

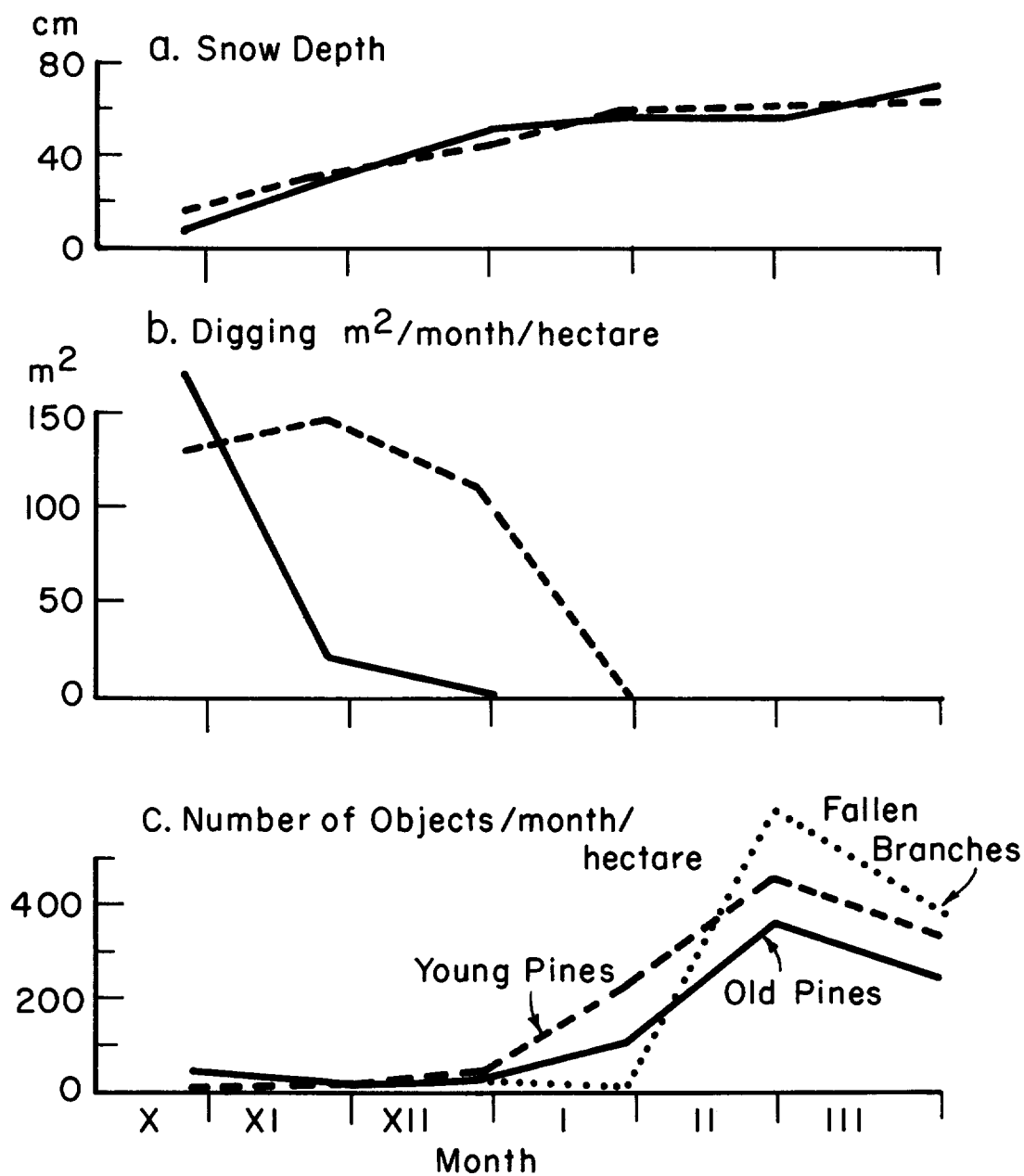


Fig. 1.—Monthly distribution of snow and grazing by reindeer in the Oulanka area in winter 1971/72. A. Snow depth in clearings (—) and in dry pine forests (---). B. Monthly amount of digging for lichens in pine forests (---) and for grass in clearings (—). C. The number of instances of feeding on beard lichens from branches brought down by storms (...); from young pine (---) and old pines (----).

The reindeer ceased digging in pine forests in early November, but digging in clearings continued until January (Fig. 1). The distribution of digging in extensive clearings closely followed that of the stands of grass (Fig. 2). The extent of digging remained limited in both

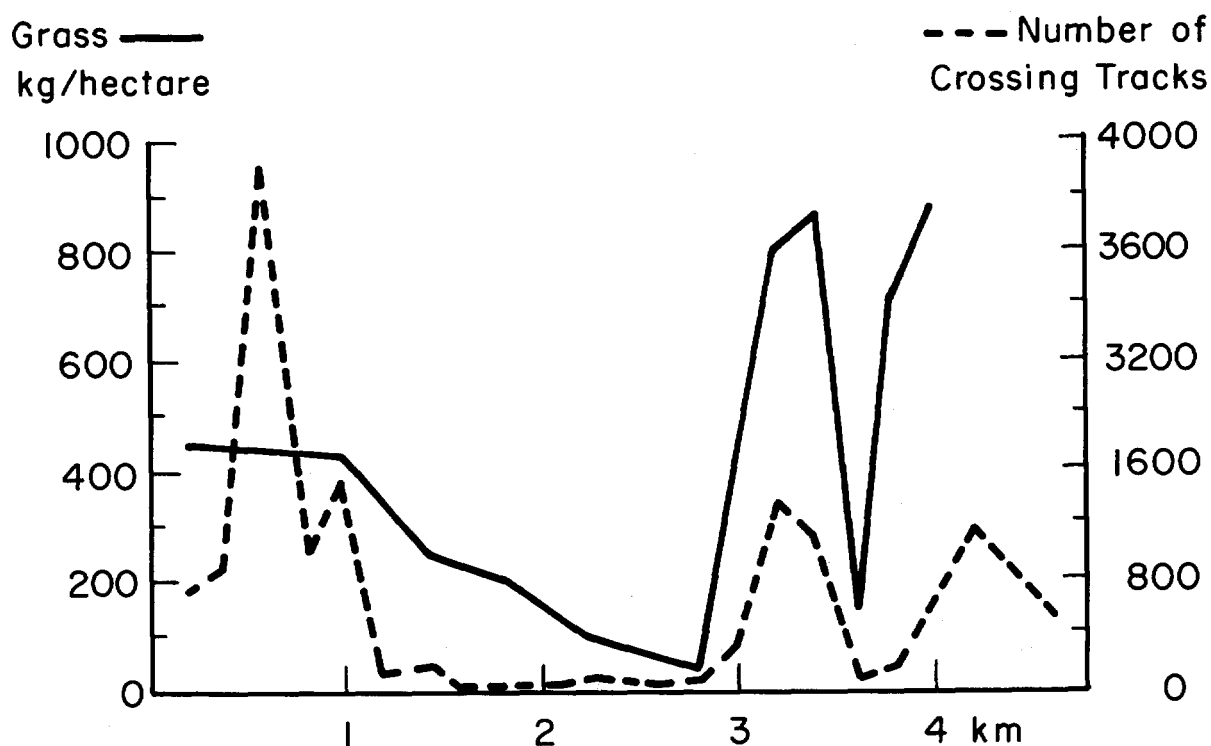


Fig. 2.—The biomass of *Deschampsia* grass (—) and the frequency of reindeer (number of tracks encountered, ---) along the survey line in a wide clearing near Oulanka during October-December 1971.

biotopes, however, covering 1.9 per cent of the ground surface in lichen forests and 3.9 per cent in clearings over the whole winter; while in winter 1968/69, 23 per cent of the lichen-covered surfaces in pine forests had been dug by January.

The increase in the depth of the snow to 40-50 cm seemed to curtail digging in clearings in January 1972. It is possible that the reindeer could no longer catch the scent of the grass through the snow (cf. Bergerud and Nolan, 1970). The earlier termination of digging in the pine forests was probably caused by the freezing of the lichens in the icy snow. This did not happen in the clearings where the grass remained mainly in the air space under the snow.

Nutritive values did not affect the digging activity, since these values were well preserved at least until February, the values (per cent of dry matter) for crude protein for example being on average 9.5 in *Deschampsia* ($n = 3$), 4.2 in *Alectoria* (6) and 4.2 in *Cladonia* (2) in February.

During the rest of the winter of 1971/72, about 3½ months, the reindeer in the Oulanka area were feeding almost entirely on beard lichens, the most favored biotope for gathering these being the pine forests in the valley of the Oulanka River (Fig. 3). About one-third of the reindeer fed on beard lichen from felled trees at timber cutting sites.

The snow in which the reindeer were digging in December and January was considerably harder than that in which barren ground caribou in Canada cease digging (60

g/cm², Pruitt, 1959), although the reindeer of the Oulanka area may sometimes stop digging earlier. This happened in lichen forests in the winter of 1970/71 in January, for instance, when in the upper portion of the snow cover there existed a layer 16 cm thick with a hardness of 100 (90-125) g/cm². Finnish reindeer seem generally to dig in greater hardnesses of snow than wild caribou and this is probably caused by the restricted ranges available to the Finnish domesticated reindeer.

Number of Crossing Tracks /day/km

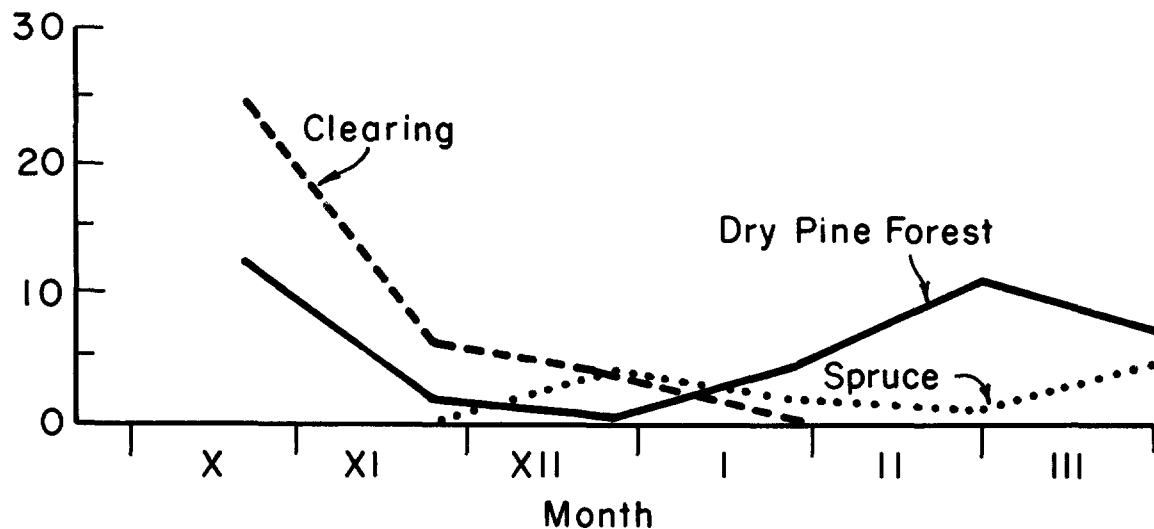


Fig. 3.—Distribution of reindeer in the principal winter pasture types in winter 1971/72 in the Oulanka area according to numbers of tracks encountered along the line surveys.

The effect of the snow cover seems to be very variable and often differs from winter to winter. These studies will continue through the next winter, and it is hoped that different conditions will again prevail.

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ANALYSIS OF THE NELCHINA CARIBOU RANGE

R. E. Pegau
Alaska Department of Fish and Game
Nome, Alaska

ABSTRACT—Trend of the Nelchina caribou range was determined from vegetation examinations of 36 ten and fifteen year old exclosures. Condition of climax lichen stands, primarily *Cladonia alpestris*, began to degenerate with two to three years of use and has declined substantially in the last 10 years. Within 15 year old exclosures lichens are just starting to recover and most are about one inch or less in length. Even with a marked reduction in winter use by caribou for 15 years, lichen condition has continued to deteriorate. Trampling by caribou and moose has been an important factor in suppressing lichen growth and contributing to their poor condition. Apparently lichens on the Nelchina range require long periods of total protection, possibly 25 years or more, to reach climax condition, yet it only takes five to eight years of use to destroy climax lichen stands. The lichen flora of the Nelchina range cannot withstand the present numbers of caribou and moose.

The Nelchina caribou (*Rangifer tarandus*) herd has long been considered one of the most important herds in Alaska because of its ready access from populated areas. The Nelchina caribou range is located in Southcentral Alaska, centered about 160 km (100 mi) northeast of Anchorage (see Hemming, this volume, Fig. 2., for map). Roughly, it is bounded on the south by the Glenn Highway and the Tazlina and Matanuska rivers, and on the west by the Alaska Railroad and the lower Susitna, Chulitna and upper Nenana rivers. The summit of the Alaska Range forms its northern boundary and the Wrangell Mountains bound it on the east. The Nelchina range encompasses about 51,799 km² (20,000 mi²). The climate of the Nelchina area is similar to that of Interior Alaska, but with slightly milder temperatures, ranging from 35° C to -45° C, and greater precipitation, averaging 33 cm. Snowfall occasionally exceeds 100 cm.

The principal caribou habitat lies above timberline in elevations between 914 m (3,000 ft) and 1,524 m (5,000 ft) except for Lake Louise Flat. Because the Nelchina range has such varied topography, a multitude of micro-climates exist. One factor of particular importance is wind, which influences caribou distribution in the summer by providing relief during the peak period of flying insect harassment. Snow conditions are variable and the depth accumulation, as well as icing and layering, determine which areas can be utilized by caribou during the winter months. Little information has been obtained about snow conditions and distribution of snow accumulation, etc.

Range studies have been more intensive with this herd than any other herd in Alaska. Major studies were conducted by Hanson (1958) and Skoog (1968). In 1970, I reexamined the exclosure and reviewed and summarized all the data that had been collected since 1949 (Pegau and Hemming, 1972).

Vegetation of the Nelchina range is similar to other tundra and taiga regions in the northern hemisphere. Twelve vegetation types have been described on the Nelchina range (Skoog, 1968). Six of these are most important to caribou. Black spruce (*Picea mariana*) and white spruce (*P. glauca*) occur throughout, at elevations below 914 m (3,000 ft) with

scattered trees extending to 1,066.8 m (3,500 ft). The largest area of spruce cover occurs in the Lake Louise Flat and in the Copper River drainage. Interspersed among the Spruce communities are stands of Aspen-poplar, Meadow, Water Sedge and Bog. Shrub Birch (*Betula glandulosa*) is the co-dominant with Spruce at elevations between 914 m (3,000 ft) and 1,066.8 m (3,500 ft). Willows (*Salix* spp.) occur on most drainages and Fescue Grass (*Festuca altaica*) is commonly found in association with the Shrub Birch type. The Heath type (*Ericaceae*, *Carex* spp. and *Cladonia* spp.) is normally found above timberline and is a very important vegetation type in the ecology of the Nelchina herd. Heaths usually occur from 914 m (3,000 ft) upward on dry well-drained sites. The Meadow (*Carex* spp. and *Eriophorum* spp.) type occurs on sites with poor drainage up to considerable elevations in the mountains; however, the majority occur below 1,219.2 m (4,000 ft).

PROCEDURES

During 1955 and 1956, 15 exclosures were constructed on the Lake Louise Flat where the Nelchina herd had traditionally wintered. At each range station, two similar plots, each approximately 9.4 m² (5 x 20 ft), were delineated; Plot A was fenced to exclude all large animals and Plot B was left open to normal grazing by all animals.

The small size of the exclosures has often been criticized. The criticism is justified if the objective is to determine quantitative data on carrying capacity from these small exclosures, as there are several unknown factors (forage availability, snow depth, icing, accurate enumeration of animals utilizing a site for a known length of time, etc.), that negate obtaining carrying capacity estimates by the classical means. However, these exclosures can provide qualitative information on the effects of caribou and other animals on the range in relation to different intensities of grazing and use patterns, successional stages of the vegetation protected from and exposed to grazing, and other factors that are useful in the management of a caribou herd.

The disadvantages of the small size are offset somewhat by the fact that the exclosures were built to provide data on the ground vegetation (lichens, mosses, sedges, grasses and dwarf shrubs) rather than the taller shrubs and trees and that all plots are at least 3 to 5 ft (.9144 to 1.524 m) inside the fence. The effect of the fence on micro-climate has not been determined but during 1970 when a considerable change in the vegetation was noticeable at several of the range stations, there was no instance where the fence had an apparent effect on the vegetation. Skoog (1968) remarked that at the time of his winter examinations of the exclosures he could not detect any difference in snow accumulation due to the fence. In my own observations of six exclosures in the Nome area, as well as two in the Selawik and Kobuk valleys, I have not noticed any indication that the fence influences snow depth, melt, runoff or growth of the vegetation.

In 1960, 24 more exclosures were constructed on major Nelchina caribou wintering areas. No attempt was made to do the vegetation analysis that year, as construction of as many exclosures as possible was desired. In 1961 and 1962 vegetation was examined in the exclosures constructed during 1960. A fenced plot and an unfenced control plot, each containing two m² quadrats, were established at each range station. The vegetation was analyzed by the modified Hult-Sernander method recommended by Hanson (1958).

RESULTS AND DISCUSSION

Northwestern Quadrant of the Nelchina Range

This area, which contains Range Units 1-4, is mostly mountainous except for Monahan Flat and nearly one-fourth is bare ground. Shrub Birch, Heath and Meadow predominate. For over 20 years prior to 1956, caribou seldom used the area. Caribou resumed use of this area in 1956, and in the early 1960's it was a major wintering area. Winter use by caribou continued to a lesser extent in the late 1960's. Range examination in the late 1950's and early 1960's revealed excellent lichen stands with *Cladonia alpestris* often being 15 to 20 cm high. Forage lichens were abundant in the Heath and Shrub Birch types. Sedges were also abundant and provided considerable winter forage (Skoog, 1968).

Several range exclosures constructed and examined in 1960 and 1961 revealed the excellent condition of the range. By 1967, there was an evident deterioration of the range outside of the exclosures, reflecting the resumption of utilization by caribou in the early 1960's.

Within a five-year period, from 1962 to 1967, rapid destruction of lichen cover, especially of *Cladonia alpestris*, had occurred. Scattered disrupted lichen stands with numerous gray podentia (the decadent portions) of *C. alpestris* were common in 1967 and clearly showed that this species cannot withstand continued heavy utilization. It deteriorates rapidly under moderate caribou use, which has been demonstrated in other studies, particularly in Sweden (Skuncke, 1969).

Examination in 1970 revealed that with the disruption of the lichen cover, the growth of shrubs was stimulated. There was little noticeable change in other vascular plants.

The effect of trampling on the vegetation, especially lichens, by caribou and moose is demonstrated at several of the exclosures in the northwestern sector, especially in the vicinity of Soule Lake. In 1961, when the Soule Lake exclosure was constructed, lichen condition was excellent. There were numerous small moss hummocks and grass tussocks. Caribou resumed their use of the area shortly after the exclosure was constructed. In the summer of 1966 nearly the entire Nelchina caribou herd passed through the Soule Lake area. The destruction of the habitat was remarkable. It looked almost as if the area had been spaded, with bare ground exceeding vegetative cover. Lichens outside the exclosure were completely trampled. Other studies in Alaska (Palmer and Rouse, 1945; Pegau, 1970a), Sweden (Skuncke, 1969) and the Soviet Union (Makhaeva, 1963; Davydov, 1958), have also shown that the effect of trampling during snow-free periods may exceed the damage caused by grazing.

Central Region

This region containing Range Units 5, 8 and 12, lies between two mountain ranges, and rolling foothills are prominent. Shrub Birch, Heath, Meadow, Spruce and Willow are the principal vegetation types. This sector received some of the most intensive use, as it is the prime summer and calving range with occasional winter use as well. Lichens were abundant in some areas in 1953 but were markedly reduced by the late 1950's. The preferred species, such as *Cladonia alpestris*, *C. rangiferina* and *C. arbuscula* were in poor condition and being replaced by secondary types such as *Cladonia uncialis*, *C. gracilis*, *Cetraria cucullata* and *C. nivalis* (Skoog, 1959). Lichens have continued to decline in condition through the early 1970's due primarily to trampling during snowfree periods of the year. Inside one 15-year-old exclosure *Cetraria nivalis* was the only lichen that appeared to be recovering from prior use. Shrubs, especially blueberry (*Vaccinium uliginosum*) and narrow-leaved

Labrador tea (*Ledum decumbens*), have increased but total cover has decreased. Overall, the central region is poor winter range but does provide considerable summer forage. There has been some destruction of the vascular plants as well, reflecting the continuous heavy use.

Northcentral Region

This area, containing Range Units 6 and 9, consists mostly of gentle slopes and rolling terrain. Shrub Birch and Heath types predominate. Lichens are prominent in the Shrub Birch stands, but they are mostly unavailable to caribou due to the density and height of the shrub birch. Exclosures located in the Shrub Birch stands contain excellent lichen undergrowth and there is little evidence that they have ever been utilized by caribou. Lichen stands in the few areas exposed to winter grazing have deteriorated in condition during the last 10 years. The region contains a considerable amount of good summer and early fall forage.

Eastern Region

From the late 1960's to the present a major portion of the Nelchina caribou wintered principally near the Wrangell Mountains, which is outside what was previously considered 'normal' range. No range studies have been conducted to date in this area and such studies should have high priority.

Southwestern Region

This area containing Range Units 10, 11, 14 and 15, is mountainous and nearly one-fourth unvegetated. Heath, Spruce and Meadow are the principal vegetation types. Caribou utilize the area primarily during the winter.

Skoog (1959) and Skoog and Keough (1961) examined several areas that had been used during the winter to determine the amount of area utilized by caribou in the winter. He reported (Skoog and Keough, 1961) that nine months of winter use (three winters of three months each) by over 20,000 caribou on an area of about 258 km² (100 mi²) had resulted in 9 per cent of the lichen forage being destroyed and 18 per cent grazed lightly. Almost all of this damage occurred in the Heath type, and indicated that under continued heavy use of such intensity, the range probably would deteriorate rapidly. The buffering effect of the Meadow type could not be determined.

Southeastern Region (Lake Louise Flat)

Over 95 per cent of this region lies below 914 m (3,000 ft). Snowfall and winds are light to moderate and the ground becomes free of snow early in the spring. The area is characterized by numerous lakes and ponds with poor drainage. Spruce covers over 75 per cent of the Flat. Water covers 8 per cent and associated sedges form extensive stands. Fire has had considerable impact on the flora of the area and the growth of lichens is mostly poor to fair due to the poor drainage, heavy caribou use and frequent fires.

On most stands the lichen cover is comprised primarily of secondary species, usually *Stereocaulon* spp. The lichen mat is trampled and its height is usually less than 2.5 to 5 cm. This area had been the major wintering grounds from early in the 1930's until the mid-1950's. Since 1955, however, only small portions of the herd have wintered on the Flat, although many thousands usually swing across the Flat each year during the October-December period before moving to other wintering areas. This pattern of range use

continues, and from vegetation examinations of the range exclosures it appears to be sufficient to suppress lichen recovery. However, there are large quantities of sedges remaining, particularly *Carex aquatilis*, which is a valuable early winter forage.

Because the Lake Louise Flat was the major wintering ground, it received considerable attention and numerous vegetative studies have been conducted including 14 exclosures built in 1955 and 1956. These stations have been examined periodically and range condition and trend data have been obtained.

Aerial surveys indicate that 56 per cent of the Spruce type in the Lake Louise Flat has burned (Skoog, 1968). Presently the lichen growth in predominately secondary types, such as *Stereocaulon* spp., *Cladonia gracilis*, *C. uncialis*, *Cetraria cucullata* and *C. islandica*. Isolated patches of the preferred lichens *Cladonia arbuscula* and *C. rangiferina* occur, usually in depressions of the polygons where they are unavailable during the winter and also in protected sites under the shrubs.

Throughout the Nelchina range, from the earlier studies in 1953 to those in 1970, the most palatable lichens were usually encountered only in isolated, scattered locations where they were protected from grazing, trampling or fire. The effects of fire have been spotty, and lichens occurring on a dense moss mat, which would be moist and resistant to burning, often were not burned. Frost polygons are characteristics of the Lake Louise Flat and lichen growth usually occurs on the top of the slightly elevated polygons. Usually shrubs are less dense and the area is more exposed to grazing and trampling. These sites are the most severely damaged. Luxuriant stands of lichens often can be found in the border depressions adjacent to an elevated mound. This is due to the increased moisture content and moisture retention by the moss cover and protection by the shrubs. Overall, the shrubs, particularly blueberry, cranberry (*Vaccinium vitis-idaea*), narrow-leaved Labrador tea, shrub birch and willows, were increasing at almost all stations examined. Sedges (*Carex* spp. and *Eriophorum* spp.) are usually a principal component of such a stand, although there has been very little indication of increase in the sedge cover at any of these stations. Observations indicate that the Nelchina herd has utilized sedges to a large extent, but, unfortunately, only one or two of the stations are in representative stands and very little change in the sedge cover has occurred with either protection or normal grazing. Apparently the sedges are quite able to withstand the current level of use.

All exclosures are showing signs of recovery of the lichen growth after 14 or 15 years of total protection. The recovery is by lichen species that occurred at the time the exclosures were built. These include *Stereocaulon* spp., *Cladonia uncialis*, *C. arbuscula* and *C. rangiferina*. There has been almost no recovery by *Cladonia alpestris*. Very likely *C. rangiferina* and *C. arbuscula* should be considered climax for the Flat due to the intense frost action and use by both moose and caribou. Most stations showed a continued deterioration of the lichens outside of the exclosure with the lower level of use that has occurred since the mid-1950's. This is particularly true at Corky and Harris Lakes, which are close to the calving grounds. The caribou move across these stations annually in large numbers. Deterioration of the total range, especially the lichens, has continued, but also numerous moss pedestals are apparent at several of the stations. Total cover has been severely reduced and large amounts of bare ground are now exposed. Several of the stations are located in stands that are suitable for studying recovery from fires, especially at Betty Ann Lake which experienced a rather recent fire. This station showed that six to 15 years of total protection were required for the first lichens to establish themselves. After 20 years the primary species, such as *Cladonia gracilis* and several of the funnel-form *Cladonias*, were still almost the only lichens present. Some of the stations on an old burn that occurred in 1924 or before showed that the recovery by *Cladonia arbuscula* and *C. rangiferina* usually occurred 30 to 40 years following the fire. Station 12 shows the relatively slow progress

made in 15 years of total protection on an old burn. It appeared that recovery by the lichens had occurred within 30 years and that since that time, there had been very little change in the lichen cover or composition.

The condition of lichens in the Lake Louise Flat is considered poor and they are still deteriorating. Lichen recovery will require a minimum of 15 years of total protection, which is unfeasible, since the caribou will likely be using the Flat in the future. Very likely moose will continue to be in the area and their movements will tend to retard improvement of the condition of lichens, as will frost action. The Flat contains an abundance of sedge forage and caribou are evidently utilizing this source to a large extent. Effort should be made in the future to more accurately determine the role of sedges in the winter diet of caribou because it is obvious that the Flat cannot be considered a major wintering site based on the condition of lichens. The recovery by lichens within exclosures has shown marked changes in the last four years, and it appears that within the next 10 years, there will be very rapid changes in the condition and composition of lichens to a more nearly climax condition with total protection.

CONCLUSIONS

Palmer and Rouse (1945) reported that lichens on tundra ranges are quick to react to any disturbance and the length of time required for their recovery is directly proportional to the degree of disturbance. In the Heath type recovery was rapid following light grazing, but slow with heavy grazing. Palmer and Rouse also found that a depleted lichen range under complete protection required from 20-40 years for restoration of the original density and height. Their work is substantiated by the fact that in a Heath type at Unalakleet total recovery of the original density of lichens has not occurred after 33 years because the shrubs have become difficult to displace (Pegau, 1970b).

The nutritional biology of caribou is very important and has been discussed by Klein (1970a). With a wide diversity of habitats, a considerable variety of nutritional plants are available throughout a prolonged period during the brief summer when body maintenance and a rapid rate of growth take place (Klein, 1970a). The caribou's feeding behavior enables them to select the highest quality forage available on the range. However, low population density and the opportunity to range over wide areas, as pointed out by Klein (1970b), are essential to the well-being of caribou. His studies of the St. Matthew Island reindeer herd (Klein, 1968) indicated that the drastic population decline occurred after the population reached a level at which the animals were no longer able to select a high quality diet because of the high population density and consequent deterioration of the range.

From the exclosure studies, it is apparent that the successional trend of the Nelchina range is towards a drier condition and increase in shrubs. The exclosure studies and the study of Palmer and Rouse (1945) show that use by caribou stimulates the growth of shrubs and the lichen cover is reduced. The shrubs have increased at almost all range stations on the Nelchina. Dwarf shrubs increase on heavily utilized tundra ranges, and once they become established, they are able to suppress recovery of the fruticose lichens (Palmer and Rouse, 1945; Pegau, 1970b). Shrubs increase the value of a summer range but reduce the quality of winter range. There has been no indication that shrubs are important in the winter diet of caribou.

On the Nelchina range, it is apparent that whatever recovery of the lichens occurs usually involves those species that were already on the site when the exclosures were established. There was some change in species composition, but normally the recovery has been primarily of those species already present at the time the areas were first protected.

Skoog (1968) presented considerable data on historical and recent population size of

the Nelchina caribou herd. Evidently large-scale population fluctuations have been characteristics of the herd since its earliest recorded history. Skog (1968) states, "A low point in numbers probably was reached during the late 1930's or early 1940's."

The Nelchina herd continued to increase during the 1950's and early 1960's, possibly reaching a peak in the early 1960's (Hemming, 1971). The increase in total numbers of the Nelchina herd was accompanied by an expansion of the 'normal' Nelchina range, especially during the winter. During the 1960's the caribou traditionally utilized a major portion of the Wrangell Mountains area as part of their wintering range. Areas that previously had been used, such as the Lake Louise Flat, now receive only sporadic use. Also during the early 1960's, the caribou used the northwestern quarter of the Nelchina range extensively, an area virtually untouched by caribou for at least 20 to 30 years.

Some of the earliest investigations on the Nelchina Range pointed out the fact that trampling constituted a major portion of the damage to lichens. Is it possible that the characteristically large population fluctuations of caribou are mechanisms that have evolved along with lichen suppression and recovery? Apparently even though the animals move out and utilize new areas, the continued sporadic use of previously heavily used areas is sufficient to suppress lichen growth and prevent restoration of the lichens. From the exclosure studies it appears that lichens on the Nelchina need almost total protection for lengthy periods of time (over 25 years?) to recover fully, yet it takes only five to eight years of intensive use to destroy climax lichen stands. The Nelchina caribou herd has been and possibly still is, undergoing the classic population dynamics of building up, expanding into new areas and then declining. The range is continuing to deteriorate and indications are that the recent population levels of the Nelchina herd may very well have been in excess of what the lichen flora could support.

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WOODLAND CARIBOU AND SNOW CONDITIONS IN SOUTHEAST MANITOBA

Richard R. P. Stardom
Department of Zoology
University of Manitoba
Winnipeg, Manitoba, Canada

ABSTRACT—Two winters of field research was conducted to determine the effect of snow conditions on woodland caribou activity in the various vegetation types found within the project area. Bimonthly snow cover data were obtained for each vegetation type and caribou activity was recorded utilizing both aerial and ground reconnaissance. Groups of two to 22 individuals fed mainly on arboreal lichens in open bogs until the snow cover approached 60 cm in depth and possessed a crust hardness of 400 gm/cm². This resulted in a movement to mature jackpine-lichen rock ridges where the caribou spent the major portion of their time until the open bog crust allowed travel with ease. Lakes were utilized to a greater extent during the second winter, a year of above average snowfall. The caribou demonstrated a definite response to nival conditions and preferred habitat providing several vegetation types and subsequently several snow accumulation types.

Although a great deal of research has been undertaken on the genus *Rangifer*, far too little is known about the role snow plays in the winter ecology of the genus in the many geographical areas to which it is indigenous. In continental North America, the word 'caribou' conjures up visions of vast migrating herds of barren ground caribou forced by severe tundra snow conditions to find refuge in forest snow accumulation types. In comparison to this species, much less investigation has been carried out on the woodland caribou. These small resident or semi-migratory bands are scattered throughout much of the taiga and must react to variations in nival conditions within their forest ecosystem.

Snow data have been obtained in winter studies of other cervids (Telfer, 1968). These data are difficult to apply to woodland caribou ecology unless caribou activity data are also available for that particular forest type snow regime. Assessment of the nival environment of barren ground caribou in their winter forest habitat (Banfield, 1949; Bergerud, 1971; Pruitt, 1959) may be useful as an index of the effect of snow on woodland caribou in those particular habitat types. Morphological and behavioral differences between barren ground and woodland caribou may be slight but are sufficient to produce different nival thresholds and reactions to sensory cues afforded them by this annual phenomenon of snow accumulation.

During the winters of 1970-71 and 1971-72, I undertook a study of the winter ecology of western woodland caribou, *Rangifer tarandus sylvestris* (Richardson) (Cringan, 1956), in southeastern Manitoba. According to Banfield (1961), these woodland caribou from Manitoba do not differ significantly from eastern specimens and so should be referred to as *Rangifer tarandus caribou* (Gmelin). My primary objective was to determine the effect of the nival environment on the movements and feeding activity of the species in the various vegetation types found in the project area. Other objectives were to determine population size and distribution of various groups in the area, to study annual winter movement patterns and to assess the degree of association with other ungulates present in the area:

moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*).

AREA

The area chosen for the project is a portion of the Precambrian Shield (Fig. 1) that is

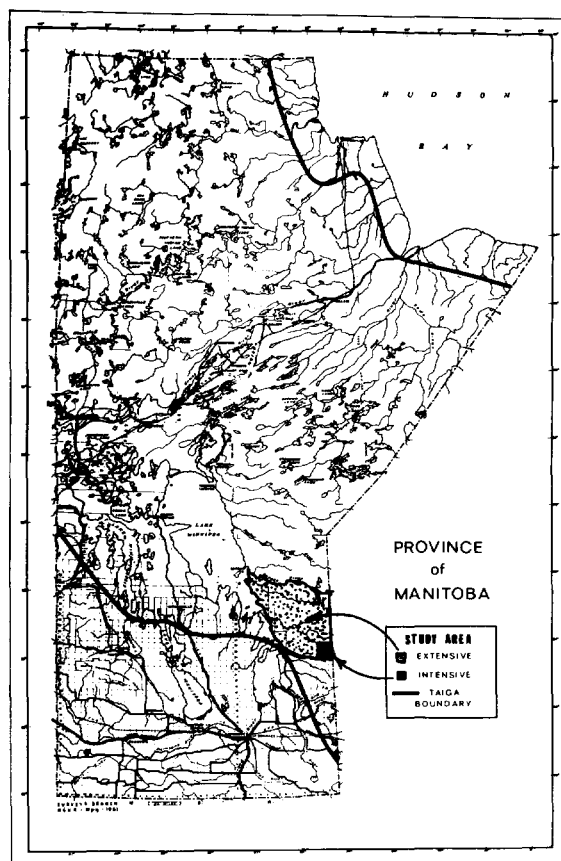


Fig. 1.—Map of the Province of Manitoba showing the study area.

relatively unaffected by man although its southern boundary is accessible by road. This area belongs to the Hudsonian biotic province as designated by Dice (1943). Rowe (1959), in his classification scheme, includes this portion of Manitoba in the Boreal Forest Region and further subdivides it into three sections.

The area grades from 1,100 ft (335 m) elevations along the Ontario boundary down to the 713 ft (217 m) elevation of Lake Winnipeg in three major levels. The topography of the eastern level, the Northern Coniferous Section, consists of rugged jackpine rock ridges, often 60-100 ft (18-30 m) in height, cradling many lakes and stream valleys. The central Nelson River Section is of a more rolling terrain with numerous glacial sand flats and bogs. The Manitoba Lowlands Section, adjacent to the Lake Winnipeg shore, is for the most part flat bogs with numerous rock outcrop 'islands'.

The extensive study area of approximately 3,250 km² is bounded by Lake Winnipeg on the west, the Ontario boundary to the east, the Berens River to the north and the Wanipigow River to the south. There are no permanent roads, few human residents and a

sufficient population of caribou to provide good activity data. There is also the advantage of a meteorological station in Bissett at the southern boundary of the study area. Snow transect work and determination of the population size and winter movements of undisturbed caribou groups in the area were accomplished with the aid of aircraft.

The vegetation varies from open tamarack (*Larix laricina*) bogs to heavy, mature white spruce (*Picea glauca*) stands. As much of the area has been burned several times since 1926 and at least once since 1948, all successional forest types are present with the climax vegetation being spruce and a sub-climax of jackpine (*Pinus divaricata*). It is important to note that due to glacial action most open bog areas and lakes are oriented in a northwest-southeast direction while elevation differences cause all major drainage systems to flow in a westerly direction to Lake Winnipeg. This orientation of the terrain to the prevailing winter winds is a major factor in vegetation distribution and snow cover.

Within this large area, an intensive study site of 673.4 km² was set up. Here, the emphasis was on the snow cover with respect to the various vegetation types and its subsequent effect on the activity of a resident group of caribou. Logistically, this area was ideal since it also afforded a base camp and available outcamps.

METHODS

Since the winter ecology of the caribou is so closely associated with the vegetation, both as a food source and as a main factor in snow accumulation, a vegetation map of the intensive study area was necessary. Eight major vegetation or habitat types were delineated with the aid of timber type maps from the Manitoba Department of Mines and Natural Resources. I attempted to monitor successional changes in the snow cover within and between the habitat types at bimonthly snow stations. Snow data were also obtained in association with animal activity in the various vegetation sites.

Aerial transects, using a Cessna 180 and Piper PA-12, were flown over the intensive study area monthly during the first winter and bimonthly during the second winter. The east-west transects were at three-mile intervals and flown at a height of 500 to 700 feet. I used the data obtained to determine group movements and to assess the amount of time spent by the caribou in various habitats.

I located the caribou groups by aerial reconnaissance. I then carried out ground reconnaissance on the most accessible group with the use of snowmobile and snowshoes. Since nival characteristics can change rapidly, fairly close contact with the caribou group was necessary during which time I recorded animal activity and snow conditions.

The snow kit used during the first winter was modified from the National Research Council of Canada snow instruments and although bulky it had advantages such as instant reading large spring scale, hardness gauges with screw-on face plates, 500 cc density cutters to simplify density calculations and rapid reading thermometers. These features of the instruments reduced the amount of time per snow station in comparison to the time taken when using the standard NRC kit. During the second field season I was fortunate in being able to use a new Swedish 1000 cc density cutter which, coupled with hand held spring scales, reduced both the size of the snow kit and length of time in taking density readings.

At each snow station, I recorded the location, date, habitat type, weather conditions and animal activity present. I exposed a vertical snow profile and measured air and pukak temperatures. Other measurements taken were the total snow thickness, and the thickness, hardness, density, snow crystal type and size of each of the layers exposed by the profile. Substrate observation added detail to the habitat type and provided an index of the quality and quantity of food available to the woodland caribou.

RESULTS

For the purpose of this paper, I will limit the results to data gathered within the intensive study area. A major portion of the results will deal with the comparison of woodland caribou activity during the first field season, a winter with below average snowfall, and the second winter, one with above average snowfall (Fig. 2).

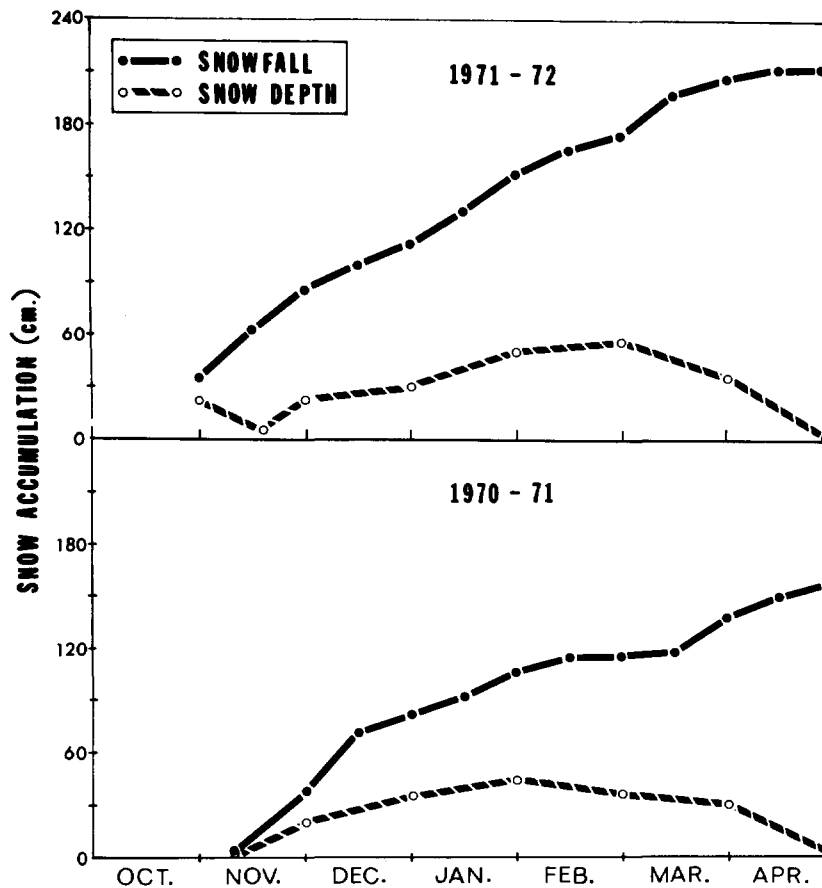


Fig. 2.—Comparison of two successive winters of data on snowfall and snow depth recorded at the meteorological station in Bissett, Manitoba.

I spent most of my time the first autumn becoming familiar with the intensive study area. My winter schedule began with the first permanent snow cover on November 10, 1970. A large amount of time was spent in creating a network of trails in an attempt to maintain contact with the caribou groups and to link the various outcamps. Due to the rugged terrain, the easiest access routes were in open tamarack and black spruce bogs which at this time of the year were also utilized to a large extent by the caribou. I observed extensive feeding on arboreal lichens in these bogs during November and December of 1970. The caribou spend as much as 70 per cent of their daily activity periods in these bogs even though the snow cover was close to 10 cm thicker there than in the ridge areas or on the lakes (Fig. 3).

Such frequenting of bogs and major feeding on tree lichens existed until January 20, 1971 when the first high winds of the winter, up to 20 mph (32 km/hr), created za-es-chā (wind-drift crusts) in all major open and semi-open bogs. The immediate result was a shift in

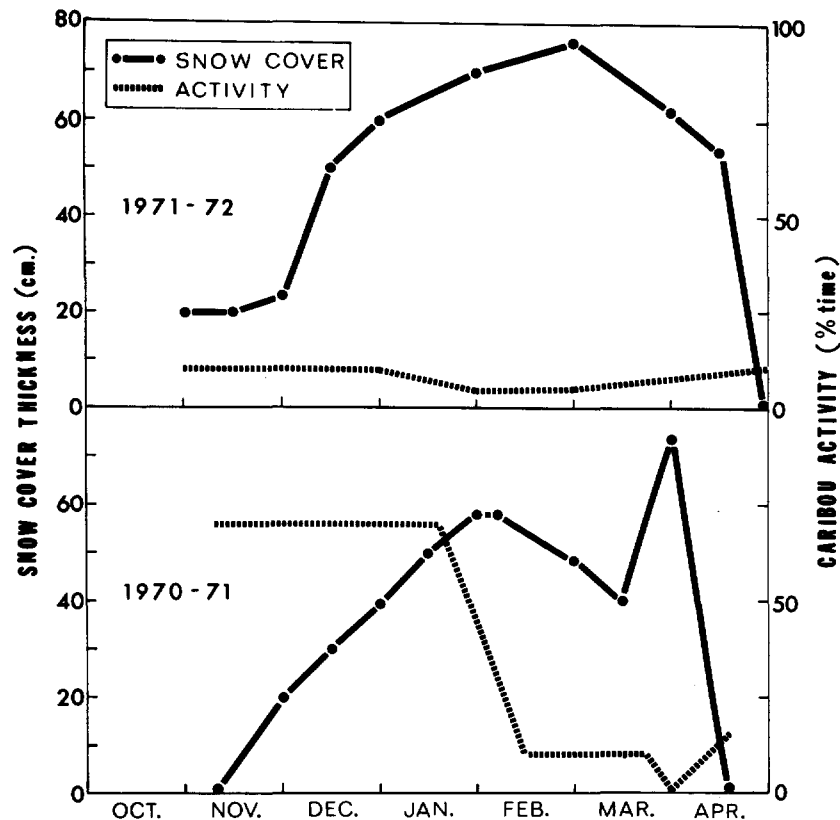


Fig. 3.—Comparison of two successive winters of data on snow cover thickness and caribou activity in open bogs in the intensive study area.

caribou activity from the open bogs to jackpine rock ridges. The bog snow cover remained at 50 to 55 cm in thickness but the maximum hardness changed from 80 g/cm² to 500 g/cm² with the mean being 164 g/cm². The maximum density changed from .10 to .26 with a mean density of .19. The ridge snow was now approximately 15 cm less in thickness but now became a conglomerate of various sized blobs with hardnesses of 100 g/cm² and densities of up to .37 in a soft snow matrix averaging 20 g/cm² in hardness and .17 in density. Movement in this conglomerate snow type was awkward and energy-consuming.

Ground lichens now became the major food source and 75-90 per cent of all caribou activity took place on these ridges from mid-January to mid-March (Fig. 4). Movement across bogs and lakes made up the remainder of their activity. I noted that when the caribou crossed bogs they chose the shortest route between ridges and generally traveled in single file, regardless of the number of individuals in the group. While crossing lakes, the groups would spend short periods of time digging for slush where it was available.

During the month of March, 1971, I observed frequent pawing for slush on lake edges or creek mouth slush-holes; such activity often was associated with feeding on *Carex* spp. along the nearby marshy shores (Fig. 5). Major feeding on ground lichens now shifted from protected jackpine areas to the exposed south or southeast facing slopes of rocky lakeshores where only limited cratering was necessary to feed on partially exposed lichens. Although the amount of lichen available in these areas is approximately 25 per cent of that found up on the ridges, much less energy would be consumed in feeding since the snow was 15 to 25 cm less in depth (Davydov, 1963).

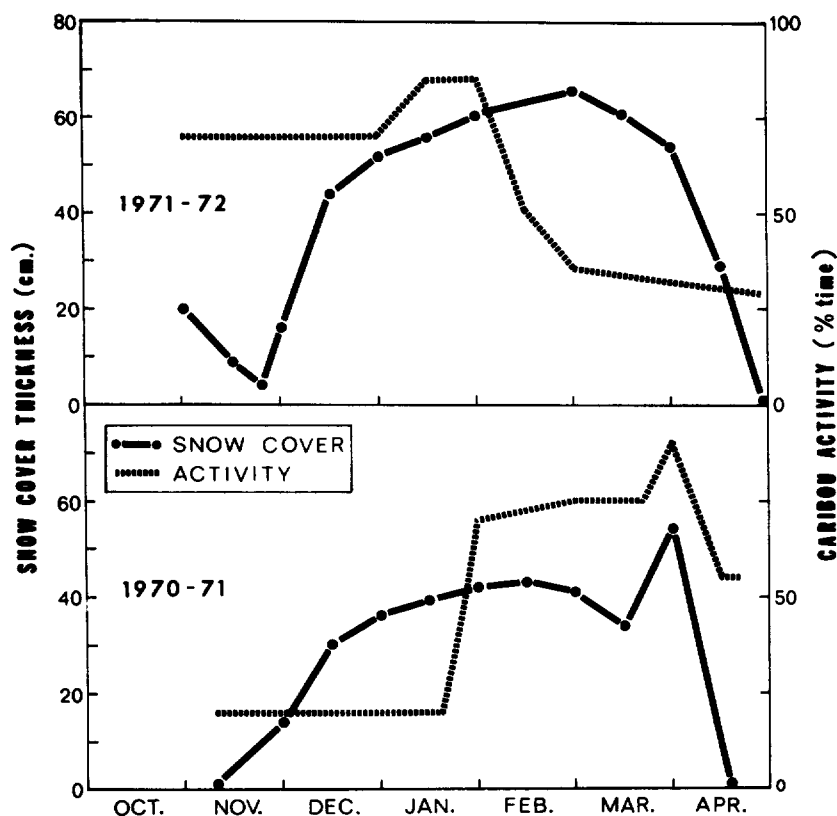


Fig. 4.—Comparison of two successive winters of data on snow cover thickness and caribou activity on jackpine (*Pinus divaricata*) rock ridges in the intensive study area.

By mid-March, I noted that single individuals and pairs were beginning to split off from the various groups, but this was halted at the end of March by a snowfall of 21 cm. All major caribou movement stopped. I maintained contact with a group of 18 individuals which had been feeding on a rock ridge 1.1 km² surrounded by open bog. They did not move out of this small area for six days until thawing and settling reduced the bog snow cover from 78 cm to 43 cm, which permitted ease in travel. During the time spent on this ridge, compacted trails were used by the caribou in order to move back and forth along the ridge top while feeding on ground lichens and, when available, tree lichens. I observed very little grazing on low shrubs, such as *Vaccinium* spp. and *Ledum* spp. Thawing conditions in the forested areas and slush conditions on the lakes ended winter field work on April 6, 1971.

I began the second winter of field work with the first permanent snowfall on October 31, 1971. The 23 cm of snow deposited by the storm remained only in vegetation types which insulated it from substrate warmth but on rocky ridges it melted entirely. Heavy snowfall and high winds created conditions during November and December which restricted caribou activity almost entirely to small areas on jackpine rock ridges and adjacent lakes which had little snow cover due to late freeze-up. I found ground reconnaissance almost impossible during December and January due to the severe nival conditions which the caribou were also experiencing.

By the end of January, the snow thickness in the bogs had increased to 70 cm and in many areas the early snow had insulated the bog so well that the substrate remained

unfrozen and very soft. The 57 cm average thickness of ridge snow cover was much more conducive to caribou activity. This restriction of animals to ridges was even more apparent as the bog snow thickness approached 80 cm by the end of February. The snow cover in the jackpine-lichen areas increased to 65 and 70 cm in thickness, maintaining an obvious thickness difference between the two habitats. The snow thickness in jackpine-lichen areas now approximated the caribou snow thickness threshold while bog snow thickness exceeded the threshold value by approximately 15 cm. The maximum densities in the two habitat types were between 0.20 and 0.25 but an early windcrust hardness in the bogs was 400 g/cm² as compared to the maximum hardness of 80 g/cm² in jackpine stands.

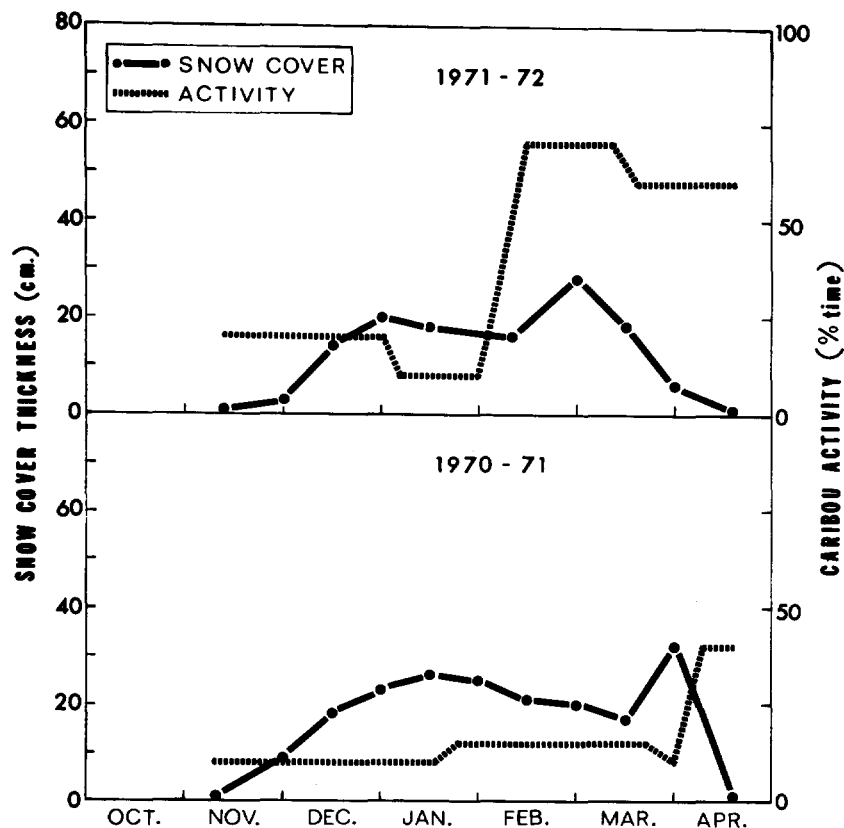


Fig. 5.—Comparison of two successive winters of data on snow cover thickness and caribou activity on lakes in the intensive study area.

By the end of February and until the end of the snow season almost all caribou activity was on jackpine ridges and lakes with as much as 70 per cent of their time spent on small lakes. Heavy accumulations of snow during January and February caused extensive slush which froze during periods of intense cold below -40° C. The slush freezing near the snow surface reduced the snow cover on the lakes from 25 cm in early winter to 10 cm by mid-March.

There was no slush formation in March but I did note that groups of caribou would frequent the locations where slush had formed the previous spring. These slush locations are in areas where the caribou are normally found at this time of year. Caribou groups of two and 22 individuals remained on these small lake-rock ridge systems during March and April, feeding on ground lichens made available by the thawing of old feeding craters along south

facing slopes. Along the lake shores, arboreal lichens were utilized wherever they were available, generally on beaver-killed jackpine and on windthrows and qali breaks of the previous winter.

Disbanding of the caribou groups did not begin until the first week of April, three weeks later than the previous spring. By mid-April the largest group to be found in the area was one of seven individuals.

The number of individuals in the intensive study area was 35 as of March, 1971 and 37 as of March, 1972. This resident band consisted of five groups in the first winter, an average of seven individuals per group as compared to four groups with an average of 9.25 individuals per group during the second winter.

The winter range occupied by the caribou consisted of a 235 km² area made up of three major habitat types: open tamarack or black spruce bog, intermediate to mature jackpine rock ridges and many small lakes. The open bogs comprised 26.8 per cent of the winter range and produced the greatest amount of arboreal lichen, 45.5 per cent of the area was composed of jackpine stands, the major source of ground lichens. Lakes formed only 10 per cent of the total habitat but were important as travel routes and loafing areas especially when deep slush was absent and the snow cover in adjacent areas was greater than 60-65 cm. The remainder of the area was closed spruce bog and ridge stands, not caribou habitat.

Association between any of these groups of caribou and the other ungulates of the area was almost non-existent due to ecological segregation.

DISCUSSION

Vegetation and weather interact intimately to produce a snow cover which exerts a great influence on caribou winter ecology. The woodland caribou are found first in vegetationally suitable areas and then react to the various nival conditions within this winter range (Edwards, 1956). The winter range in the intensive study site was surrounded by vegetation types unsuitable as food sources and exhibited snow conditions beyond the nival threshold of the caribou. Their winter habitat did not vary in area during two winters which exhibited the two extremes in snow cover thickness.

Investigations of barren ground caribou by Scotter (1964: 56) indicated that "Arboreal lichens are apparently important sources of forage during critical periods...". My own results agree with the fact that arboreal lichens are an important food source but during periods of favorable nival conditions. During critical periods use shifted to ground lichens. This response was evident during both winters of field work.

The woodland caribou certainly possess morphological adaptations to this boreal environment. Based on observations of their behavioral responses to snow factors, which exist during one-half of their annual activity, they should be regarded as chionophiles as classified by Formozov (1946). This also concurs with Pruitt's (1959) classification of barren ground caribou.

Based on the results of this project, the threshold of sensitivity to snow depth of woodland caribou in this area is approximately 65 cm. This is greater than the 60 cm snow depth threshold of barren ground caribou as described by Pruitt (1959) and further substantiated by Henshaw (1968). It is also greater than the 50-60 cm critical limit of wild reindeer in the U.S.S.R. as described by Formozov (1946) and Nasimovich (1955).

Snow hardness, especially crusting conditions higher than 25 cm from the substrate, had the greatest effect on caribou activity during the two winter study periods. The caribou would prefer to enter areas of snow above their thickness threshold of 65 cm rather than be subjected to vesicular ice or snow crusts of hardness greater than 400 g/cm². This response was manifested during the second winter of study when severe snow conditions caused a

reduction in the area of their winter range that they utilized in their search for food. This behavioral response resulted in a greater aggregation of caribou in these nival suitable areas. Although the total band size was similar during both winters, there were fewer and larger groups during the second winter.

The presence of qali (snow retained on the trees) provides a general index of the existing nival conditions. Early winter qali formation indicated a soft, light snow cover over the entire winter range and a much thinner snow cover in forested, ground lichen productive areas. It also indicated favorable conditions in major arboreal lichen productive bogs. Secondary qali formation during successive periods of the winter indicate only the maintenance of thinner snow cover in forested areas. The absence of qali at any time during the winter is an indication of high winds, the major factor in creating (1) crusting in bog areas; (2) qali blob formation in forest areas; (3) thinner, hard lake snow cover; (4) extensive snow shadow effects.

CONCLUSIONS

- (1) Woodland caribou in southeast Manitoba require winter habitat which provides a spectrum of snow accumulation types caused by the interdigitation of several vegetation types and small lakes.
- (2) In a winter of thin snow cover, the groups making up the resident band in the intensive study area were smaller and fed more extensively over their winter range. Conversely, in a winter of thick snow cover, there was a greater aggregation of individuals into larger groups which fed intensively in small areas of their winter range.
- (3) During early winter, the caribou feed intensively on arboreal lichens under windless, thin snow cover conditions but if the reverse conditions exist, intensive feeding shifts to ground lichens often found on ridge areas. During the remainder of the snow period major feeding is on intermediate and mature jackpine ridges where the snow cover is softer due to the lack of wind crusts and thinner due to qali formation.
- (4) The two most important vegetation types in this area are open tamarack bogs and mature jackpine rock ridges, the former for arboreal lichen production and the latter for the production of ground lichens. Ground lichens (*Cladonia* spp.) are more important than tree lichens as winter food items since hard and deep snow conditions limit the utilization of major tree lichen areas during 60 per cent of the snow season.
- (5) Major utilization of lakes occurs only during periods of thick snow cover when the nival conditions on lakes are more conducive to loafing and travel than adjacent forest types. Slush formation, a result of this thick snow cover, also restricts the utilization of these lakes.
- (6) Orientation of the terrain to prevailing winds is important in producing snow drift effects: areas where the caribou's energy consumed/activity ratio should be low. These areas are generally characterized by a thinner or softer snow cover.
- (7) The threshold of sensitivity to nival conditions appears to be higher than that of barren ground caribou. The threshold of thickness sensitivity appears to be approximately 65 cm. The hardness threshold appears to be approximately 80 g/cm² for jackpine ridge areas, 400 g/cm² for open bog areas and 700 g/cm² on lakes. The density threshold appears to be approximately .20 to .36 for jackpine ridge areas, .18 to .24 for bog areas and .25 to .33 for lakes. These thresholds vary with the thickness of the snow cover in the three types and height of hard, dense layers above the substrate.

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THE IMPACT OF REINDEER GRAZING ON SELECTED
AREAS OF WINTER RANGE IN SUCCESSIVE YEARS,
MACKENZIE DELTA AREA, N.W.T., CANADA

Julian T. Inglis
Department of Biology
Carleton University
Ottawa 1, Ontario
Canada

ABSTRACT— Five 7.3m x 7.3m exclosures were constructed on winter range following grazing. All feeding craters within the sites were permanently marked. The exclosures were later examined, disassembled and the crater outlines super-imposed on vegetation maps. The procedure was repeated on these sites the following year. The number, size and vegetation of the craters was similar in both years. The area of the site cratered was related to vegetation type and was modified in one case by snow conditions. Lichens composed 75 per cent of the vegetation and included *Cladonia mitis*, *C. rangiferina*, *Cetraria nivalis* and *Peltigera aphthosa*. An average of 41 per cent of the sites was cratered during the two years and of the areas cratered the first year, 26 per cent were reutilized. Maximum values of 51 per cent and 39 per cent respectively were recorded. It is concluded that lichens compose a major part of the mid-winter diet and that, on heavily cratered sites, most of the available forage is utilized in two years of intensive grazing. Differential snow accumulation, in successive years, may reduce the impact of grazing on sheltered sites.

Range studies have been carried out on the Reindeer Grazing Reserve on several occasions (Porsild, 1929; Cody, 1964; Scotter, 1968; Lambert, 1969). These studies have been primarily concerned with the overall condition and trend of the range and its classification for seasonal use. General recommendations for range management have stemmed from this work and the seasonal movements of the reindeer herd within the Reserve are well established. Estimates of carrying capacity range from 85,000 (Porsild, 1929) to 30,000 (Scotter, 1968). Scotter (1969) points out, however, that these estimates are based on the whole 45,600 km² Reserve. Currently less than one-fourth of the range is in use, and significant expansion seems unlikely in the near future.

Before revised and meaningful estimates of carrying capacity can be applied to the present range, an understanding of reindeer — range relationships in critical areas is essential. The Canadian Wildlife Service initiated a program of range research in 1968 which should result in an accurate prediction of future range requirements.

The object of the present study was to assess the impact of reindeer grazing on selected areas of winter range following two years of intensive use. The winter range was chosen for the work as it forms both the economic and biological basis for the success of the Canada Reindeer Project.

DESCRIPTION OF STUDY AREA

The study area comprises a 1,200 km² section of the Reindeer Grazing Reserve and is located 40 km northeast of Inuvik, N.W.T., Canada. This area forms the core of the present winter range and falls within the forest – tundra transition zone. The physiography and vegetation zones have been described by Mackay (1963). Lambert (1972) recognizes nine major vegetation types from a mosaic of plant communities within the study area. Those types associated with the presence of extensive lichen mats, such as open spruce woodland, dwarf birch – heath, and lichen – heath, are particularly important components of reindeer winter range.

Approximately 2,000 reindeer grazed in the study area in both winters, and remained on the winter range from December to late March. Selected climatic data are presented for Inuvik in Table 1. The data indicate that conditions were typical for this station during the winter of 1969. In 1970, however, the depth of snow on the ground from January to March was lower than the mean.

METHODS

Grazing studies were undertaken in the study area from 12-20 March 1969 and 20 January to 12 February 1970. A group of reindeer on the periphery of the herd was selected for detailed study on five occasions during the first period. A suitable reference marker, such as a tree or shrub, was chosen and feeding activity closely monitored once the group had passed this point. Observations were continued until all animals had left the area. A 7.3 m x 7.3 m area was laid out from the reference point and the site fenced to minimize further disturbance. All feeding craters, walking trails and resting sites were delimited using a combination of wooden tripods and short metal spikes. Snow depths were recorded at each site and a detailed photographic record was made.

Five exclosures were completed on three main vegetation types: dwarf birch – heath – lichen, (E 3, E 5), open spruce – lichen woodland, (E 1, E 2) and a lichen – heath dominated ice wedge polygon site (E 4). A sixth site (E 6) was added the following winter on a well wooded spruce – lichen site.

The distribution of feeding craters, and their relationship to vegetation and microtopography, was assessed by establishing a grid of 36 contiguous quadrats in each site and plotting crater outlines and vegetation within each quadrat to scale. The area of each site utilized for grazing was measured directly from the resulting map (Fig. 1).

Following analysis, the exclosures were dismantled and the crater outlines permanently marked with colored spikes. All surplus fencing materials and tripods were removed. The reindeer were herded in the study area during the second period and were allowed to graze, under observation, through each of the exclosure sites. The procedures for marking and mapping the feeding craters were repeated as before.

RESULTS

The broad variation in average size and number of feeding craters between the sites in 1969 is shown in Table 2. The number of craters was consistent for five of the sites in 1970, while average size varied. For three of the exclosures (E 1, E 3, E 4) the results were very similar in both years. On a sheltered spruce – lichen site (E 2), however, substantially more craters were excavated during the second winter than the first, while average crater size on the site remained constant. Average crater size in each winter was almost identical (1.00 m² in 1969; 1.01 m² in 1970). The smaller craters of E 5 (1969) reflect the mapping technique

TABLE 1.--Selected climatic data for Inuvik, N.W.T.

	Monthly mean temperatures (°C)					Snow on ground (cm)				
	1957-71	S.D.	1968	1969	1970	1957-71	S.D.	1968	1969	1970
January	-31.1	3.5	-28.4	-32.7	-31.5	56.8	15.6	76.2	43.2	35.6
February	-29.8	4.1	-31.1	-31.7	-28.7	60.0	11.4	71.1	53.3	40.6
March	-24.7	3.5	-20.7	-24.7	-24.1	65.5	12.5	71.1	61.0	43.2
November	-21.6	2.6	-22.7	-24.9	-17.7	33.6	16.1	33.0	20.3	30.5
December	-26.9	3.9	-29.9	-20.4	-29.5	46.6	14.0	43.2	38.1	45.7

initially employed on this site and are not included in the above calculations. Photographs of the site from 1969 indicate that the feeding sites were similar in size to those of 1970.

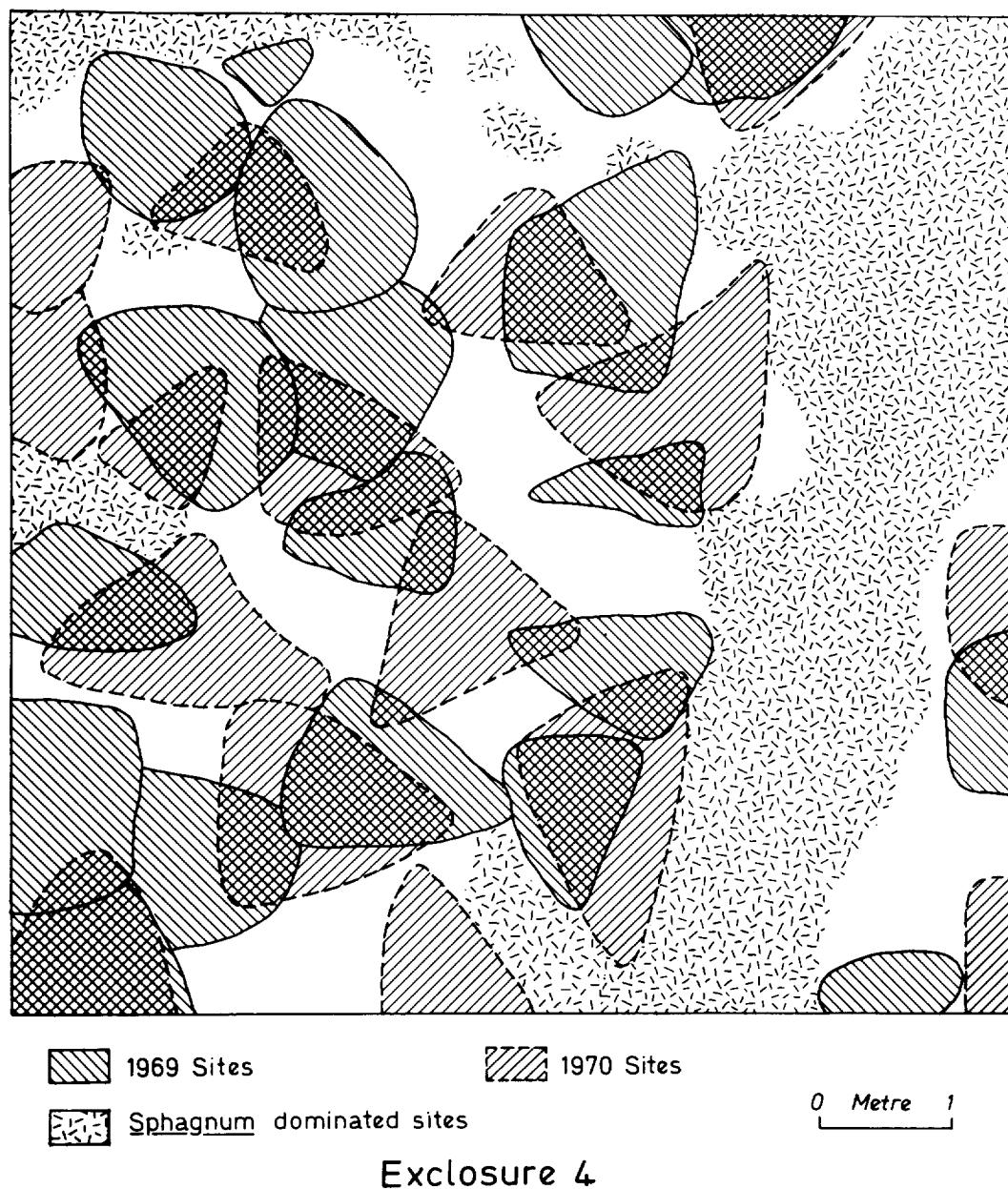


Fig. 1.—Reindeer grazing patterns on a lichen dominated ice wedge polygon.

The area of each site utilized for feeding activities is presented in Table 3. Average values of 22 per cent (1969) and 26 per cent (1970) were recorded. The second winter's data is consistent with that of the first with the exception of E 2 and E 5 as noted above. The results from five of the sites (E 2 — E 6) in 1970 are remarkably uniform with a range of 6 per cent. Most intensive utilization occurred on the lichen — heath site and was generally higher on open sites than on those located in treed areas.

TABLE 2.--The number and average area of reindeer feeding craters on six selected sites.

Site	1969		1970	
	Number of craters	Average crater area (m ²)	Number of craters	Average crater area (m ²)
E 1	11	0.83	9	0.83
E 2	9	0.88	17	0.96
E 3	13	1.32	15	1.09
E 4	19	1.03	16	1.16
E 5	16	0.62	15	1.16
E 6	--	----	17	0.83

The reindeer appeared to graze and move at will through all of the sites with the exception of E 2, in 1969, when grazing was sporadic and the animals were restricted to narrow trails through the site. In 1970, however, the herd moved through this site in a broad front and grazed the area heavily (Table 3). Snow depths were consistently greater in 1969 than in 1970 on all exclosure sites (Table 1). While values did not generally exceed 40 cm in either year, snow depths ranging from 35-78 cm were recorded in E 2 in 1969 and were responsible for the marked decrease in activity compared with 1970. Pruitt (1959) stated that the snow thickness threshold for caribou appeared to be approximately 60 cm.

TABLE 3.--Per cent utilization of six selected sites for winter feeding activities.

Site	Area cratered		Total area	Crater overlap	Area utilized
	1969	1970			
E 1	17	12	29	1	28
E 2	14	28	42	4	38
E 3	25	28	53	6	47
E 4	34	30	62	13	51
E 5	19	31	50	7	43
E 6	--	25	25	--	25

Many of the areas cratered in 1969 were reutilized in 1970, and these contributed substantially to the area utilized during the second winter. In general, the amount of overlap in feeding craters increased with the proportion of the exclosure utilized. This is particularly evident in E 4 where 44 per cent of the area cratered in 1970 had been grazed the previous winter (see Fig. 1). An average value of 26 per cent was obtained for the five exclosures.

The importance of lichens in the mid-winter diet of reindeer was confirmed following analysis of feeding crater vegetation. *Cladonia mitis*, *C. rangiferina* and *Cetraria nivalis* composed over 75 per cent of the vegetation. *Peltigera aphthosa* occurred in three exclosures and was very abundant in the feeding sites of E 3. Scotter (1967) found that *Peltigera* spp. were abundant in the rumens of 20 barren ground caribou (*Rangifer tarandus groenlandicus*) from northern Canada. *Betula glandulosa*, *Vaccinium vitis-idaea* and *Ledum decumbens* were constant components of the cratered areas, and a frequency analysis of the

contiguous quadrats reflected their ubiquitous nature.

While dwarf birch, ericoids and other vascular plants were evidently grazed, the distribution of the feeding sites was closely related to the distribution and abundance of lichens. In E 4, for example (Fig. 1) the lichen mat was heavily grazed to the edge of areas dominated by *Sphagnum* spp. A similar pattern could be identified at each site.

Disturbance to the vegetation was minimal following one year of grazing. Following the second winter, however, the impact on the vegetation was pronounced in all sites. Lichens were fragmented and scattered and were completely removed from the raised polygonal ridges of E 4.

DISCUSSION

These results correspond closely with those from similar studies in the U.S.S.R. Sablina (1960) estimated that from 18 per cent to 23 per cent of an upland lichen moor in Karelia was utilized in one winter by a small reindeer herd. Makhaeva (1961), using 10 m x 10 m study plots on old reindeer feeding grounds, demonstrated utilization levels of up to 41.8 per cent on a pine — lichen forest site. In both these studies, the relationship between the degree of utilization of a site and vegetation type was stressed and was directly related to lichen cover. Makhaeva concluded that in the Murmansk Oblast, approximately one-half to one-third of the available lichen was utilized by reindeer. A comparable level was found in the present study as seen, for example, in Figure 1 where almost all of the lichen mat (unshaded) has been utilized for feeding activities. The lower levels in some sites may reflect the lower availability of the lichens due to hummocky microtopography and extensive shrub growth. Precise values for the proportion of each site which is unsuitable for grazing are difficult to assess.

The feeding patterns correspond closely in both years except where secondarily modified by snow cover. Differential accumulations of snow in successive years may serve to lessen the impact of grazing on sheltered sites. Where snow is not limiting however, the impact of repeated grazing on lichen rich sites may be severe. Overgrazing has occurred on an Alaskan caribou range which had been grazed for three years (Pegau, 1972).

The evidence from this study indicates that serious overgrazing may result on areas intensively used by the reindeer herd for more than two consecutive years.

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RANGE USE AND FOOD SELECTIVITY BY WILD REINDEER IN SOUTHERN NORWAY

Terje Skogland
Norwegian State Game Research Institute/Norwegian IBP
Tundra Biome Studies
Trondheim, Norway

ABSTRACT—Year-round direct ground observations are in progress to determine the portion of active time that reindeer spend feeding in different vegetation types within the arctic-alpine ecosystem. Reindeer ranged through nine phytosociological plant communities during their annual cycle of movement in 1971. *Cladonia* heaths received 60 per cent of the annual use and approximately 95 per cent of the December-April use. *Deschampsia* dominated grass meadows received 14 per cent of the annual use and approximately 50 per cent of the early spring and late fall use. *Salix* and herb-dominated snowbeds received 22.5 per cent of the annual use and approximately 95 per cent of the early and late summer use. Bogs received 3 per cent of the annual use and approximately 45 per cent of the midsummer use. Grazing succession followed a gradient of altitude, and aspect related to snow conditions and phenology of key *Salix* and *Deschampsia* spp. Concentration of feeding on the relatively level and low midwinter range (1,100 m altitude), changed towards south-facing slopes and higher altitudes (1,400 m altitude) during late winter and the early spring snowmelt. A reversed movement downward toward wet areas (1,200 m altitude) relates to emergence of dwarf *Salices* in bogs and along riverbanks. In late summer reindeer followed the spring growth of north-facing snowbeds upward toward the edge of glaciers (1,450 m altitude). Toward winter reindeer descended eastward to their winter range. Observations of feeding rates were used as an index of food intake. Statistical analysis revealed significant differences in eating rate related to slope and aspect in late winter and spring. The X^2 test showed no significant differences in eating rates between age and sex groups. Between lactating females and other herd members a 't' test showed significant differences at post-calving.

METHOD

Year-round field observations of wild reindeer herds on the Hardangervidda arctic-alpine plateau of 7,500 km² and lying at 60° N were done in 1971.

The distribution pattern of alpine vegetation in the Scandinavian mountains has been studied by phytosociological methods by several workers; in Norway particularly by Nordhagen (1943), Dahl (1956) and Gjaerevoll (1956). The plant sociological system applied by these workers was found useful for identifying the grazing pattern of the wild herds in the alpine tundra of Hardangervidda. Successive 10 minute observations on herd grazing were done throughout the daylight period. Plant alliance, plant species, slope, aspect and altitude of the grazing were noted. Feeding behavior in relation to environmental and social factors was studied by timing randomly selected deer with a stopwatch. Thus eating rates within the active periods of the herds were determined. Eating rate is defined as the percentage of active time a deer ingests. A total of 2,400 eating rate minutes were gathered

in 1971.

Food selection was studied by observations of grazing in relation to phenology and nutrient level of selected food plants. Data on range use patterns and individual deer performance were also gathered. Data on the food habits of the Hardangervidda population has been obtained from rumen samples of sacrificed and esophageal fistulated deer on the range. These results have been published as progress reports elsewhere (Gaare, Skogland and Thomson, 1970; Gaare and Skogland, 1971). Studies of the snow as an environmental influence on food selection and feeding behavior are in progress, but are as yet too premature for inclusion in this report. Laboratory analyses of the nutrient level of hand picked food plants are not yet available. With most of the present work still under way no definitive conclusions on grazing performance can be drawn.

RESULTS

Habitat

Plant communities.—During their annual cycle of movement the wild reindeer herds roam a wide variety of range types and plant communities within the alpine environment. Most vegetation receives some use. The reindeer pattern of feeding is very extensive; nibbling at the ground as they move, they also aggregate in spots of feeding interest and disperse again when food is abundant and widespread. Distances moved each day vary with season and external factors such as weather and harassment by insects or predators.

By making continuous observations a record of the annual range use pattern was established. During 1971 five different range types including nine different plant alliances received 100 per cent of the annual use.

Table 1 shows the annual distribution of range utilization. The winter range, the dry lichen heaths with *Cladonia* spp. predominating, received greatest use. After snow melt utilization on the summer range was distributed over several types. Changes in the range use pattern were seasonally related and were tied in with snow cover, snow melt and the emergence of green growth. Figure 1 shows how the reindeer use was distributed through 1971 on different plant alliances. After the first snowfalls in late October a progressively larger use of the continental lichen heaths belonging to the *Arctostaphylio* — *Cetrarion nivalis* (Dahl, 1956) alliance began. Grasses like *Deschampsia flexuosa* in the *Phyllodoce Vaccinion myrtilli* (Dahl, 1956) alliance were eaten until they became unavailable toward the end of the year by the increasing snow pack. In early winter when the snow pack is still relatively shallow *Betula nana* — *Cladonia alpestris* associations in the lower part of the *Arctostaphylio* — *Cetrarion nivalis* (Dahl, 1956) alliance received most use. Toward late winter snow pack increase and the wind hardening of the snow confined feeding to the most exposed ridges where *Empetrum hermaphroditum* — *Cetraria nivalis* associations are most prevalent.

As solar radiation increases in late April, the snow cover recedes on south-facing slopes and by calving time in late May exposed ridges of the calciphile *Kobresio* — *Dryadion* (Nordhagen, 1943) alliance, with *K. myosuroides* on the high calving grounds, receive limited use. The *Nardo* — *Caricion bigelowii* (Nordhagen, 1936) alliance, with *Carex bigelowii* in the lower parts of the snow-free south-facing slopes, receives an increasing use during the calving and post calving period. Dry tufts of *Juncus trifidus* were free of snow early and received use before the emergence of green growth. The first green shoots of the dwarf shrub *Salix herbacea* within the *Cassiopo* — *Salicion herbacea* (Nordhagen, 1936) alliance appeared at the beginning of June and received a progressively larger proportion of the grazing through early summer. Toward midsummer riverbanks with the *Lactucion alpina*

TABLE 1.--Annual distribution of reindeer grazing time per range type.

Range types	Phytosociological alliances	% range utilization
Lichen dry heaths	<i>Arctostaphylion</i> - <i>Cetrarion nivalis</i> (Dahl-56)	
	<i>Kobresio</i> - <i>Dryadion</i> (Nordh.-43)	60.0
Grassy meadows	<i>Phyllodoce</i> - <i>Vaccinium myrtilli</i> (Dahl-56)	
	<i>Nardo</i> - <i>Caricion bigelowii</i> (Nordh.-36)	14.5
Dwarf-shrubs snowbeds	<i>Cassiope</i> - <i>Salicion herbacea</i> (Nordh.-36)	
	<i>Polarion</i> (Du Rietz-42)	11.8
Herb snowbeds	<i>Ranunculo</i> - <i>Oxyrion digynae</i> (Nordh.-36)	
	<i>Lactucion alpinae</i> (Nordh.-43)	10.7
Bogs	<i>Salicion myrsinites</i> (Kalliola-39)	
	<i>Leuco</i> - <i>Scheuchzerion</i> (Nordh.-36)	
	<i>Oxycocco</i> - <i>Empetrion hermaphroditi</i> (Nordh.-36)	3.0
		100.0

(Nordhagen, 1943) alliance and several bogs, notably *Salicion myrsinitis* (Kalliola, 1939), *Leuco-Scheuzherion* (Nordhagen, 1943) and *Oxycocco – Empetrion hermaphroditi* (Nordhagen, 1936), produce green shoots and these are sought by the reindeer. Toward late summer north-facing slopes with late melting snow beds receive more use.

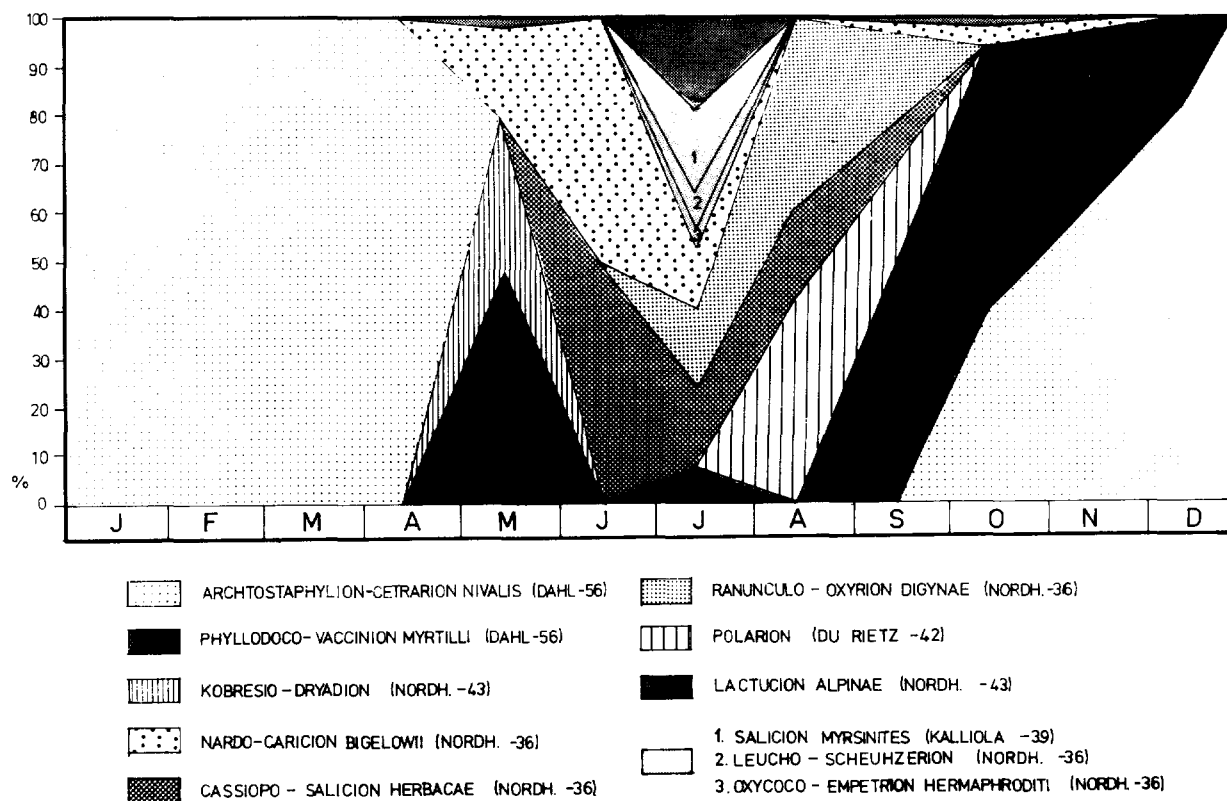


Fig. 1.—Seasonal variation in wild reindeer grazing on vegetation types, Hardangervidda 1971.

The herb rich *Ranunculo – Oxyrion digynae* (Nordhagen, 1936) alliance receives more use as summer progresses. By late August the reindeer are following the emergence of *Cassiope – Salicion herbacea* (Nordhagen, 1936) and *Ranunculo – Oxyrion digynae* (Nordhagen, 1936) alliances behind the retreating snow line on the north-facing slopes up to the edges of the glaciers were *Salix polaris*, in the *Polarion* (Du Rietz, 1942) alliance within the high-alpine zone, are grazed. As summer recedes in September, the reindeer slowly descend eastward toward the winter pastures, and *Deschampsia flexuosa*, within the *Phyllodoco – Vaccinium myrtilli* (Dahl, 1956) alliance, receive most of the early fall use. Thus a yearly grazing cycle has been completed.

Range gradient.—During the annual grazing cycle the reindeer cover a wide gradient of the entire range. The eastern continental winter range is fairly flat with low gently rolling hills. The majority of the terrain varies between 1,000 and 1,200 m above sea level. As the snow pack increases in late winter the reindeer leave this area and move westward toward higher elevations where a larger portion of the habitat is available for grazing on wind swept ridges. Figure 2 shows the variation in range use pattern by altitude. Table 2 shows the

TABLE 2.--Seasonal grazing pattern in relation to topographical features.
 Figures are percentages of monthly observations in 1971.

Month	Slope				Aspect							
	Flat	1-5	6-10	11-40	N	NE	E	SE	S	SW	W	NW
Jan.		22.2	77.8							100		
Feb.												
Mar.	100											
Apr.	28.4	25.9	3.7	1.2	11.1				17.3	33.3	4.9	4.9
May	6.3	71.4		22.2	1.6				42.8	25.4	14.3	9.5
June		100			38.9			61.1				
July	48.9	29.7	21.2		29.7				10.6	2.1		8.9
Aug.		3.7		92.5	51.8	3.7	22.2	18.5	3.7			
Sept.												
Oct.	5.9	39.7	23.5	30.9		8.8	5.9	25.0	38.2	16.2		
Nov.												
Dec.		77.2	22.7					45.4		54.5		

grazing pattern in relation to slope and aspect of the habitat. The gradient of use must be viewed in the light of the above described yearly grazing succession. Slope, aspect and the different vegetational zones in the alpine environment result in a wide spectrum of snow cover and plant growth which the reindeer fully exploit. From the lowest elevations reached in midwinter, about 1,100 m on gentle (6-10°) southwest-facing slopes, they move into progressively higher terrain in late winter and early spring. Here they graze the level ridge tops and southwest-facing slopes in April, and south-facing and southwest-facing slopes in May. In June the reindeer are still ascending as green growth progresses upward and 61.1 per cent of all grazing is on southeast-facing gentle slopes. In late June and early July they move down to an altitude of about 1,275 m to graze the flat bogs. In August 92.5 per cent of all grazing is on steep, north-facing slopes. In October and early winter they again descend to the eastern and lower south- and southwest-facing, gentle slopes.

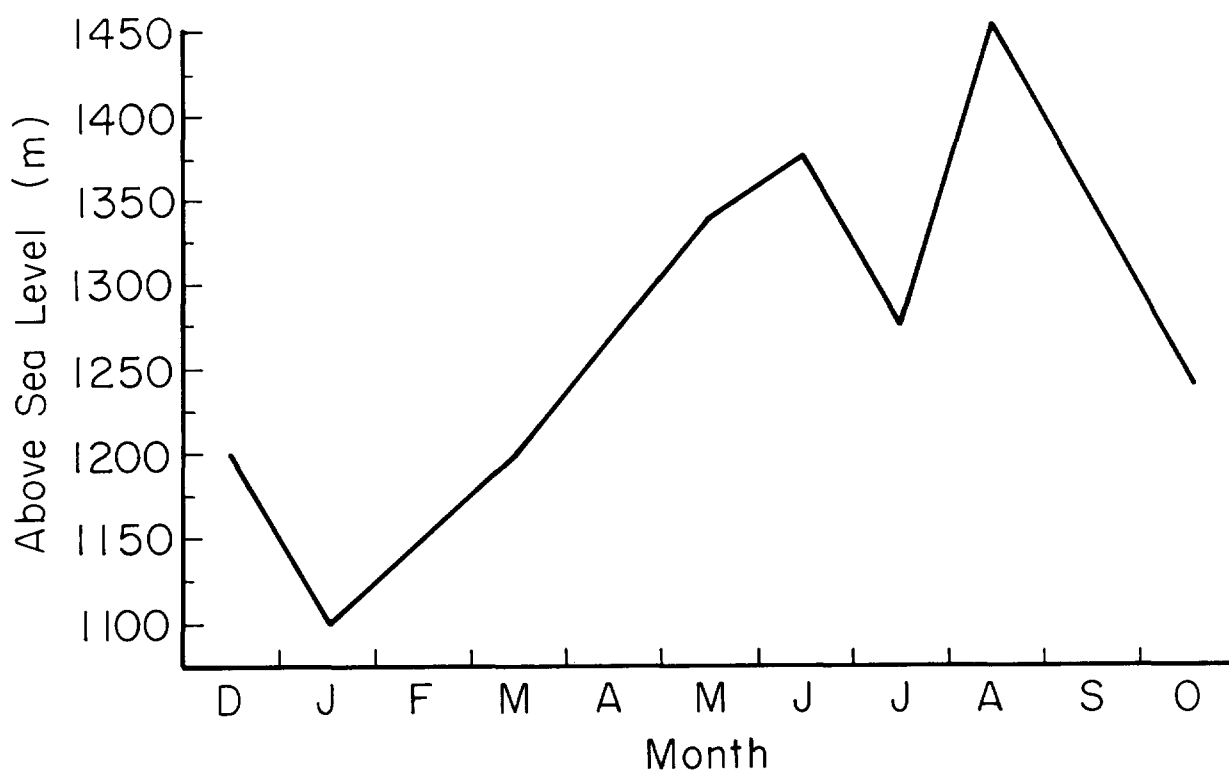


Fig. 2.—Seasonal topographic variation in range use by reindeer at Hardangervidda in 1971. Weighted means of number of observations.

Selectivity.—To gain some understanding of reindeer selectivity, observations of the grazing of plant species were examined in relation to the phenology of plants. Figure 3 shows the results for the most important plant species. Below the grazing observation figure for certain species is shown linearly the phenology of the grazed species from the emergence of visible flowering buds till flowering. Emergence of green shoots often takes place under the snow cover which makes accurate observations on the timing of this difficult and this is not reflected in Figure 3. It is apparent from the data that grazing of the most important

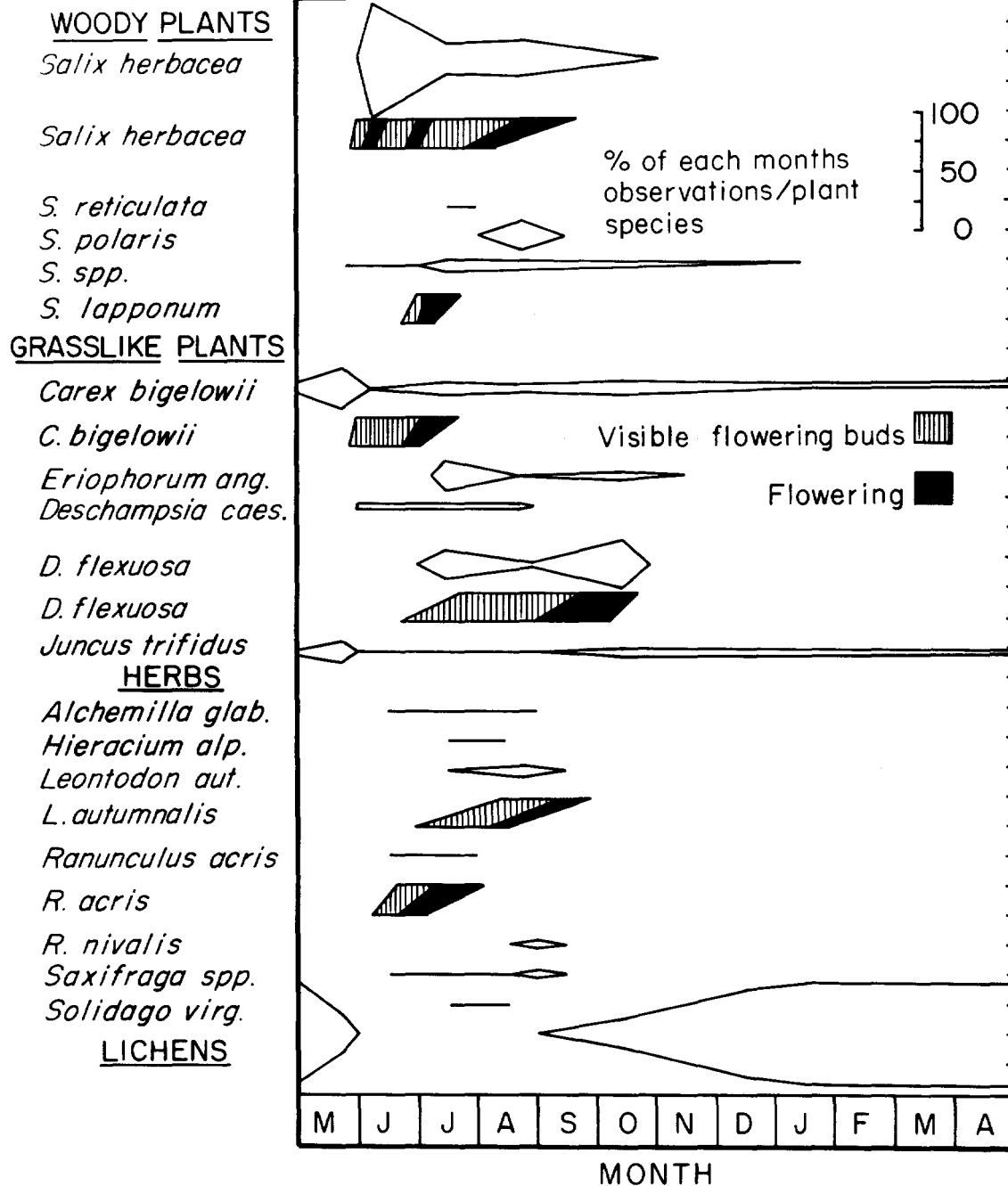


Fig. 3.—Plants observed grazed by reindeer in relation to the growth stages of some plants.

species, *Salix herbacea*, *Carex bigelowii*, *Deschampsia flexuosa*, *Leontodon autumnalis* and *Ranunculus acris*, is closely correlated with visible flowering buds and flowering. No such observations were possible for lichens because no reliable method of determining the periods of active growth of lichens in the field is available. Figure 3 indicates that lichens gain importance as a major food source after the flowering stage of phanerogams.

Feeding behavior.—Feeding behavior is a dynamic process involving learning, specifics of the habitat, nutritional status of the animal, individual preferences and social interactions between herd members. Eating rate expresses the actual time a herd member spends ingesting. The process of ingesting is dependent upon availability of feed and the activity expenditure of obtaining the food.

Figure 4 shows the per cent of reindeer active time spent ingesting throughout the

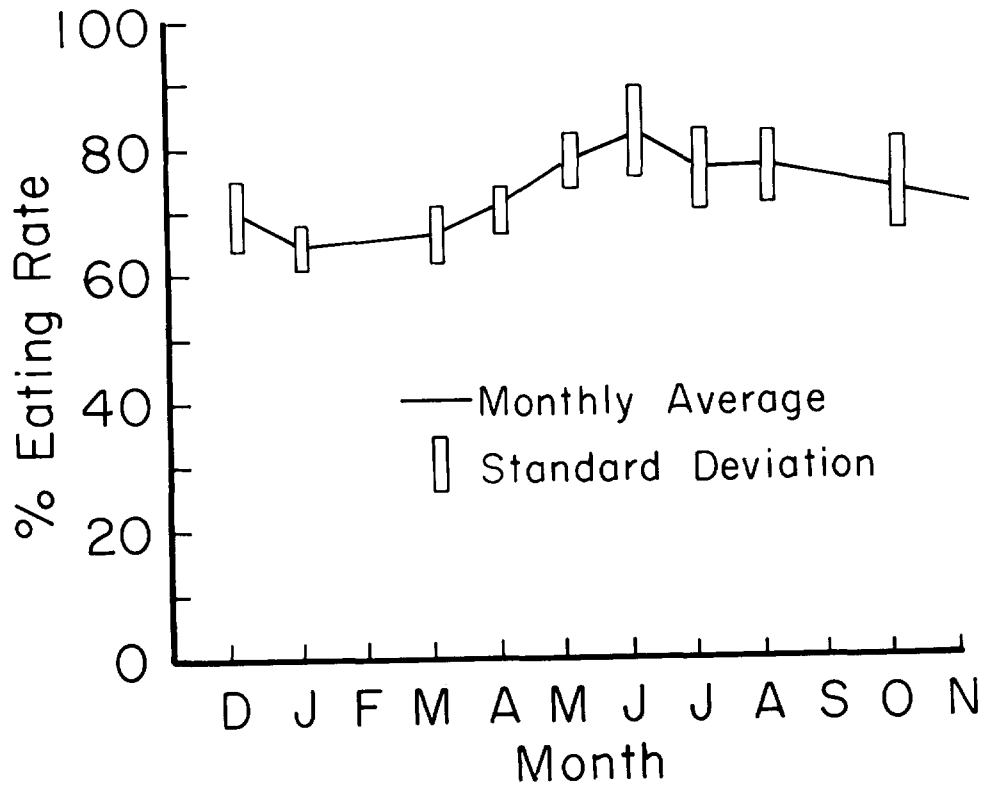


Fig. 4.—Per cent of reindeer active time spent eating. Hardangervidda 1971.

year. The eating rate is lowest in midwinter (63 per cent) and increases to a high (80 per cent) in the post calving period. During summer the eating rate is fairly constant between 75-80 per cent. During fall and early winter the eating rate declines slowly toward the midwinter low. To understand eating rate in terms of the animal energy balance, eating rate must be viewed in relation to the activity pattern of the animals. Thomson (1971) studied the activity pattern of the Hardangervidda population. The graph in Figure 5 shows the seasonal activity pattern that Thomson found in relation to the eating rates. During midwinter eating rate is low while daily activity time is higher. In late winter this is reversed

toward higher eating rates and a lower activity time. The difference is largest at the time of snow melt during calving and post calving. This is a time when the highest physiological drain is laid on females with new born calves. The 't' test showed a significant difference in eating rates between lactating females and other herd members at this time ($P < 0.01$). Fresh green growth is also emerging at this time and the deer have a high eating rate and a lower daily activity time. Tentative data (unpub., Gaare and Skogland, 1972) suggest that 2 g of dry matter is consumed per minute of eating. Thus it seems possible that reindeer can regulate food intake when preferred food is readily available by increasing eating rate and at the same time lowering total activity expenditure. Eating rates were related to environmental and social interaction influences. Snow conditions in midwinter and availability of southwest-facing slopes in late winter had significant effects on eating rates.

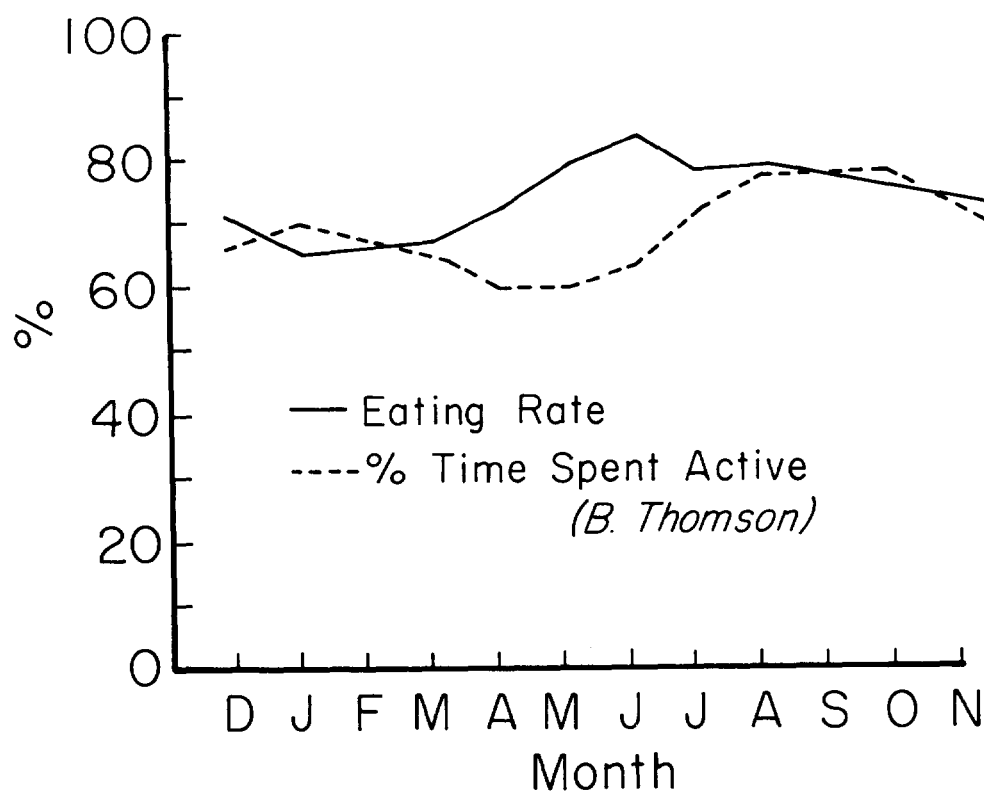


Fig. 5.—Eating rates versus activity time.

Table 3 shows the eating rates for different interacting sex and age groups when the majority of the herd was active and when the majority of the herd was resting. A chi-square test failed to show statistically significant differences in eating rates between sex and age groups in relation to herd activity. It is felt that more data are needed on this point.

TABLE 3.--Test of social group influence on deer eating rates.

Time	Sex/age group	Mean eating rate when the herd is:		Chi-square	P
		Active	Resting		
Jan. 1971	♂ calf	70.96 68.27	60.42 62.35	0.0796	0.8<P<0.7
April 1971	♀ calf	72.88 69.81	79.31 68.57		
Dec. 1971	♂	69.93	64.13	0.191	0.5<P<0.3
	♀	74.15	59.83		
Feb. 1972	♂	57.68	42.43	0.262	0.7<P<0.5
	♀	45.31	51.06		

DISCUSSION

For a species evolved to maintain itself on a low protein, high carbohydrate diet of lichens for about five months of the year, the flush of new green growth in spring must play a vital role in the nutrient balance of the deer. To compensate for the low nutrient diet of winter the evolution of a high degree of feeding selectivity must be expected. Bell (1969) showed how the habitat pressure on different ungulates in Africa occupying the same feeding ground had resulted in the evolution of species specific feeding selectivity which was clearly expressed during the annual grazing succession. This selective force must have a significant effect on the feeding behavior of the species and it would seem that innate reactions determine selection by grazing deer and that these reactions have developed during the evolution of the species (Arnold, 1969).

The reindeer grazing succession during the summer period indicates that they are selecting for the early growth stages of plants within different vegetation types. Klein (1970) found by chemical analyses of range plants in Alaska that the early growth stage had the highest nutrient level and that differences between plant species were largely related to differences in growth stages. When there is an abundance of food in the summer the grazing deer can therefore express its preference freely in association with a high eating rate. As food availability decrease in early winter the animal must eat less acceptable plant material or starve. The animal appears to compromise and eat previously neglected species. At the same time it will spend a high proportion of its daily activity time on favored species of low accessibility. Thus its eating rate is lowered and its daily activity time increased in midwinter when the snow covers all vegetation. Later in winter more food is available through the action of wind and sun that lays southwest-facing slopes bare, and the eating rate increases. Food in such areas has a low nutritive value and activity expenditure is kept at the annual low. Campling (1969) discusses the physical regulation of food intake in domestic herbivores. Distension of the reticulorumen is presumably responsible for day to day regulation of food intake, but it is also possible to integrate physical control with the long term regulation of energy balance that adult animals exhibit. Changes in the physiological status of an animal due to lactation may modify and increase the capacity of the reticulo-rumen for increased food intake during lactation. The high eating rate found for lactating females on Handangervidda is suggestive evidence for Campling's hypothesis. Thus it seems possible to explain grazing and range use patterns in terms of animal energy balance.

Several workers have tried to explain individual and seasonal differences in food intake. Lát (1956) suggested that there are individual differences in excitability. Excitable rats showed preference for large amounts of carbohydrates in their diet while less excitable animals preferred protein (casein) and fat (margarin). A diet of high protein lowered excitability and high carbohydrates increased this level. Lát went on to suggest a linear relationship between level of excitability and calories ingested per unit of body surface. Rundquist and Bellis (1933) reported that the basal metabolic rate of active animals was higher than that of inactive ones. McEwan and Whitehead (1970) report that caribou seem to have a lowered metabolic rate in winter and that this might be an innate adaptation. Arnold (1969) found a functional relationship between food digestibility and food intake for sheep. There were parallel significant differences between adults and juveniles. Luick and White (in press) found a late winter increase in glucose metabolism due to lactation. This increase parallels the eating rate increase. The large standard deviations for the sums of herd eating rates each month found in this study suggest that several of the above mentioned factors might be influencing eating rates. Differences in eating rates between individuals were only detected for lactating females and other herd members. Environmental influences

including snow in midwinter, slope in late winter and availability of green food in summer gave seasonal differences in eating rates for all herd members. The relationship between eating rate and activity is suggested to be one of energy balance, assuming that reindeer have evolved a feeding behavior guided toward obtaining the necessary amount of digestible energy with the least physical effort in order to maintain themselves.

ACKNOWLEDGMENTS

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A METHOD FOR MEASUREMENT OF ENERGY EXPENDITURE IN UNRESTRAINED REINDEER AND CARIBOU

B. A. Young
Department of Animal Science
University of Alberta
Edmonton, Alberta

E. H. McEwan
Canadian Wildlife Service
University of British Columbia
Vancouver, B. C.

ABSTRACT—A suitable method for measurement of energy expenditure of unrestrained animals has been sought for considerable time by researchers. Recently a method involving the measurement of CO₂ entry rate by an isotope dilution procedure and prediction of rate of energy expenditure from empirically determined relationships was developed for free grazing domestic sheep and cattle. This new method was evaluated for use on reindeer and caribou. Where similar infusion and sampling procedures are used for determination of CO₂ entry rate a single relationship apparently exists between CO₂ entry rate and rate of energy expenditure of sheep, cattle, reindeer and caribou.

The study of the energetics of wildlife species has been limited by the lack of a suitable method for measurement of energy metabolism in unrestrained animals. Thus the limited information currently available on the energy metabolism of reindeer and caribou is based upon measurements made on a few captive animals held in close restraint within the laboratory (McEwan, 1970; McEwan and Whitehead, 1970).

Several attempts have been made to develop methods for measurement of energy expenditure of unrestrained large animals. Portable equipment for determination of respiratory gaseous exchange of humans has been adapted for use on domestic ruminant species (Flatt *et al.*, 1958; Corbett *et al.*, 1969; Young and Corbett, 1972). Tracheostomy has been used to allow grazing activity by the animals. However, these respiratory gas exchange methods are not often used because of the surgical interference to the animals and the considerable instrumentation that must be borne by the animal.

Attempts to utilize readily measureable physiological indices of energy expenditure, for example heart rate (Booyens and Hervey, 1960; Webster, 1967; Brockway and McEwan, 1969), have often been suggested for use with man and animal subjects. The recent advances in radio-telemetry of physiological parameters have allowed substantial freedom of subjects and greatly assisted in the collection of information from unrestrained subjects. The physiological index methods for prediction of rates of energy expenditure have not found wide application probably because of the need to calibrate individual animals and the influence of factors other than energy expenditure on the measured parameter.

The possibility of using the flux of radioactive traces as measurements of metabolism was suggested by Odum and Golley (1963). Chew (1971) reported that the rate of elimination of ⁶⁵Zn showed promise as an indicator of energy metabolism in small rodents. Other tests using ⁵⁴Mn (Chew, 1971) and ³²P (Wagner, 1969) have not shown such a close

relationship with energy metabolism. Lifson and McClintock (1966) developed a method for estimation of carbon dioxide output, and hence energy metabolism of unrestrained small animals, from differences in the apparent flux of the hydrogen and oxygen of body water. The apparent flux of hydrogen and oxygen was measured by administering doubly labelled water ($D^{18}O_2$) and following the disappearance rate of the label from the body. This method has been used successfully with small rodents and birds (Lee and Lifson, 1960; LeFebvre, 1964; Mullen, 1970). The cost of the oxygen isotopes prohibits the use of this measurement method with larger animals.

The apparent rate of entry of carbon dioxide (CO_2 flux) into the body pool of CO_2 has been used as an index of CO_2 production and thus energy metabolism of domestic animals (Young *et al.*, 1969; Corbett *et al.*, 1971). Empirical relationships were established between CO_2 entry rate as determined by continuous infusion of $NaH^{14}CO_3$ and the rate of energy expenditure. After allowing time for equilibrium between the infused label and the body pool of CO_2 , the rate of entry of CO_2 can be calculated from the equation:

$$CO_2 \text{ entry rate (m-mole/min)} = \frac{\text{rate of infusion of label (}\mu\text{Ci/min)}}{\text{specific activity of } CO_2 (\mu\text{Ci/m-mole)}}$$

in which the specific activity of CO_2 is derived from a sample of a body fluid such as blood, urine or expired gas.

The recent successful use of the CO_2 entry rate method for estimating rate of energy expenditure of large domestic ruminant species (Young and Corbett, 1968, 1972; Young, 1970; Corbett *et al.*, 1971) encouraged investigations to evaluate the use of this method on large wild ruminant species. This paper presents the results of the evaluation of the CO_2 entry rate method on reindeer and caribou and compares the results with values obtained from cattle and sheep.

METHODS

Two, 5-year-old reindeer, one male (R_4) and one female (R_1) and a 7-year-old female caribou (V_{24}) were used. All three were reared and kept in captivity (McEwan and Whitehead, 1969). In addition, five female domestic sheep and two female cattle were used. The sheep and cattle were routinely used for research studies and were kept within the laboratory. The reindeer and the caribou were fed a pelleted maintenance ration while the cattle and sheep received a maintenance ration of chopped alfalfa hay.

During each measurement period of five to eight hours each animal was restrained by a head halter or in a stanchion (cattle) and given a continuous interperitoneal infusion of $NaH^{14}CO_3$ at about 200 $\mu\text{Ci/min}$ in 0.1 ml of isotonic saline. The catheter for infusion was inserted with the aid of a guide wire, and under local anaesthesia (xylocaine), 10 cm into the right flank and into the peritoneal cavity. A light-weight battery powered pump (Model 1300, Harvard Apparatus, Mass., USA) was used for the infusion. Harnesses have been developed so that these pumps can be readily carried by sheep (Leng *et al.*, 1968) and cattle (Young, 1970) while infusing.

Jugular blood samples from an indwelling catheter, and expired gas sample from the respiratory mask, see below, were obtained at 15 or 30 minute intervals throughout the infusion period. The CO_2 was isolated from each sample and its specific activity was determined by the procedures described by Corbett *et al.* (1971).

Expired gas was collected continuously from each animal during the infusion periods by means of a ventilated mask and an open circuit system. Samples of gas were collected over 15 minute intervals and used for determination of the specific activity of expired CO_2 .

The expired gas was also continuously analyzed for oxygen content, and rates of energy expenditure (kJ/min) were calculated as 20.5 x litre of oxygen consumed per minute.

RESULTS

Equilibrium between the infused label and the body pool of CO₂ as reflected by a plateau in the specific activity of CO₂ in blood and expired gas occurred after approximately 180 minutes in the sheep, 240 minutes in the reindeer and caribou and after about 300 minutes in the cattle. Mean entry rates calculated from the plateau values of specific activities of CO₂ derived from samples of blood and expired gas and the corresponding mean rates of energy expenditure of each animal are shown in Table 1.

TABLE 1.--Mean and SE of CO₂ entry rates, calculated from samples of jugular blood and expired gas, and energy expenditure in sheep, reindeer, caribou and cattle.

	Animal number	Weight kg	CO ₂ entry rate (m-mole/min)		Energy expenditure (J/min)
			from jugular blood samples	from expired gas samples	
Sheep	48	78	19.3±0.4	24.3±1.2	7,038±170
	46	70	30.8±2.2	32.9±2.2	6,882±115
	24	62	28.3±0.9	30.5±3.1	8,044±385
	38	65	27.0±1.6	26.7±1.7	6,619±363
	48	78	30.2±1.0	28.5±0.2	8,200± 80
Reindeer	R1	115	56.2±5.4	55.6±2.9	14,248±383
	R4	140	90.2±6.3	87.9±0.6	17,607±418
Caribou	V24	97	39.6±2.3	38.2±0.9	12,968±154
Cattle	3	290	89.1±2.2	90.8±2.5	19,106±574
	2	402	122.6±1.8	142.6±4.2	31,304±390

The regression equation describing the relationship between rates of energy expenditure (EE, J/min) and CO₂ entry rate (m-mole/min) estimated from samples of jugular blood (ER_b) and expired gas (ER_g) were:

$$\begin{array}{lll} \text{EE} = 215 \text{ ER}_b + 1707 & \text{SE of } b = \pm 12 & (1) \\ \text{EE} = 195 \text{ ER}_g + 2239 & \text{SE of } b = \pm 10 & (2) \end{array}$$

The correlation coefficients were 0.96 and 0.98, and residual standard deviations were 1,947 and 1,465 J/min, equivalent to 14 and 10 per cent of the mean values, for equations (1) and (2) respectively.

DISCUSSION

The time for equilibrium to be reached between the infused NaH¹⁴CO₃ and the body pool of CO₂ appeared to be related to the body weight of the animals. The reindeer and caribou with weights intermediate between sheep and cattle required more time than sheep but less time than cattle for the infusate to equilibrate. About 4 h was required for

equilibration in the reindeer and caribou. Therefore, if the CO₂ entry rate method is adopted for use on reindeer and caribou, the infusion must be maintained for at least 4 h before samples of a body fluid are taken for determination of CO₂ entry rate.

Several routes of infusion of NaH¹⁴CO₃ into free ranging animals have to be examined (Young, 1970; Corbett *et al.*, 1971). Irritation and disturbance to the animal tends to be less with subcutaneous or intraperitoneal routes than with intrajugular infusion. With subcutaneous infusion, Corbett *et al.* (1971) observed that on some occasions the infusate tended to accumulate near the tip of the catheter. The method of intraperitoneal infusion through the mid right flank region proved to be satisfactory in the present study. Several different body fluids, for example, venous or arterial blood, urine and expired gas, may be sampled for isolation of CO₂ for specific activity. Corbett *et al.* (1971) have shown that with different routes of infusion or when different body fluids are sampled for specific activity determination, slightly different regression relationships are obtained between CO₂ entry rate and rate of energy expenditure. Thus for field application of the CO₂ entry rate method the empirically determined relationship must be determined in the laboratory using the same infusion and sampling procedures as are used on the field animals.

Portable infusion apparatus and harnesses described by Leng *et al.* (1968) and Young (1970) for domestic sheep and cattle could be readily adapted for use on free-ranging caribou or reindeer. Recently, Farrell *et al.* (1970) have described apparatus suitable for collection of blood from free-ranging animals. This apparatus allows for a sample to be collected continuously over periods of 12 h and would be suitable for collection of blood for specific radioactivity analysis of CO₂.

Although the present results were obtained from only a few animals they indicate that the CO₂ entry rate method could be readily applied to reindeer and caribou and possibly other wildlife species. Furthermore, where similar infusion and sampling procedures are used for determination of CO₂ entry rate a single relationship apparently exists between CO₂ entry rate and rate of energy expenditure of sheep, cattle, reindeer and caribou.

ACKNOWLEDGMENTS

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RESPONSES OF REINDEER, *RANGIFER TARANDUS*, TO HEAT STRESS

M. K. Yousef and J. R. Luick
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska

ABSTRACT—Although reindeer experience exposure to heat stress as a result of their effective insulation even at moderate temperatures and/or exposure to heat during the summer season, little is known of their physiological responses to heat stress. To evaluate their physiological adjustments to heat, three yearling female reindeer were exposed for five hours to ambient temperatures (T_a) of 10, 20, 30, 35, 40 and 45° C. Relative humidity was 40-43 per cent, and feed and water were available *ad libitum*. Heart rate (HR), respiratory frequency (Rf), rate of oxygen consumption (VO_2), rectal temperature (T_e) and blood hematocrit (Hct) were measured during each temperature exposure.

At 35° C and above, all the measured physiological parameters increased. An increase of 4-5 fold in Rf was sufficient to prevent a further rise in T_e . Thus thermal polypnoea represents an adequate mechanism for evaporative cooling in reindeer. Indices of heat tolerance for reindeer were calculated from data on T_e and Rf and compared to other large mammals. In conclusion, it appears that reindeer are as heat tolerant as some domestic cattle and wild African ungulates.

Responses of arctic mammals to cold have been well investigated. Maintenance of warmth in large arctic mammals is accomplished by a combination of two mechanisms: effective insulation and peripheral heterothermy (Irving, 1964, 1966); this means that peripheral tissues of animals are functional at temperatures considerably cooler than the interior of their bodies. Observations on adaptation of *Rangifer tarandus*, the domestic reindeer and caribou, have shown that metabolic adaptation is rarely a major factor in protection against hypothermia (Irving, 1966; Hart *et al.*, 1961; Lentz and Hart, 1960; Yousef *et al.*, 1971; Yousef and Luick, 1971). The efficiency of insulation for heat conservation poses a physiological problem during heat stress. Bartholomew and Wilke (1956) found that fur seal bulls may die from overheating when driven at 10° C temperature.

Although *Rangifer tarandus* may experience exposure to heat stress as a result of their effective insulation even at moderate temperatures and/or by exposure to high ambient temperatures during the summer season, little is known of their physiological response to heat. Rosenmann and Morrison (1967) concluded that reindeer have a good capacity for heat resistance when water is available, but very poor resistance to water deprivation with or without heat stress. The following experiment was designed to study some physiological responses to various ambient temperatures.

MATERIAL AND METHODS

Animals

All experiments were carried out on three yearling female reindeer. Each was approximately nine to 12 months old and weighed about 50 kg. The reindeer were obtained from the Bureau of Indian Affairs model herd in Nome, Alaska. The animals were air-freighted to Fairbanks, Alaska, and maintained in a semi-natural fenced yard. They were fed brome hay supplemented with a commercial livestock ration (Purina Cattle Starter No. 1, Ralston-Purina Corp., St. Louis, Missouri). Water was available at all times. As a result of frequent handling, the reindeer soon became quite tame and submitted voluntarily to laboratory procedures including standing quietly in stanchions for five to six hours at a time while wearing a metabolism mask.

Experimental Protocol

All experiments were carried out during March 1968 in a climatic chamber (3.0 x 4.5 m) at the Institute of Arctic Biology, University of Alaska. Reindeer were exposed to the following ambient temperatures: 10, 20, 30, 35, 40 and 45° C; relative humidity ranged from 40 to 43 per cent. Each reindeer was exposed to each temperature treatment for a period of five hours and then removed to an indoor-outdoor holding pen where the temperature ranged from -2.8° C to -22.2° C. Water and food were available *ad libitum* in the climatic chamber. Data were collected on only two reindeer during the 40 and 45° C temperature studies as the third reindeer had died from pneumonia just prior to these experiments.

Physiological Measurements

Heart rate (HR) was obtained at each temperature by inserting electrodes through the skin. The heart rate was recorded using a GME portable cardioencephalograph as described by Rosenmann and Morrison (1963, 1967). Respiratory frequency (Rf) was transmitted from a belt-mounted stretch transducer and recorded. Recording of HR and Rf of 15 seconds duration was obtained at 15 minute intervals during the five hour exposure. Rate of oxygen consumption (VO_2) was measured three to four hours following initial exposure to each given ambient temperature, using an open-circuit system consisting of a gas tight metabolism mask previously used on sheep (Luick *et al.*, 1960) and sealed with an inflatable cuff. The exhaled air was pumped through a dry gas meter to measure its volume. A portion of this air was directed to a Beckman oxygen analyzer, Model F3 and to a CO_2 analyzer, Model 1 R 215. The analyzers were connected to a dual-channel, recording potentiometer, Honeywell Model 15. The system was calibrated with gas mixtures of known concentrations. Oxygen consumption, corrected to STPD, was calculated as usual (Consolazio *et al.*, 1951). Rectal temperature, T_{re} , was measured using a standard veterinary clinical thermometer once every 30 minutes during the experimental period. At the end of the five hour exposure to each temperature a blood sample was obtained from the jugular vein for determination of hematocrit using Wintrobe tubes and centrifugation in a clinical centrifuge.

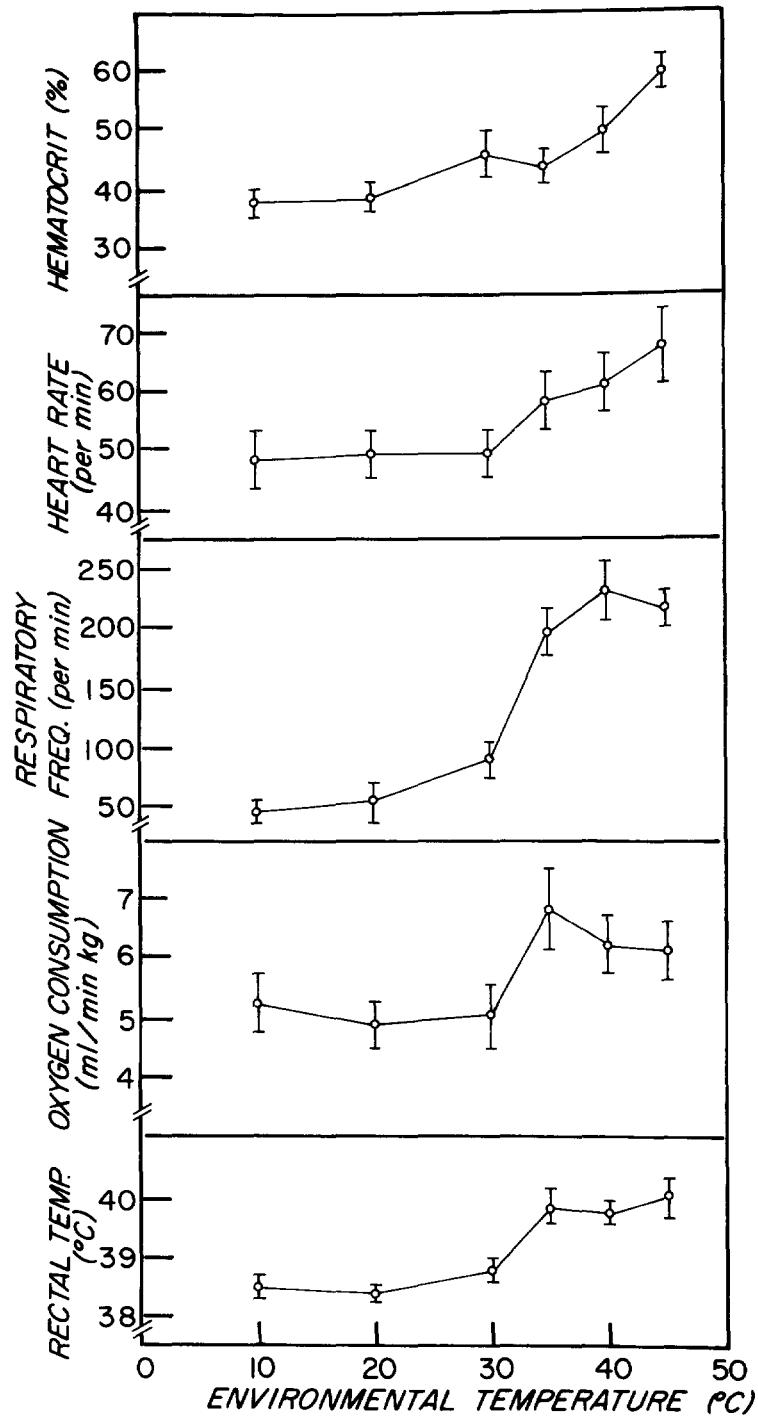


Fig. 1.—Effects of environmental temperatures on rectal temperature, rate of oxygen consumption, respiratory frequency, heart rate and hematocrit in reindeer.

RESULTS

The physiological responses of the three reindeer to various ambient temperatures, T_a , are shown in Figure 1.

Rectal temperature, T_{re} : The average T_{re} varied between 38.4 to 38.8° C at a T_a between 10 and 30° C. At 35° C and above, T_{re} rose to 39.9° C. The time course of change in T_{re} at 45° C is shown in Figure 2. Within one hour of exposure, T_{re} reached its maximum

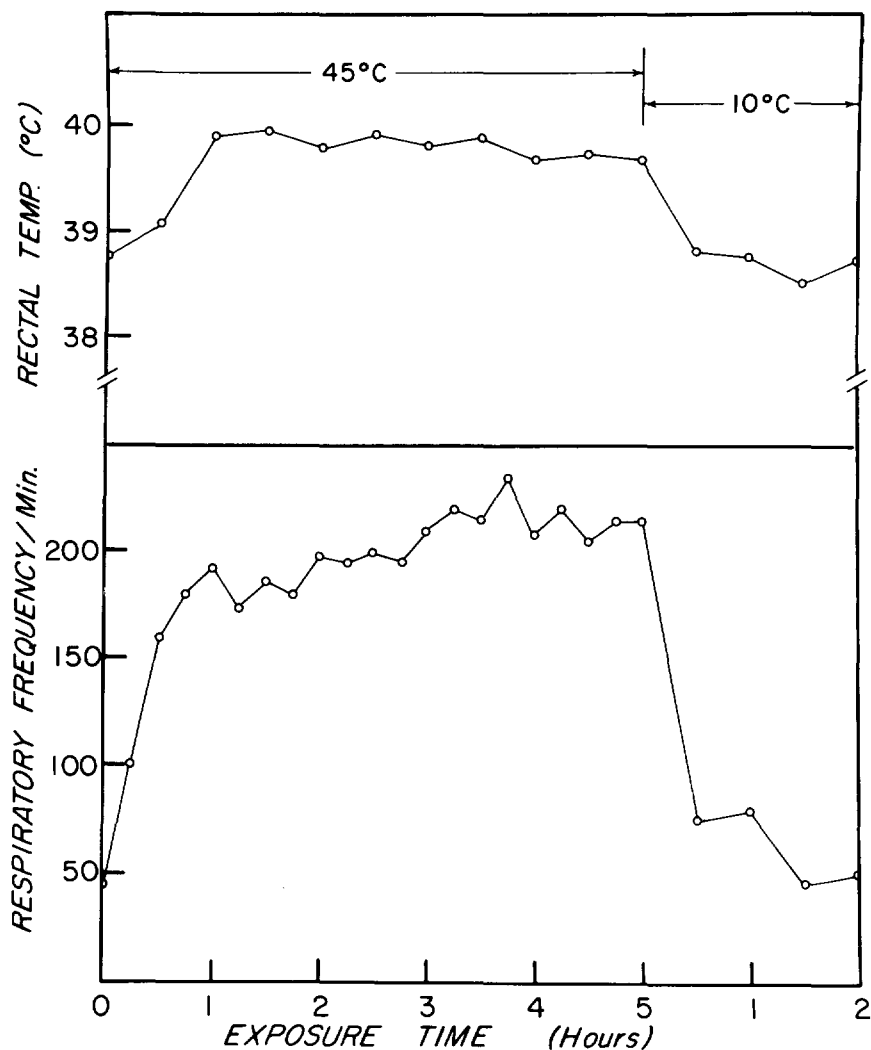


Fig. 2.—Time course of changes in respiratory frequency and rectal temperature during exposure to heat, 45° C, in reindeer.

increase of 1.1° C. This increase was maintained for two hours after which there was a decline of about 0.2° C.

Rate of oxygen consumption, VO_2 : The average VO_2 expressed in ml/min per kg body weight varied between 4.9 to 5.3 at T_a between 10 and 30° C. At 35° C the average VO_2 increased sharply to 6.8 whereas at T_a of 40 and 45° C the VO_2 averaged 6.1 and 6.2 respectively.

Respiratory frequency, Rf: The average Rf/min ranged between 45 and 55 at 10 and 20° C respectively. At 30° C, the Rf increased to 90 and was between 190 and 225 at 40 and 45° C.

Heart rate, HR; and hematocrit, Hct: The average Hr at Ta below 30° C was 48 beats/min. At Ta above 30° C, the HR increased gradually reaching its maximum of about 70 at 45° C. The Hct averaged 38 per cent at 10 and 20° C. Above 20° C, the Hct increased gradually reaching its maximum value of 58 per cent at 45° C.

DISCUSSION

The average Tre of reindeer at 30° C is 38.8, a value similar to early reports on reindeer (Rosenmann and Morrison, 1967; Segal, 1965; Hammel *et al.*, 1962) and its conspecific, the barren ground caribou (McEwan *et al.*, 1965). When Tre of reindeer is compared to data obtained on East African ungulates, it is found to be similar to Eland, Oryx and Wildebeest but about 0.6 to 1.0° C less than Waterbuck, Thompson's and Grant's gazelle (Table 1).

TABLE 1.--Some physiological characteristics of reindeer and East African ungulates kept at 30° C.

Ungulate	Tre, °C	HR/min	Rf/min	VO ₂ ml/kg·min	Reference
Waterbuck	39.6	-	25	4.4	Taylor <i>et al.</i> (1969)
Grant's gazelle	39.8	-	42	-	Taylor (1970)
Thomson's gazelle	39.4	-	25	-	Taylor (1970)
Oryx	38.4	-	17	4.0	Taylor (1970)
					Taylor (1969)
Wildebeest	39.0	-	34	-	Taylor (1970)
Eland	-	-	-	3.9	Taylor (1969)
Reindeer	38.6	48	50	5.1	Our study

Therefore, no general conclusion can be made regarding phylogeny and Tre as related to adaptability of large mammals to arctic and desert conditions. Exposure to heat (35° C or above) increased Tre about 1.1° C, an observation contrary to the results of Rosenmann and Morrison (1967). They found no displacement of the normal level of Tre even after seven and one-half hours of exposure to 43° C in hydrated reindeer but Tre increased 1.2° C in dehydrated reindeer. The discrepancy between our data and Rosenmann and Morrison (1967) probably results from the degree of the previous state of acclimatization, i.e., their study was carried on during July-August whereas our study was undertaken during March. Recently, Yousef and Dill (1971) concluded that the previous state of acclimatization of Kangaroo rats, *Dipodomys merriami*, is an important factor in their adaptation to heat. This conclusion may be extended to reindeer, thus summer acclimatized reindeer appear to be more heat tolerant than winter acclimatized ones.

The time course of rise in Tre at 45° C (Figure 2) indicates that despite the three-fold increase in Rf after 15 minutes exposure, Tre continues to rise and reaches a maximum in one hour of exposure. It seems that a four to five-fold increase in Rf was sufficient to prevent a further rise in Tre which remained below Ta. Thus thermal polypnoea in reindeer is a physiological mechanism permitting adequate respiratory evaporative cooling. Whether

reindeer under heat stress depend primarily on panting for evaporative cooling or depend on both panting and skin evaporation remains a problem for further investigation. An animal that depends on panting can dispose of its body heat and at the same time maintain a higher skin temperature to minimize heat flow from the environment (Taylor, 1969). The increased evaporation of water was accompanied by increased water consumption. Unfortunately quantitative measurements of water consumption were not made, but both reindeer were observed to drink more than two to three times their normal water intake. Maintaining T_{re} at 39.9° C throughout the exposure period to 45° C indicated that the thermoregulatory center can be reset at a higher level and maintained for at least five hours.

The average Rf of reindeer at 30° C is compared with data on East African ungulates and shown in Table 1. It is evident that Rf/min in reindeer is higher than the antelope. The significance of this is difficult to ascertain since information on lung volumes and capacities is not known. Rosenmann and Morrison (1967) reported values for normal Rf/min in three reindeer ranging between 15 to 105.

The ability of animals to endure the impact of exposure to heat without suffering ill-effects has been measured by changes in T_{re} and Rf (Bianca, 1963). Two indices were developed to measure heat tolerance in farm animals: Rhoad's coefficient and Benezra's index (Bianca, 1963). The formulas used for calculation of heat tolerance are:

$$(1) \text{ Rhoad's coefficient} = 100 - [18 (T_{re} - 38.3)]$$

$$(2) \text{ Benezra's index} = T_{re}/38.3 + Rf/23$$

The indices of heat tolerance for reindeer were calculated from these equations and compared to the available indices on cattle. We have also calculated the indices for the waterbuck, an African ungulate, from data reported by Taylor *et al.* (1969). From Table 2,

TABLE 2.--Comparative data on heat tolerance of domestic, wild East African and arctic ungulates.

Ungulate	Rhoad's coefficient		Reference
	%	Benezra's index	
Ayrshire	65	4 to 11	Bianca (1963)
Waterbuck	55	6	Taylor <i>et al.</i> (1969)*
Reindeer	69	11	Our study

*The indices were calculated from data by Taylor *et al.* (1969).

regardless of the index used, it appears that reindeer are as heat tolerant as some desert ungulates.

The average HR below 30° C (Fig. 1) is within the normal range of HR reported by Rosenmann and Morrison (1967). Exposure to 35, 40 and 45° C caused a continuous increase in HR, an observation contrary to Rosenmann and Morrison (1967) who found that heat alone without dehydration did not modify the HR. The increase in HR coincides with increased Hct. The increase in Hct represents hemoconcentration, i.e., higher viscosity of blood, thus an increased HR is needed to maintain blood circulation.

The VO_2 for resting reindeer (Fig. 1) at 30° C and below was almost 40 per cent higher than could be predicted by the Kleiber equation (1961): $\text{kcal/day} = 70 (\text{kg}^{.75})$ and assuming that one liter O_2 is equivalent to 4.8 kcal. Hammel *et al.* (1962) also reported a value for reindeer that is higher (70 per cent) than the value predicted from the equation. The VO_2 at 30° C of reindeer is compared to values reported on East African ungulates as shown in Table 1; the value on reindeer is about 14 to 24 per cent higher than values for

these desert ungulates. This may not represent any metabolic adaptation since the values on the African ungulates are also higher than the values predicted from Kleiber's equation.

Exposure to 35° C or above increased VO_2 . The increase in VO_2 is probably due to the rather high cost of panting, since Kibler (1957) and Macfarlane (1964) concluded that panting is expensive in terms of energy. However, Whittow and Findlay (1968) estimated that the VO_2 cost of panting at a T_{re} of 41.4° C in the ox represented only 11 per cent of the total VO_2 . Therefore, the increase in VO_2 during exposure to heat is probably caused by Vant' Hoff effect (Q_{10}) resulting from increased T_{re} and perhaps increased activity of the neuroendocrine system in addition to the cost of panting.

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M. K. Yousef, current address: Department of Biological Sciences, University of Nevada, Las Vegas, Nevada 89109 and Laboratory of Environmental Patho-Physiology, Desert Research Institute, Boulder City, Nevada 89005.

THE CIRCULATION IN THE GROWING REINDEER ANTLERS

J. O. Krog and M. Wika
Institute of Zoophysiology
University of Oslo
Norway

ABSTRACT—The circulation in the growing antlers of reindeers is very large. In the present studies the relative values for circulation in the different parts of the antlers were determined by means of thermograms. The site of rapid growth at the tips of the antlers was found to be the warmest parts. Heat loss from the antlers seems to be a function of the large local blood flow necessary for the rapid growth and not due to a special thermoregulatory adjustment as has previously been suggested.

The reindeer, as most arctic animals, has a very efficient thermal barrier between the skin surface and the environment. The thickness of the fur coat varies greatly from one part of the body to another. The extremities have a relatively thin fur coat as compared to the back and the side of the animal while the growing antlers are covered with fur consisting of short, soft hair having the appearance of velvet. Antlers are grown both by male and female reindeer. The male sheds his antlers earlier than the female, the latter keeping hers until the calf is born. At that time, in the spring, the bulls have already started growing their new antlers.

The center of the antler is hard, and the largest blood vessels pass just underneath the skin. Growth occurs at the end of the antler bud. The skin of the antler can therefore be compared to the bark of a tree where the vascular bundles carry water and nutrients to the branches. Grooves in the scraped antler indicate the former presence of the major vessels that conducted the large blood-supply necessary for antler growth.

Fig. 1 shows a section through the bud of a growing reindeer antler. It is interesting

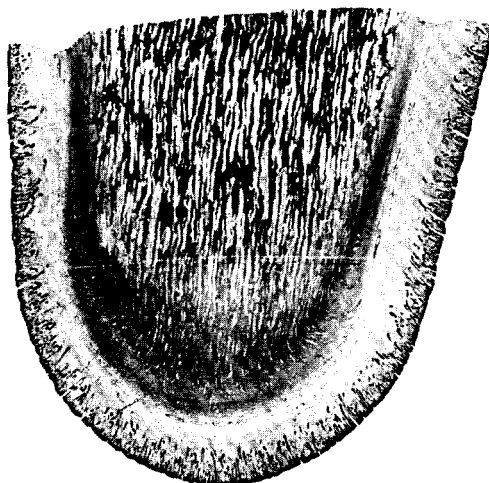


Fig. 1.—Section through the tip of a growing reindeer antler.

to observe the great open spaces and sinuses filled with blood at the end of the antler, rapidly growing bone cells are seemingly 'bathed in blood'. Organized capillaries are not visible in this part. After the antler is fully grown and ossification has stopped, the skin gradually atrophies and spontaneous thrombosis of the vessels must take place at the same time that shedding of the velvet occurs. Some bleeding from the skin of the antlers is usually seen during shedding but none so serious as to endanger the life of the animals. This seasonal build up and break down of the antler vascular bed is regulated by hormonal factors and shows some resemblance to other disposable vascular beds, e.g., the placenta, which also have a more limited lifespan than the rest of the organism.

The rapid growth of the antlers and especially of the nerves supplying them, is extremely interesting, as it is without doubt the fastest growing nervous tissue known. Antlers of one meter or more length are not unusual in male reindeer, this length being obtained in about three to four months.

MATERIALS AND METHODS

In work on thermoregulation, it is necessary to take the utmost precaution not to disturb the animal as that would upset normal heat balance and as well as regional patterns of heat loss. The measurements reported were made in the summer with unrestrained domestic reindeer in northern Finland and while the animals were resting quietly outside the observation building. An infrared recording device, known as 'thermovision' and produced by Swedish Company AGA, was used to determine heat distribution and the avenues of heat loss from different parts of the reindeer's skin. The reindeer were observed at different times of the day in warm as well as in cooler weather in the summer. No effort was made to get 'absolute' temperature readings as relative values for skin surface temperatures of the animal were entirely satisfactory for our purposes.

RESULTS

Figure 2a shows an infrared color thermogram reproduced in black and white of a reindeer at rest during warm conditions of 17° C in the air. The scale from light to dark colors is given at the bottom of the pictures. From the color scale the relative temperatures of the different areas can be distinguished. Figure 2b is for comparison — a black and white picture of the same deer. The light spots of the antlers are clearly visible, indicating the highest temperature in the growing parts.

Figure 3 shows a black and white thermogram taken with the same camera and at a relative warm environmental temperature. Here the legs, nose and tip of the antlers stand out clearly, indicating that the animal is dissipating heat through these parts of the body.

Figure 4 was taken during the same experiments and shows the relative importance for heat dissipation from the different parts of the animal's surface. In a later unpublished experiment performed in the mountains of Norway, reindeer were photographed after exercise and while standing in cold water. It was expected that vasoconstriction due to the cold exposure would change the temperature of the antlers. Surprisingly no change in heat loss from these antlers was detected.

DISCUSSION

Several investigators have suggested that the reindeer should have difficulty in dissipating heat during the summer due to their heavy fur coat and that antlers, even though covered with fur, should facilitate the dissipation of excess heat to the environment

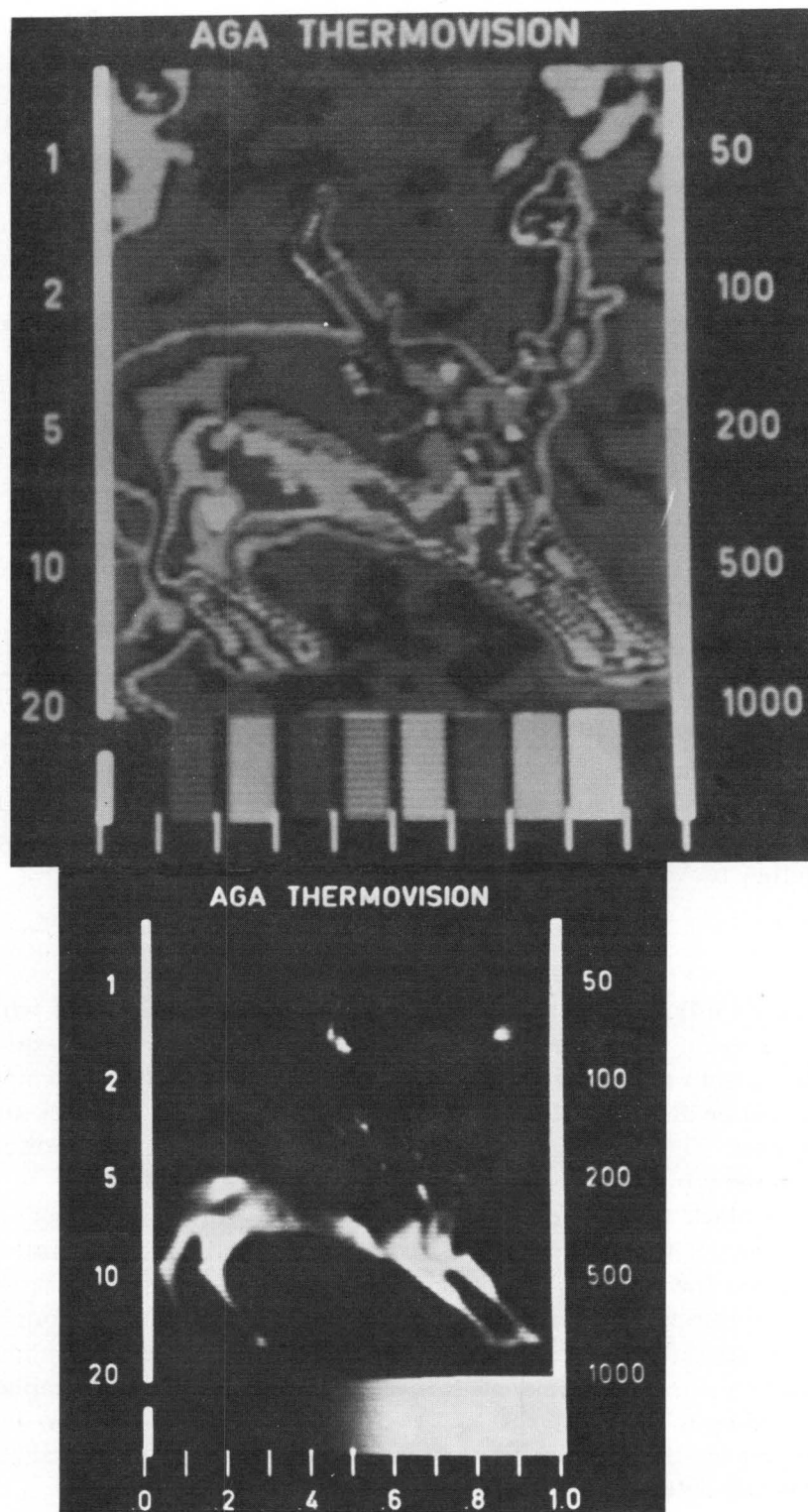


Fig. 2.—Thermograms of reindeer resting.

(Stonehouse, 1968). Direct observations of the heat distribution in peripheral parts of reindeer have been made by several investigators (Irving and Krog, 1955; Krog, Reite and Fjellheim, 1969). The measurements of Irving and Krog were taken in mid-winter and a large gradient was noted between the main part of the body and the distal parts of the legs, where temperatures as low as 4-6° C were recorded. In the winter conservation of heat is the main problem whereas in contrast, dissipation of heat may be of great importance during summer. Temperature recordings with thermovision show the sparsely haired parts of the body acting as avenues of heat loss.

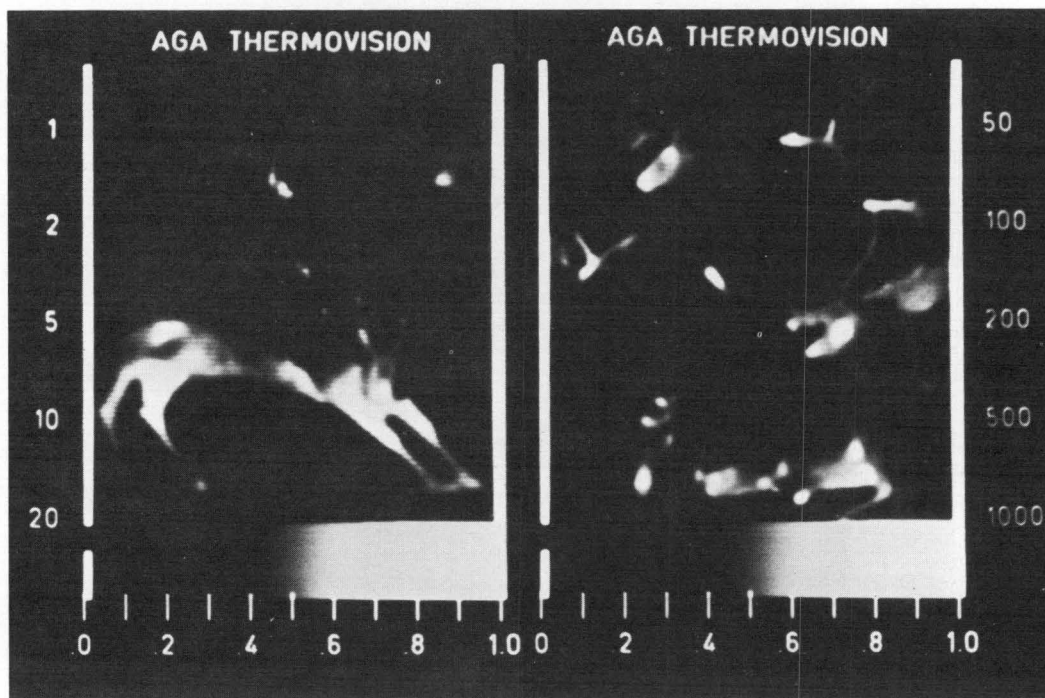


Fig. 3.—Black and white thermogram of reindeer resting.

The blood vessels of the antler react to infusion of catecholamines, such as adrenaline and noradrenaline, to the same extent as vessels from other parts of the body, including the extremities (Krog, Reite and Fjellheim, 1969). These data were obtained by perfusing antlers and legs of constant flow and measuring changes in peripheral resistance. These investigations showed that the vessels in the growing reindeer antler dilate and contract like other vessels in the body even though they may be looked upon as part of a disposable organ with a very short lifetime. This finding may indicate the capabilities of these vessels to subserve thermoregulation. The presence of sensory nerves in the distal parts of the growing antlers is well known to anyone who has handled reindeer at this time of the year. However, to our knowledge, vascular nerves have not been demonstrated anatomically. The reaction

of the vascular bed of the antler when the animal is exposed to cold does not indicate strong sympathetic innervation.

The heat distribution in the antlers shows that the region of most active growth is the warmest, and therefore possesses the greatest circulation. The large heat loss from these

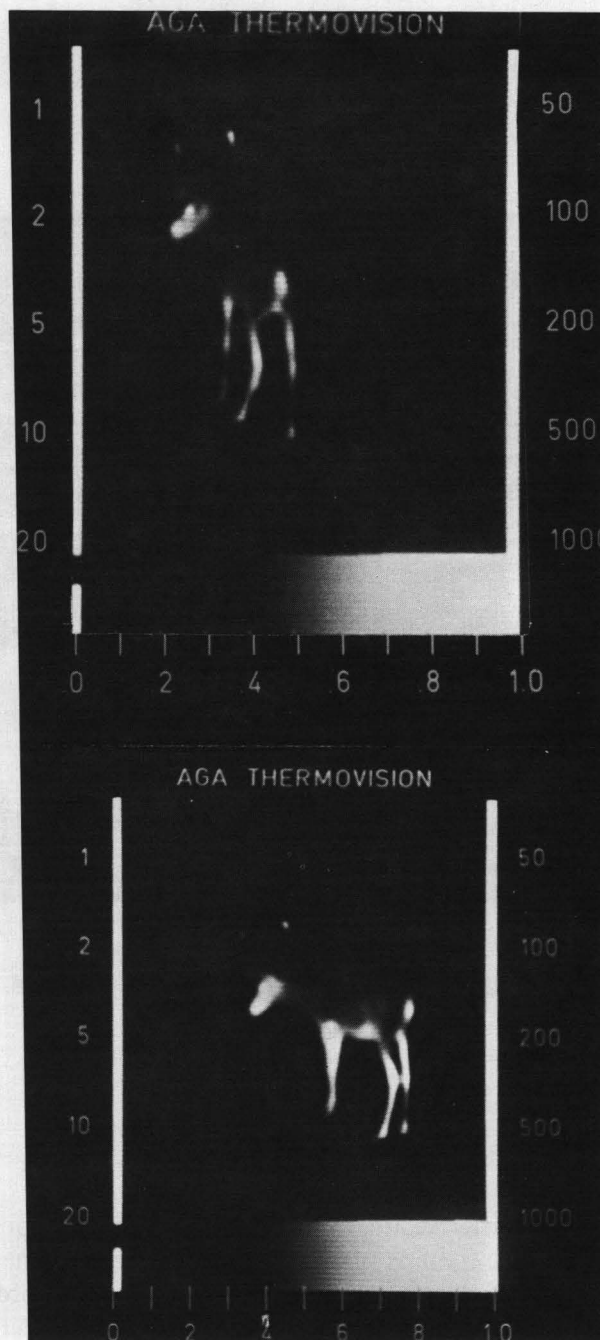


Fig. 4.—Black and white thermogram of reindeer standing.

areas seems to be a function of blood flow. It may, therefore, be looked upon as an obligatory heat loss secondary to the large blood flow necessary for rapid growth. Further studies underway include detailed investigation of the vascular pattern and blood supply of growing antlers as well as the reactivity of the vascular bed, *per se*.

CONCLUSION

Our studies indicate that the large circulation of blood in reindeer antler is of prime importance for supplying nutrients for antler growth, and not directly subserving the thermoregulatory need of the animal.

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THE ACCUMULATION OF WATER IN REINDEER DURING WINTER

Raymond D. Cameron, R. G. White and Jack R. Luick
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

ABSTRACT—Non-pregnant female reindeer grazing lichen pastures in winter or held under simulated winter conditions in the laboratory may accumulate a quantity of body water equal to nearly 15 per cent of body weight, while body weight itself remains relatively constant. Our data suggest that the primary site of this change in body hydration is the alimentary tract, particularly the ruminal fraction. The phenomenon is discussed in terms of the problems associated with predicting body composition of *Rangifer* and with regard to its possible survival value.

Under natural grazing conditions, reindeer (*Rangifer tarandus*) are subject to marked seasonal variations in both climate and food supply. Lichens constitute the principal food source from late fall to early spring and, although high in energy are extremely low in nitrogen; lichen species typical of those consumed average less than 3 per cent crude protein (Kelsall, 1968). As a result, *Rangifer* enter the spring season in poor body condition, yet pregnant females are faced with increasing fetal demands, parturition and early lactation. During summer and early fall higher quality grasses, sedges and deciduous vegetation predominate in the diet, and body weights increase with the rapid accumulation of body fat. In mature males these large fat deposits are almost completely metabolized during the short breeding season due to a nearly complete cessation of food intake. Thus, in its natural habitat, *Rangifer* is subject to nutritional extremes which presumably result in marked changes in body composition.

Although a large volume of evidence supports the generalization of chemical constancy of the lean (fat-free) body mass of mature animals (see Panaretto, 1963a; Searle, 1970), the fat mass responds dramatically to dietary variation, and the determination of body fat content provides one of the best single indices of energy balance. It has been demonstrated by many earlier studies that the percentages of total body fat and total body water are inversely related. Pace and Rathbun (1945) reported that the quantity of water in the lean body mass is nearly constant in the adult at about 73.2 per cent, and on this basis proposed a formula from which body fat can be calculated if the percentage of water in the whole body is known: $\% \text{ FAT} = 100 - (\% \text{ WATER}/0.732)$. Although subject to some degree of interspecies error, this equation permits a first approximation of body fat within a 'normal' range of total water content, but its use is seriously limited with regard to very lean animals having high percentages of total body water; thus, percentages exceeding 73.2 result in negative estimates of body fat. Further, these inconsistencies raise some doubt as to the reliability of the equation when applied to very fat animals. Such inaccuracies have been reduced in individual species by determining the quantities of body water indirectly, using tracer dilution methods, and relating these results to direct measurements of total fat, as well as protein and ash. In this manner a 'prediction equation' is formulated from which the amounts of the major body components can be calculated from a single water volume measurement. Equations such as these have been reported for rabbits (Panaretto, 1963b),

hamster (Kodama, 1971), goats (Panaretto and Till, 1963; Panaretto, 1963c) and sheep (Panaretto, 1963c, 1968; Searle, 1970) based on data obtained over wide ranges of fatness.

Using the tritium water (TOH) dilution method, Cameron and Luick (1972) have reported seasonal changes in total body water volume of grazing female reindeer which tend to reflect the cycles of fat deposition and mobilization described above. Means for TOH space ranged from 54 to 80 per cent of body weight for late summer (August) and early spring (May), respectively, while values obtained in early winter (December) were intermediate at a mean of 68 per cent. During the first year of this study when all reindeer were non-pregnant, the increases in TOH space between December and May were not accompanied by changes in body weight, indicating a significant accumulation of body water and a concomitant utilization of body solids in response to winter conditions. This report deals with further details of this study and with two subsequent experiments in summarizing this process of progressive water accumulation, and includes a consideration of the possible sites of hydration.

MATERIALS AND METHODS

Experiment 1. A field study was undertaken in which total body water volume and turnover were determined in from three to seven grazing female reindeer on a seasonal basis using, in each case, the tritium water (TOH) dilution method (Cameron and Luick, 1972). Briefly, a known quantity of TOH was injected intravenously and four to seven blood samples were collected over the two to three week period post-injection. Water was recovered from plasma by vacuum sublimation and assayed for tritium specific radioactivity.

The decrease in plasma TOH activity (A_t , $\mu\text{Ci}/\text{ml}$) with time (days) is described by a single exponential expression; extrapolation of this regression line to zero time gives A_0 , the theoretical specific radioactivity of tritium in the body water pool assuming complete and instantaneous mixing of the injected dose. The volume of the total body water pool is calculated by dividing the zero-time concentration into the injected dose (μCi), and the rate of water flux is determined as the product of the total body water volume and the fractional rate constant, k .

Experiment 2. Two non-pregnant females held in a controlled environment chamber were fed hand-picked lichens (3 per cent crude protein) for a three-month period (Cameron, 1972). Ambient temperatures were regulated between -5 and -20°C , and the daily ration ranged between 800 and 1300 g dry matter. Total body water volume was estimated as described above from daily blood samples taken over the five-day period post-injection.

Experiment 3. Two yearling reindeer were fed hand-picked lichens for a two-month period in mid-winter (January-March), and a third served as a control and was allowed an *ad libitum* intake of a commercial pelleted ration (c.p. 13 per cent crude protein) (White, unpub.). All three animals were subsequently slaughtered and the alimentary contents analyzed for water.

RESULTS AND DISCUSSION

During the first winter of the field study (i.e., December through May, Expt. 1), body weights showed no net change while total body water volume (percentage of body weight) increased from 64 to 80 per cent, representing an increase of about 13 liters of water for a reindeer of 80 per cent, kg body weight. These results are summarized in Figure 1a and are shown in detail elsewhere (Cameron and Luick, 1972). Total body water volumes in the lichen-fed reindeer (Expt. 2) increased from 70 per cent of body weight to 84 and 89 per cent (mean, 86.5 per cent), while again body weights remained fairly constant, decreasing

by only 3-4 kg over the entire period. Thus, the water accumulated amounted to 7 and 13 liters for the two animals studies, corresponding again to a difference of 13 liters for a body weight of 80 kg (Fig. 1b). Thus, in both field and laboratory experiments, the reindeer accumulated a quantity of water nearly equal to 15 per cent of body weight.

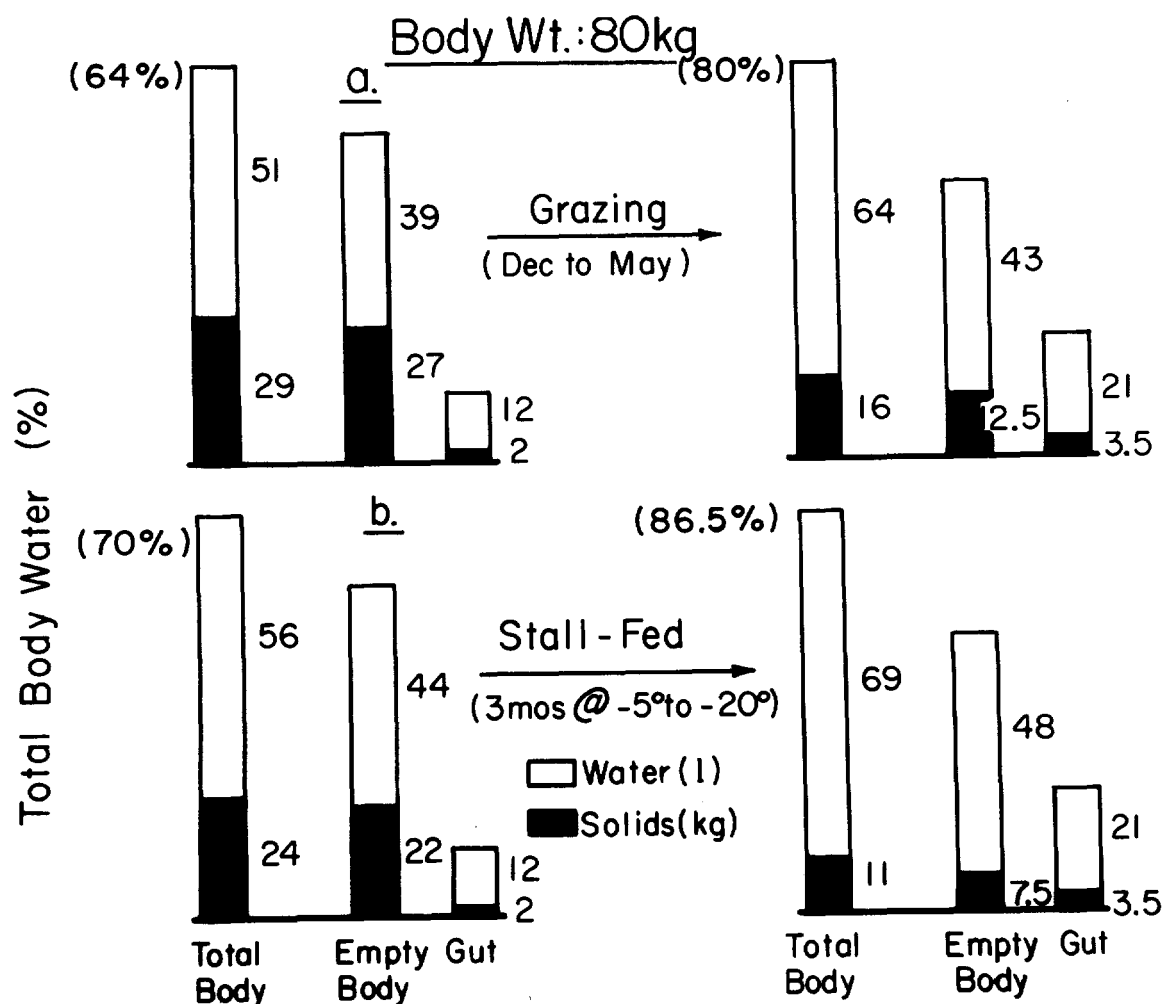


Fig. 1.—Graphical representation of changes in the distribution of total body water in non-pregnant female reindeer in the field (a) and under laboratory conditions (b). Values shown for empty body (i.e., tissue) water and alimentary water are calculated from the results of separate slaughter experiments. All results have been normalized to a constant body weight of 80 kg.

The body weights of the three yearling reindeer used in the slaughter experiment (Expt. 3) declined during the first three weeks of feeding, although the weight losses of the lichen-fed animals exceeded that of the pellet-fed control. Unfortunately, changes in total body water were not monitored, but measurements following slaughter indicate that while total alimentary water in the lichen-fed yearlings averaged 26 per cent of body weight, the same value for the control was only 15 per cent. Neither the mean moisture content of the alimentary contents nor the relative contribution of ruminal and intestinal to total fill differed significantly between nutritional regimes. Although the various water compartments of the alimentary tract appear to have increased in parallel in the lichen-fed

yearlings, quantitatively the most important increase occurred in the rumen which accounted for 86 per cent of the difference; rumen water volume in the control was 11.5 per cent of body weight while for the lichen-fed animals the value reached a mean of 21 per cent.

From the latter results it appears probable that the increases in total body water observed in the former studies were due largely to an accumulation of water in the alimentary tract, particularly in the ruminoreticulum. In Figure 1 the results of the slaughter trials have been superimposed on the total body water data from both field (Expt. 1) and laboratory (Expt. 2) experiments. If the observed changes in alimentary fill are considered, the increases in water in the empty body amount to only 4 liters in each case, in contrast to the whole body increases of 13 liters. On the other hand, losses of tissue or empty body solids (14.5 kg) theoretically exceed the whole body estimates (13 kg) because of the additional alimentary dry matter.

The gain of 4 liters of tissue water (i.e., empty body water) as shown in Figure 1 may result partially from an inherent error of the tritium water dilution method. Injected tritium is known to exchange with the protium of organic body constituents with the result that the volume of distribution of the tracer increases. Such an overestimate of the volume of the total body water pool is thought to be on the order of 2 per cent (Aschbacher *et al.*, 1965). Aside from this error an increase in tissue water as shown in this illustration is a real possibility: the additional water could represent either extracellular or intracellular increases, and it has been suggested by other workers with cattle and sheep that either or both may increase in response to undernutrition or exposure to extremes of temperature (Macfarlane *et al.*, 1959; Macfarlane *et al.*, 1966; Morris *et al.*, 1962; Siebert and Macfarlane, 1969). Also, there is some evidence that water replaces mobilized fat in adipocytes (see Farrell, 1970), but it would seem that such a process could be of only minor importance here since little depot fat was noted in the yearlings at slaughter.

In summary, the results suggest that the body water which accumulates in non-pregnant reindeer grazing predominantly lichen pastures or consuming lichens in a controlled feeding situation, is due primarily to an expansion of rumen volume and, secondarily occurs as a result of increased intestinal fill and tissue hydration. Increases in rumen fill are probably related to the consumption of low quality forages; the intake of feeds of low nutritive value has been associated with greater half-times of particle retention in the rumen (Person *et al.*, this volume) and increased rumen volumes (Longhurst, pers. comm.), both of which permit more efficient utilization of energy substrates and thus encourage microbial protein synthesis.

However, water accumulation may not result entirely from nutritional influences, since the phenomenon was not observed in pregnant reindeer grazing under similar conditions of forage quality and availability (Cameron and Luick, 1972). For example, lower ambient temperatures may influence the degree of body hydration. A larger volume of body water in general, and of rumen water in particular, favors survival in a cold environment: the high conductivity of water enhances the rapid and uniform distribution of body heat, and a process whereby this thermal buffering capability is augmented may therefore be important in avoiding any fluctuations in body temperature associated with the consumption of snow and frozen forages.

In addition to these nutritional and thermal implications, the occurrence of this phenomenon in reindeer suggests that equations established for the prediction of body composition in other species do not necessarily apply to *Rangifer*. In fact, the higher percentages of total body water noted above for both field and laboratory studies result in very small (<3 per cent) of negative values for fat content when applied to prediction equations established for sheep by Panaretto and Searle (see above). Since the estimation of

body composition is an important parameter in assessing nutritional status, this work points to a need for developing the appropriate equations for reindeer.

ACKNOWLEDGMENTS

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GLUCOSE METABOLISM IN FEMALE REINDEER

J. R. Luick and R. G. White

Institute of Arctic Biology

University of Alaska

Fairbanks, Alaska 99701

ABSTRACT—Initial studies on aspects of carbohydrate metabolism in reindeer showed that plasma glucose concentration exceeded that of other ruminants while the volume through which it was distributed was normal. Studies were then made on the kinetics of glucose metabolism to characterize the reindeer in relation to other ruminants. Net and total rates of glucose synthesis and loss (expressed as mg/min per kg^{0.75}) were estimated using dual isotope (¹⁴C and ³H) dilution techniques in grazing and penned reindeer. The net and total rates of glucose synthesis in feeding female reindeer at maintenance (respectively 4.2 and 6.6), terminal pregnancy (respectively 2.8 and 7.1) and lactation (respectively 8 to 10.1 and 12 to 15) were similar to published values for sheep and cows. Highest rates of net and total synthesis of glucose (respectively 10.1 and 15.2) were noted in lactating females in the month of June. No significant difference was noted between lactating and non-lactating female reindeer in August and the high rates noted in June through September were greater than the respective estimates for females at maintenance and were associated with abundant vegetation, declining milk production and increasing body weights.

For most of the year (November to May), the net rate of synthesis of glucose in grazing female reindeer is at or below maintenance and the glucose requirement of the animal is met by recycling glucose carbon. This effect is most pronounced in late pregnancy; almost twice as much glucose was resynthesized as was formed *de novo*. Peak rates of glucose resynthesis are considerably higher than previous reports for other ruminant animals.

Glucose is known to be an important intermediate for the metabolism of nervous tissues, erythrocytes and fetal-placental tissues in mammals. In ruminants little glucose is absorbed from the alimentary tract and all glucose must be synthesized from dietary precursors. During pregnancy and lactation the requirement for glucose increases (see reviews by Leng, 1970; Lindsay, 1970); for instance in sheep as much as 70 per cent of the rate of *de novo* synthesis of glucose is used for fetal requirements and in the lactating goat a continuous supply of glucose is an absolute requirement for milk production (Linzell, 1967; Annison and Linzell, 1964; Annison *et al.*, 1968). It is not known whether the requirements of reindeer and caribou for glucose are similar to domestic ungulates; however if they are, synthesis of glucose from dietary sources may be an important process affecting fetal growth and milk production. Late winter and early spring are periods of high glucose demand in caribou for females are generally either pregnant, or lactating; this is also a period when food is frequently unavailable or of low quality. Undoubtedly, reindeer and caribou have well developed mechanisms to overcome such limitations. This paper describes our field studies on the synthesis of glucose by pregnant and lactating reindeer. The seasonal pattern of change in glucose synthesis is discussed in light of influences of diet and physiological status; the ability of reindeer to synthesize glucose is compared with estimates

for domestic sheep and cattle. Some of these findings have been previously published in detail (Luick *et al.*, 1973) or are in preparation for publication (White and Luick, 1974).

MATERIALS AND METHODS

Initial experiments were made on female reindeer held in outside pens at the Institute of Arctic Biology, University of Alaska. The reindeer were offered *ad libitum* a commercial pelleted ration (Purina Cattle Starter No. 1). Food intake was not measured but body weight was maintained constant over the period of the trial (January) confirming previous reports of a 'winter dormancy' phenomena in this species (McEwan, 1968).

All other female reindeer were taken from semi-natural grazing at the University of Alaska's Reindeer Research Station at Cantwell, Alaska. A description of the summer vegetation available to these animals has been published elsewhere (Luick *et al.*, 1973). Supplementary feeding with commercial pellets was required during winter and early spring, however, supplementation ceased at least three weeks before experiments started.

The exact regimen for conducting these experiments has been described (Luick *et al.*, 1973); briefly, animals were taken from the field, cannulated and experiments were started within 45 minutes. The experiment consisted of intravenous infusions of radioactive glucose and sampling of blood through indwelling venous catheters at 30 minute intervals for a three-hour period.

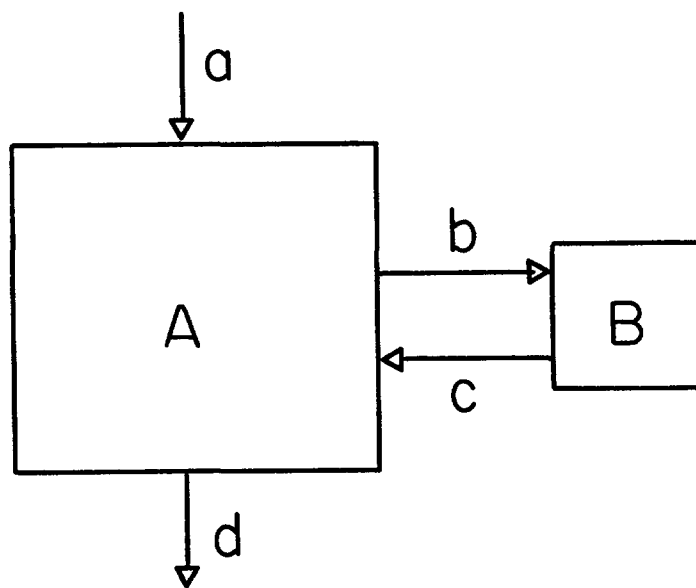
The rate of entry of all glucose carbon into the pool of glucose was estimated with a single injection of either [3-³H] glucose or [2-³H] glucose and this rate is given as the sum of *a* and *b* in Figure 1. The rate of net, or *de novo*, synthesis of glucose was estimated from primed infusions using [U-¹⁴C] glucose and is given as *a* in Figure 1. In conditions of steady state, the rate of *de novo* synthesis is equivalent to the rate of irreversible disposal of glucose (*d* in Fig. 1). The amount of glucose recycled to the glucose pool (termed glucose resynthesis) was calculated as the difference between the estimates of total synthesis and net synthesis (i.e., *c* or *b* in Fig. 1). The methods used to calculate these parameters plus the glucose pool size and space have been outlined by Luick *et al.* (1973).

Glucose concentration in plasma was estimated by the method of Hoffman (1937) and glucose was isolated from plasma as the glucose pentaacetate derivative (Jones, 1965). Independent assay of ¹⁴C and ³H in a Nuclear Chicago Scintillation Spectrometer (Mark III) were made by dual channel counting using external standardization for quench correction. [U-¹⁴C], [2-³H] and [3-³H] glucose were obtained from Amersham/Searle Corp., Des Plaines, Ill. and were made up in 0.9 per cent (w/v) Na Cl solutions.

RESULTS AND DISCUSSION

In initial studies, it was noted that the plasma glucose concentrations of reindeer (109-119 mg/100 ml) were considerably higher than estimates for domestic sheep and cattle (48-83 mg/100 ml) (Table 1) and may be closer to those of horses (cecalates) and other non-ruminants. The space of distribution of glucose was normal at 17-36 per cent of body weight and the mechanism by which this high glucose concentration is achieved is not known. Errors in techniques, such as chemical analysis and excitability of the animals, have been eliminated as factors causing spuriously high estimates.

Since all reindeer were taken directly from the pen or field, it is suggested that the estimates of glucose metabolism should reflect those of a fed animal. The rate of irreversible loss, or *de novo* synthesis of glucose, in reindeer at maintenance 4.3 ± 0.7 mg/min per kg^{0.75} is similar to estimates of sheep (3.9 - 4.5 mg/min per kg^{0.75}) at maintenance (Table 2). However, the rate of total synthesis of glucose may be slightly higher than that for sheep



$$\text{NET ENTRY} = a = \text{NET LOSS} = d$$

$$(\text{IRREVERSIBLE LOSS})$$

$$\text{TOTAL ENTRY} = a+c = \text{TOTAL LOSS} = b+d$$

$$\text{RESYNTHESIS} = \text{TOTAL ENTRY} - \text{NET ENTRY}$$

$$= (a+c) - a = c$$

Fig. 1.—Simplified model for glucose metabolism in reindeer. Pool A represents the body pool of glucose which is interconnected with a product pool, B. Pool B is probably made up of glucogenic intermediates such as lactate, glycerol, glycogen and glucogenic amino acids. Glucose entering pool A arises from gluconeogenic precursors (c) and dietary and tissue precursors (a): absorption of glucose from the alimentary tract is considered to be very small. Net entry into glucose pool was estimated with a primed infusion of $[U-^{14}\text{C}]$ glucose, and total entry with a single injection of $[2-^3\text{H}]$ glucose or $[3-^3\text{H}]$ glucose.

reflecting the slightly higher demand for glucose in reindeer taken from outside pens compared with that of sheep housed indoors. Recent unpublished results of Cameron, Luick and White have shown that the digestible energy intake for maintenance of reindeer, in a winter photoperiod, is slightly higher than that for sheep. However, the difference in intakes was small and per unit digestible energy intake, reindeer and sheep synthesize approximately the same amounts of glucose from dietary precursors.

Figure 2 shows the annual cycle of total and net synthesis of glucose in grazing reindeer. The horizontal lines (Jan. - Mar.), represent total and net synthesis of glucose in non-pregnant, non-lactating reindeer cows at maintenance. It is clear that net synthesis of glucose by reindeer in mid- to late-pregnancy (January and April, respectively) is below estimates for non-pregnant reindeer at maintenance. However, particularly during late

TABLE 1.--Species variation in plasma glucose concentration and space (all animals non-pregnant, non-lactating).

	Glucose concentration (mg/100 ml)	Space (% B. Wt)
Domestic sheep ¹	60-72	15-32
Cattle ¹	48-83	14-27
Horse ²	102	20
Reindeer ³	109-119	17-36

¹Leng, 1970.

²Evans, 1971.

³This study.

TABLE 2.--Comparison of net glucose synthesis (or irreversible loss) in sheep and reindeer at maintenance (all animals non-pregnant, non-lactating).

Species	Total	Net	Resynthesis	Significance of difference in total and net synthesis
Sheep ¹	4.8-6.5	3.9-4.5	0.8-2.5	N.S.
Reindeer ²	6.65	4.26	2.39	p<.05

Units, mg/min per kg^{0.75}.

¹White *et al.* (1969).

²White and Luick (1974).

pregnancy, the rate of total synthesis is about the same as that for non-pregnant reindeer at maintenance; the increased rate of glucose synthesis was apparently brought about by resynthesis (*c* in Fig. 1) of glucose from products of glucose metabolism (e.g. lactate). During early- to mid-lactation (May - June), both total entry rate and irreversible loss of glucose are approximately twice the rate estimated for non-pregnant, non-lactating reindeer at maintenance. Rates of net synthesis of glucose in reindeer during early- to mid-lactation (8-10 mg/min per kg^{0.75}) were similar to estimates of 8-11 mg/min per kg^{0.75} for domestic sheep (Bergman and Hogue, 1967) but were slightly lower than estimates for domestic goats (Annison and Linzell, 1964) and for cows (Davis and Brown, 1962; Brown and Lindsay, 1966; Annison *et al.*, quoted by Lindsay, 1970) of respectively 9-18 and 6-16 mg/min per kg^{0.75} (Table 3). These values were obtained with domestic animals given adequate food. The higher rates of net glucose synthesis during early- to mid-lactation in reindeer may possibly be the result of adequate dietary precursors of glucose. Judson and Leng (1968) and Lindsay (1970) have shown that the rate of net synthesis of glucose is highly related to digestible organic intake in non-pregnant, non-lactating sheep, whether this relationship holds during undernutrition and in pregnant and lactating animals remains to be shown. In the present study, during early lactation a decline in body weight, noted in lactating reindeer, was attributed to the high metabolic demands of lactation (White and Luick,

1974). Hence, at this time glucose was probably being synthesized from body reserves and dietary precursors. Of all glucose irreversibly lost from the glucose pool, only 16 per cent could be attributed to the synthesis of lactose (Table 4) whereas in lactating domestic livestock 28-55 per cent of glucose disposal can be accounted for as lactose. It is suggested that the reindeer may divert more glucose carbon to the synthesis of other milk constituents such as lipid and protein, during the first two weeks of lactation. This could explain the lower lactose and higher lipid and protein contents of reindeer compared with cows' milk (Luhtala *et al.*, 1968; Jenness and Sloan, 1970) particularly at a time when the availability of dietary lipid and protein is scarce.

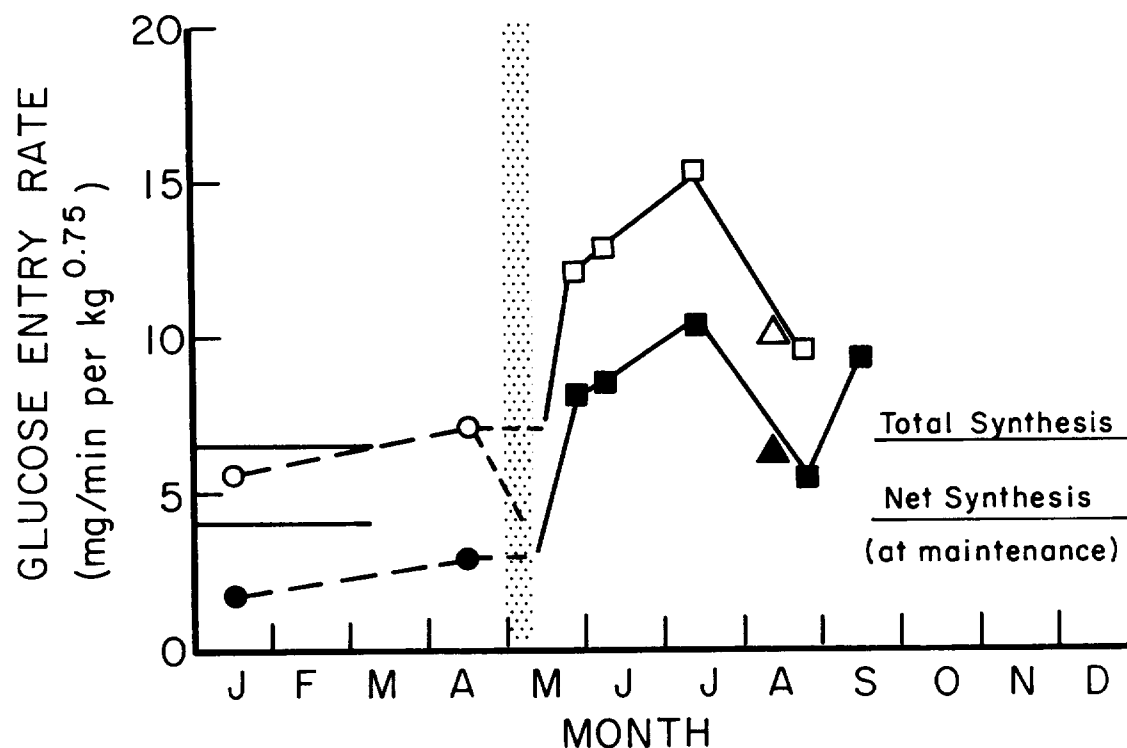


Fig. 2.—Seasonal changes in the rate of total (unfilled symbols) and net (filled symbols) synthesis of glucose in pregnant (○—○, ●—●) and lactating (□—□, ■—■) reindeer; △, ▲, individual estimates of glucose entry rate in non-pregnant, non-lactating cows in August; ▣, calving period; horizontal lines represents estimates of total and net glucose synthesis for non-pregnant, non-lactating reindeer cows at maintenance.

Peak rates of glucose synthesis were noted after the reindeer had been lactating 8-9 weeks. Preliminary evidence from this laboratory (Holleman *et al.*, 1972) shows that milk production is low at this time compared with that during the first 2 weeks (McEwan and Whitehead, 1971; White *et al.*, 1971). The findings that food quality and availability are high and requirement for lactose synthesis is low, suggests that glucose carbon at this time may be available for synthesis of body tissues. The peak rates of net synthesis of glucose in reindeer were similar to those of domestic sheep but were considerably lower than in cows and goats, both of which have been highly selected for milk production.

We have only one comparison of the rate of net synthesis of glucose in lactating

compared with non-lactating reindeer. These results, shown in Table 4, were for reindeer in late-lactation (August). No significant difference in the net synthesis of glucose was noted and both groups were synthesizing glucose at approximately 1.3 times that for non-pregnant, non-lactating reindeer at maintenance.

TABLE 3.--Species variations in peak rates of net glucose synthesis (irreversible loss) during lactation.

Species	Week of lactation	Net synthesis (mg/min per kg ^{0.75})	Fraction converted to lactose
Goats ¹	6	18	0.30
Cows ²	-	16	~0.28
Sheep ³	4	11.1	0.55
Reindeer ⁴	8-9 (2)	10.1±1.7 (8.0)	0.03 (0.16)

¹Annison and Linzell (1964).

²Brown and Lindsay (1966).

³Bergman and Hogue (1967).

⁴White and Luick (1974).

Values in parentheses are estimates for reindeer during peak conversion of plasma glucose to milk lactose.

TABLE 4.--Comparison of glucose synthesis in lactating (L) and non-lactating (NL) reindeer (studies were made in late lactation, Aug.).

	Glucose concentration (mg/100 ml)	Space (% B. Wt)	Net synthesis (mg/min per kg ^{0.75})	
NL	110	21	9.00	
L	125	18	9.20	N.S.

White and Luick (1974).

Glucose resynthesis in grazing reindeer constitutes an important contribution to total glucose synthesis. Estimates for grazing, pregnant and lactating reindeer ranged from 3-5 mg/min per kg^{0.75} and are in excess of that for female reindeer at maintenance (2.4 mg/min per kg^{0.75}) and are higher than previous reports for sheep (1-3 mg/min per kg^{0.75}) [calculated from the results of White *et al.* (1969) and Dunn *et al.* (1972)]. The fact that reindeer may synthesize from 1.4 to 2.3 times as much glucose from products of glucose metabolism than from dietary precursors suggests a well-developed gluconeogenic pathway. The implications of a lowered diversion of glucose carbon to lactose formation, the high rates of glucose resynthesis and the high, though apparently normal, concentration of plasma glucose (see Tables 1 and 2), are currently being studied in our laboratory.

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**SOME PRELIMINARY OBSERVATIONS ON INTRASPECIFIC
ACOUSTIC COMMUNICATION OF SEMI-DOMESTIC REINDEER,
WITH EMPHASIS ON THE MOTHER-CALF RELATIONSHIP**

Carol A. Ericson
Alaska Department of Fish and Game
Fairbanks, Alaska 99701

ABSTRACT—This study provides a general description of the overt acoustically related behavior of reindeer during the calving season by means of a series of observations under naturalistic conditions. The adult vocalization is a low-pitched grunt, while calves emit higher-pitched bleats. During the calving season these vocalizations are primarily associated with mother-infant interactions. As a result of this study, it is hypothesized that grunts and bleats serve as alerting signals but play no role in actual individual recognition.

A wide variety of non-vocal sounds, such as belches, coughs and sneezes, are emitted by adults during relaxed rumination. These sounds provide a means of herd cohesion and reassurance of the individual's 'in-group' feeling. Snorts are frequently used in connection with agonistic behavior and during alarm situations. Bleats are infrequently emitted by calves during apparent paradoxical sleep.

Sounds emitted by reindeer and caribou (*Rangifer tarandus*) have been mentioned in nearly every comprehensive study of the species. The tremendous babble of grunts and snorts associated with the large post-calving aggregations of animals, coughing, sneezing, panting and the various sounds of the rutting male, as well as the clicking sounds produced by the sesamoid bones during locomotion, have been described by numerous investigators (Caton, 1877; Seton, 1929; Jacobi, 1931; Murie, 1935; Flerov, 1952; Grudin, 1953; DeVos, 1960; Semenov-Tian-Shanskii, 1960; Lent, 1964; Espmark, 1964 and 1968; Kelsall, 1968).

Maternal-infant vocalization in particular has been variously reported as low-pitched, hoarse, cough-like grunts for the cow and bawling or bleating cries for the calf (Jacobi, 1931; Murie, 1935 and 1944; Flerov, 1952; Banfield, 1954; DeVos, 1960; Pruitt, 1960; Preobrazhenskii, 1961; Lent, 1966; Kelsall, 1968). Mother-infant acoustic signals are observed to be most frequent during herd movements or disturbances or when, for other reasons, one member of the pair becomes alarmed and cannot locate the other member (Seton, 1929; Murie, 1935:32 and 1944:155; Lent, 1966:726 *et seq.*; Baskin, 1969:75; Kelsall, 1968:42). Even when no general distress situation is apparent, the cow grunts while she is searching for her calf or while it is searching for her (Jacobi, 1931:217; Pruitt, 1960:31; Preobrazhenskii, 1961:124; Lent, 1966:738). Grunting is also noted when the cow wishes to elicit approach or following by an infant; most frequently this is done in conjunction with other approach-eliciting behavior (Jacobi, 1931:217; Murie, 1944:156; Pruitt, 1960:32; Lent, 1966:734, 735, 750, 752; Kelsall, 1968:42; Baskin, 1969:75).

While intraspecific acoustic communication signals have been documented for a number of social ungulates, there has not been a systematic examination of this possibility in reindeer and caribou despite the numerous references to their emission of and reaction to a wide variety of sounds. Therefore, this study was designed to obtain basic information on the acoustic behavior of reindeer when they are relatively undisturbed. It is intended to be a preliminary framework of summarized observations and hypotheses upon which future

acoustic communication studies to test these hypotheses can be built. Because these observations were made during the calving and early post-calving period, the emphasis of the study is necessarily upon the acoustic signals associated with that part of the animal's annual cycle.

MATERIALS AND METHODS

The study was conducted from April 29 to June 13, 1970 by the author and an assistant. During the 45-day span of the study, a total of 171 hours were spent in observing the small herd of semi-domestic reindeer confined in a 1.5 ha (3.6 acre) paddock at Cantwell, Alaska. The observer, equipped with 7 x 35 binoculars, a watch, a stop-watch and paper and pencil stood or sat in an advantageous position within the paddock to view the entire herd. The observations had two primary objectives: to quantify the number and kind of sounds produced by individuals, and to determine the kinds of behavior associated with each sound. An Uher 4000 Report-L magnetic tape recorder at a recording speed of 7.5 ips, with an AKG model D-900E parabolic range microphone (frequency response range 40-13000 Hz), was used to record acoustic signals for 18 of the observational hours.

The reindeer herd observed in this study consisted of 18 individuals: six calves born immediately before or during the study, and their six mothers, three cows without current calves, two males and one steer. These animals belong to the Reindeer Research Section of the University of Alaska's Institute of Arctic Biology, whose research personnel continued their own physiological experiments during the course of this study (for details see Luick, 1970).

Nine of the adult semi-domestic reindeer studied had been continuously confined for at least 18 months prior to the study. Three had been continuously confined for at least two and a half years. Three animals had been resident at the Cantwell site for 18 months prior to the study, while the remaining nine had been there for nine months. Of the six cows who had calves during this study, four had been mothers at least once before. Two of the current calves had been born a few days before the study commenced and the remaining four were born during the study period. The oldest calf was eight weeks of age and the youngest five weeks when the study terminated.

RESULTS AND DISCUSSION

Vocal Sounds

The loudest sounds emitted by reindeer are the vocalizations which will herein be referred to as 'grunts' and 'bleats'. They are the most widely described and obvious acoustic signals emitted by reindeer and seem the most amenable to investigation as distinct communication signals. Of the 202 total observed grunt events, 188 (93 per cent) were emitted by the six cows which were mothers of calves, and 14 were emitted by the six other adults. A total of 890 bleat events were observed for the six calves.

'Grunt' is an appropriate term for the adult vocalization. It is an explosively harsh, grating, low-pitched sound, rather like someone attempting very loudly to clear their throat. Most often the mouth is open during the entire vocalization, but in some cases it is open for only part(s) of the emission or remains closed entirely.

The grunt vocalization begins in one of two ways: a sudden, cough-like explosion of sound was most common, but, occasionally, the sound commenced slowly and built, within 0.10 second, into a grunt.

Though there are variations in the intensity of grunts, this is not nearly as marked as

the variations of bleats. Maternal grunts were found subjectively to be louder with increased stress and excitement. Espmark (1971) has also observed this in reindeer, and De Nahlik (1959:28) and Gilbert (1968:870) describe similar findings for fallow deer mothers (*Dama dama*). The postures of vocalizing adult or infant reindeer are fairly stereotyped. Animals which are walking or trotting during the vocalization assume one of two postures: (1) head extended with dorsal surface of the neck slightly concave, so that the head is level with or slightly lower than the spine — a posture very similar to the 'threat pose' illustrated and described by Pruitt (1960:5-7) or the 'attraction pose' illustrated and described by Lent (1966:730, 734-735); (2) head raised high and held horizontally, with an alert expression. Animals which remain standing while they vocalized also assumed an alert, head-high posture and occasionally exhibited the full alarm posture (Pruitt, 1960:14). Both Pruitt (1960) and Lent (1966) mention that grunts sometimes accompany these postures. Lent (1966) found that grunts in conjunction with the 'attraction pose' were always associated with cow-calf behavior, but the head-bobbing which he described as being frequently associated with this vocal behavior in caribou cows was never observed in this study.

'Bleat' is an appropriate description of the short, piercing cry of infant reindeer (in this study, from birth to eight weeks). Bleats vary widely in pitch, shrillness, intensity and duration among individual calves of the same age, for the same calf at different ages and even for the same calf on one particular occasion. During periods of agitation and alarm, bleats tend to be louder and of longer duration. Newborn calves seem to utter bleats which are more highly pitched and shrill, so that the sound is alarming and difficult to ignore. The bleats of older calves become increasingly low-pitched, probably due to physical maturation of the vocal tract and musculature as well as to the general increase in body size (Tembrock, 1963), so that the 'bleat' vocalization of infants becomes the loud, low-pitched 'grunt' of adults.

These observations on the physical quality of grunts and bleats are primarily subjective. While nearly 300 sound spectrographs of grunts and bleats were reproduced, no reliable conclusions on physical characteristics could be made because of the generally poor quality of these recordings made under field conditions.

Bleats and grunts occur singly, in pairs or in series in time. These series may be appropriately designated by what Tembrock (1963:764) terms 'homotypical sound sequences' in that single vocalizations are produced one after the other with random time intervals between them. Within a series of grunts or bleats, however, sound emissions tend to occur relatively regularly with each expiration of breath. This is particularly true of a vocalization series uttered under alarm conditions. The fastest series rate for adults and calves is approximately 100 bleats per minute. This rate is maintained constant for up to eight seconds after which a breathing pause of one to three seconds duration is taken; every 20 to 30 seconds a somewhat longer pause is taken to breathe several more times.

Because grunts and bleats most frequently occurred in pairs or series such collections of vocalizations, rather than single vocalizations, were taken as the units of analysis. These units were termed 'vocal events'. A 'vocal event' is herein defined as a grunt or series of grunts or a bleat or series of bleats emitted by one vocalizer on one occasion characterized by a particular behavioral context. Most vocal events were less than 30 seconds in length. Vocal events of longer than one minute occurred most commonly when blood samples were being taken by Institute of Arctic Biology personnel. During these times a restrained calf would often bleat and its mother grunt continuously and antiphonally. The event ended when workers allowed the calf to rejoin its mother.

Vocalizations as Communication Signals

Mothers vocalize far more frequently than other adults but are less vocal than their calves. While the occurrence of calf bleat events is not a clear function of age within the first seven weeks of life, the occurrence of grunt events by mothers decreases sharply after three weeks post-partum, consistent with her declining maternal instinct. Calves concurrently tend to associate increasingly with other individuals, often with other calves. DeVos (1960) makes a similar observation for caribou, and other workers (Collias, 1956; McHugh, 1958; Espmark, 1969) describe both the increasing maternal indifference and the increasing infant independence in other wild and domestic ungulates.

Although there were large differences in the total amount of vocalizations emitted by individuals, all mothers and calves vocalized in characteristic kinds of situations. During the first three weeks post-partum, this was almost always the case in connection with mother-infant attractive and bond-reinforcing behaviors. Beyond three weeks post-partum, mothers rarely vocalized except when alarmed, but calves, particularly certain individuals, bleated frequently while exploring or interacting with other herd members.

Of 368 nursing events observed, 25 per cent were preceded by the calf's bleating while only 4 per cent were preceded by maternal grunting. The percentage of nursing events preceded by bleats decreased markedly in the fifth week post-partum (Fig. 1). Nursing

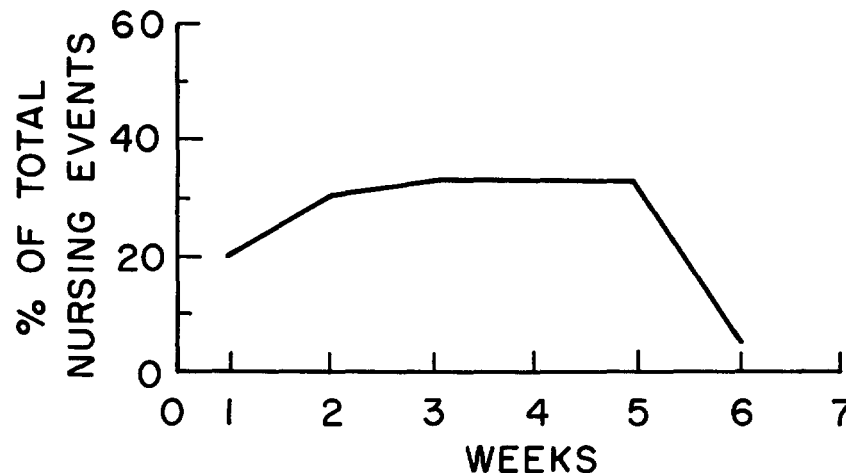


Fig. 1.—Percentage of total nursing events observed ($n = 326$) in each week post-partum which were preceded by bleating of the calf.

followed only 9 per cent of all bleat events and only 6 per cent of all grunt events. Because non-vocal mother-infant interactions, aside from nursing, were not systematically quantified, the importance of vocal events for maintaining the mother-offspring bond is not precisely clear. That vocalizations provide a means for exchange of reassuring stimuli, particularly during stress conditions, was made clear by the frequent occurrence of grunts and bleats when mothers were standing directly beside their offspring.

Individual Differences in Vocal Behavior

Certain individuals vocalized much more frequently and for longer periods of time than others. Previous maternal experience was not a consistent factor determining the vocal propensities of either a mother or her offspring, nor was there a clear direct or inverse relationship between the vocal propensities of members of each cow-calf pair (Table 1). Detailed quantification of these differences may be found in Ericson (1972).

TABLE 1.--Number of vocalizations associated with individuals and with calf age.

A. Bleats					<u>No. of bleats (wk)</u>					
					<u>Time (wk)</u>					
Individual					20c	2c	5c	10c	12c	17c
Age (wk)	1				x	8.25	53.73	8.28	20.98	34.97
" "	2				4.81	3.28	54.66	15.7	22.75	Ø
" "	3				13.12	8.67	46.63	13.33	24.75	7.96
" "	4				3.47	18.22	38.97	7.72	25.40	13.92
" "	5				10.12	12.09	62.80	6.28	25.00	12.09
" "	6				5.18	10.01	x	12.37	x	8.61
" "	7				3.69	13.29	x	19.21	x	x

B. Grunts by cows with calves					<u>No. of grunts (wk)</u>					
					<u>Time (wk)</u>					
Individual					20	2	5	10	12	17
Age of calf (wk)	1				x	1.38	10.40	3.55	40.21	10.93
" " "	2				5.50	6.56	4.05	6.54	7.84	Ø
" " "	3				3.28	5.20	1.04	Ø	3.38	1.59
" " "	4				1.73	6.07	1.58	Ø	3.10	0.61
" " "	5				2.02	2.07	2.42	Ø	14.00	0.90
" " "	6				0.69	4.21	x	Ø	x	2.03
" " "	7				Ø	12.08	x	0.62	x	x

Since it has been widely observed that vocalization in a group of ungulates invariably increases with stress and increased movement (Herscher *et al.*, 1963; Lent, 1966; Hafez, Cairns *et al.*, 1969) and was substantiated also in this study, individual differences in propensity to vocalize may be explained as individual differences in thresholds of alarm.

Baryshnikov and Kokorina (1964; see also Hafex, Schein *et al.*, 1969) have classified cattle into different 'personality types' according to their variations in excitability. Excitable individuals were found to differ from lethargic ones in many facets of their responses to disturbing stimuli. These variations in temperament may explain both the large differences in the occurrence of maternal grunts seen in this study, particularly after bleat events, and Herscher, Richmond and Moore's (1963:218) corresponding observation for sheep and goats that "some dams are particularly responsible to the bleating of the young,

answering almost any call of distress from any young, other dams almost never show vocal responsiveness."

Lent (pers. comm.) has found an interesting counterpart to the widely different vocal propensities of the reindeer calves discussed in this study. In two muskox, *Ovibos moschatus*, calf births which he observed in 1971, one calf vocalized 50 times during its first hour of life while the other did not vocalize once in the corresponding period. There was a tendency for the reindeer calves in the present study, which were born later in the season, to vocalize more in all situations. Since it has been shown that domestic calves or lambs isolated at birth vocalize infrequently or not at all (Collias, 1956; Hafez, Schein *et al.*, 1969), stimulation to vocalize may be socially facilitated by hearing the mother's or other individuals' vocalizations. But the percentage of total bleat events which actually followed maternal grunts or the vocalizations of other calves or adults was small. Lent (pers. comm.) has observed some newborn muskox calves to vocalize frequently even if they have not yet had the opportunity to hear others including, in one case, the mother. Social facilitation, then, may not provide the entire explanation for the more frequent vocal behavior of the later-born calves.

Later-born calves are born into an acoustic environment already containing the bleats of calves. It is possible that, because of this, later-born calves must vocalize more frequently to attract the same amount of maternal attention, particularly during the critical first several weeks post-partum. Lent (1966) has described how caribou calves born early in the calving season spend their first days in relatively small, slow-moving nursery bands, while calves born later find themselves part of large and noisy aggregations that are rapidly moving out of the calving areas. Maternal interest declines rapidly during the post-calving period so that calves, particularly late-born ones which become separated from their mothers during mass herd movements and stress conditions, are often abandoned (Lent, 1966). Thus, it must be advantageous for later-born calves to vocalize more frequently, though the mechanism accomplishing this was not made clear in this study. Besides social facilitation, differences in temperament, excitability and consequent "thresholds of vocal emission" remain potential explanations.

Individual Recognition

A major suspected use of maternal-infant acoustic signals is to locate and recognize the other pair member when mother and offspring are separated.

Many observers of ungulate behavior have hypothesized that mothers are able to recognize their offspring on the basis of its vocalizations alone, or calves are able to recognize their mothers, or both. Maternal recognition of the calf's voice is surmised by Smith (1965) and Smith *et al.* (1966) for domestic sheep, and by Gilbert (1968) for fallow deer. Espmark (1971) describes evidence of the ability of both reindeer mothers and calves to identify each other by voice, and McHugh (1958) and Marjoribanks-Egerton (1962) also describe supposed mutual recognition by bison cows and calves (*Bison bison*). The most widely held theory, however, is that it is the calf which recognizes its own mother's call. This is noted for reindeer (Baskin, 1969) and caribou (Lent, 1964 and 1966) as well as for dall sheep, *Ovis dalli* (Murie, 1944), mule deer, *Odocoileus hemionus* (Einarsen, 1956), the Indian antelope, *Antelope cervicapa* (Tembrook, 1968), and domestic cattle (Hafez, Schein *et al.*, 1969).

However, with the exception of Espmark (1971) and Smith (1965), neither the studies cited above, which discuss supposed vocal recognition, nor other accounts of vocalizing mothers locating vocalizing calves (the red deer, *Cervus elaphus*: Darling, 1937:139; the saiga, *Saiga tatarica*: Bannikov, 1961:148) effectively eliminated visual and olfactory clues.

It is possible that many of these studies have mistaken for maternal vocal recognition the alerting effect of *any* infant call (or even crude imitation) on a mother who is not with and cannot contact her offspring. The physical appearance of the individual mother coupled with the attraction posture frequently accompanying vocal emission undoubtedly provide important visual clues in what otherwise might seem to be totally acoustic recognition of mothers by calves (see Herscher *et al.*, 1963).

With regard to maternal visual recognition of their own infant, during the course of this study the mothers of the two very dark older calves would frequently reject each other's calf only after olfactory inspection, but they both repeatedly rejected the similar-sized piebald calf from a distance of one or two meters, without ever sniffing it.

This author agrees with Tschanz (1962), Altmann (1963), Baskin (1969) and Hafez, Cairns *et al.* (1969) that individual recognition between mothers and calves is a complex of visual, olfactory and acoustic clues. It is probably that olfactory recognition is the first to develop (Tschanz, 1962; Altmann, 1963) and is most important (Collias, 1956; Bartholomew, 1959; Smith *et al.*, 1966; Thorpe, 1968; Baskin, 1969). Visual recognition follows olfactory. In this study visual recognition was apparent in cows approximately two days post-partum, but, up to the age of two weeks, calves persisted in approaching any adult which glanced at them or which did not threaten or avoid them. Altmann (1963) mentions a similar period for elk calves (*Cervus canadensis nelsoni*) and Lent (1966) describes how young caribou calves frequently follow strange cows, even leaving their own mothers to do so.

During the critical first two weeks of the calf's life, the burden of recognition is on the strongest member of the pair — the mother. It is selectively advantageous that she respond quickly to a wide range of alarm signals. Thus she is not only more easily alarmed by unusual stimuli, but also by any acoustic stimulus resembling the often-varying distress signal of a young calf. The observations of this study lead the author to support Lindsay and Fletcher's (1968:416) hypothesis, which concerns domestic sheep but might well apply to many other ungulates. It maintains that the very young infant's call acts as a non-specific alerting signal which stimulates a mother separated from her offspring to search for it, but the infant call itself "...plays no part in actual recognition." In a like manner calves may be stimulated to seek their mothers upon hearing any adult grunt. However, Espmark's (1971) preliminary evidence for older calves' recognition of maternal calls indicates that further investigation of this question is necessary.

Non-Vocal Sounds

Grunts and bleats are primarily sounds produced by the action of the vocal cords and associated laryngeal musculature. There are numerous other sounds produced by a variety of other patterns of motion in the upper respiratory and alimentary tracts which are enhanced and made more audible, just as are grunts or bleats, through resonance in the nasopharyngeal cavities. These include sounds associated with the respiratory and digestive processes, and include coughs, sneezes, wheezes, snores, belches and sounds associated with yawning, swallowing and regurgitation. Such sounds will herein be referred to as 'non-vocal sounds'. A total of 394 non-vocal sounds were emitted by adult reindeer during the study, compared to 202 total grunt events. In contrast, calves emitted only 25 non-vocal sounds but 890 bleat events.

Snorts, the most common kind of non-vocal sound, are frequently used in connection with agonistic behavior, particularly as if to emphasize a visual threat display, and with alarm postures and gaits. Other ungulates are also known to use the snort or similar sharp respiratory sounds in conjunction with threat (Fuller, 1960; Cowan and Geist, 1961; Geist,

1966; Hunsaker and Hahn, 1965; Leuthold, 1966; Park, 1969; Van Wormer, 1969). All snorts observed were emitted by adults. Snorting is a common alarm signal among ungulates, and both DeVos (1960) and Kelsall (1968) have described its occurrence in this connection for caribou.

A few snorts were emitted by relaxed, ruminating, resting individuals, as were the other non-vocal sounds. The very small number of such sounds emitted by calves is attributed mainly to the young calves' non-ruminant method of digestion (Krebs and Cowan, 1962; Warner and Flat, 1965). Most of the adult non-vocal sounds were clearly associated with rumination, and, when not actively browsing, healthy adults ruminated while standing or lying in a relaxed manner.

Non-vocal sounds, with the exception of the snort, are not used as communication signals in the same sense that grunts and bleats are used. But it cannot be ignored that such sounds, associated with vital life processes, are virtually continuously evident, particularly in a large herd. McCullough (1969:71) found a similar "continuous array of sounds" in a herd of Tule elk (*Cervus canadensis nannodes*). He believes that such noises constitute continuous integrative signals for maintaining herd cohesion, and this author agrees. Etkin (1963:156) describes how the 'in-group feeling', so vital to the psychological well-being of highly social animals, is developed and maintained "...by the interchange of mild stimuli with other members of the group." Clearly, the continuous undercurrent of respiratory and digestive sounds, as well as other sounds incident to feeding, locomotion and life activities, inevitably present in a large herd of reindeer can serve as a source of these stimuli. The reassuring effects of all these sounds must contribute to the marked reduction in alertness of individuals in large aggregations that has been described by numerous writers (Murie, 1935; Banfield, 1954; DeVos, 1960; Lent, 1964; Kelsall, 1968).

Vocal Emissions by Sleeping Calves

Twenty soft, bleat-like sounds were emitted by calves during apparent paradoxical sleep. Apparently the signals were not in response to any obvious environmental factor because the vocalizers were not conscious. These bleats instead must be the result of internal processes, either discomfort or perhaps some activity in the central nervous system (Wiggers, 1949; Klemm, 1966; Loizzo and Longo, 1968).

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A REVIEW OF ACOUSTIC COMMUNICATION IN *RANGIFER TARANDUS*

Peter C. Lent
Alaska Cooperative Wildlife Research Unit
University of Alaska
Fairbanks, Alaska

ABSTRACT—The repertoire of acoustic messages employed by members of this species is small compared to some other ruminants. This is related to the use of relatively open habitat with corresponding dependence on visual and olfactory signals and to the lack of long-term individual roles and social structures. Vocal signals are limited to monosyllabic sounds, usually occurring in non-rhythmic sequences. The grunts of adult females and rutting males appear to be derived ontogenetically from the bleats of infants. Audiospectral analyses show that grunts by maternal cows differ significantly from the infant bleats only in the absence of harmonics over 3,000 Hz and in the presence of more energy in a non-vocal 'noise' component. Acoustic signals functioning in mother-infant contact, group cohesion, threat and courtship are described and, in most cases, illustrated by sound spectrograms. Bleats of infant caribou show very little variation within sequences made by one individual compared to those made by different individuals. The importance of acoustic information in individual recognition of mothers and offspring by their respective partners has been the subject of conflicting reports. Most workers agree that infants are able to recognize their own mothers' vocalizations. Mothers tend to react less selectively to infant vocalizations.

Terrestrial mammals use four basic modes of transmission for communicating intraspecifically: optical, acoustic, chemical and tactual. Mammalian communication like that of all other animals makes great use of redundancy in signals. There are several forms which this redundancy may take, for example, redundancy within a mode, as when an acoustic signal is used repetitively, or the use of more than one acoustic signal with the same message, or redundancy involving more than one mode of transmission, as when acoustic and optical signals convey the same message. This last form of redundancy is nearly universal in mammalian social interactions. Nevertheless, species and populations differ greatly in the degree to which they employ a given mode of communication, depending upon their evolutionary history and perhaps also upon local traditions, etc.

In this paper I will treat the topic of acoustic communication in *Rangifer tarandus* by reviewing the work and observations of others with various subspecies and including some of my own work which is now in progress with both barren ground caribou and domestic reindeer of Siberian origin.

Before turning to *Rangifer* I want to make a few brief remarks on some other ungulate species. Schloeth (1958, 1961) described 11 different vocal signals produced by the wild cattle of the French camargue. Tembrock in his review (1968) noted the use of at least 14 different voiced sounds in the genus *Sus*. Murie (1932) described approximately eight different voiced calls made by elk and notes some distinct variations of these basic sounds. Our investigations in progress with Alaskan moose have revealed a similar sized repertoire to that of elk. In each of these studies, similar signals produced by infants, females and males

are considered as separate items in the repertoire. Nevertheless, several workers have suggested a direct ontogenetic development from a given infant vocalization to a given adult vocalization (Schloeth, 1961; Tembrock, 1968). I will return to this topic in relation to *Rangifer* later.

Table 1 shows seven acoustic forms having known or suspected communication

TABLE 1.--Some acoustic phenomena with communicative functions in *Rangifer tarandus*.

Name	Emitter	Function
Bleat	Calves (rare after 6th month)	Care soliciting, contact (affin type)**
Grunt	Maternal cows (rare after five months post-partum)	Contact (affin type)
Grunt or panting*	Bulls during rut	Agonistic (threat) and courtship
Licking* or slurping*	Bulls during rut	Courtship
Snort	Adults especially	Threat (diffug type)**
Sesamoid click	Adults especially	Group cohesion (?)
Antler clatter	Bulls during rut	Affin type

*Terminology that of Bergerud (in press).

**Tembrock (1967).

functions in *Rangifer*. I have omitted many of the acoustic phenomena mentioned by Ericson (1972) and have limited this list to those acoustic phenomena which are known or suspected to cause overt behavioral changes in conspecifics. We see at the top of the table the basic vocalizations, the grunt and the bleat, which Ericson (this volume) has already dealt with. While variations in both intensity and in other qualities do occur among grunts and bleats, these variations in quality do not seem to be associated with specific messages or functions. Ericson (1972) has noted that bleats of calves tend to be louder, of higher pitch and of longer duration when the animals are under great stress. The grunt appears to be the adult version of the bleat, derived directly from it ontogenetically. A detailed audiospectral comparison of bleats and grunts tends to support this idea. All the audiospectral analyses referred to in this paper are based on sonograms made with a Kay Audio Spectrum Analyzer with a 45 Hz band width.

Table 2 shows there is no significant difference in the duration of individual signals between bleats and grunts. Furthermore they occur in similar bouts, or sequences. Occasionally a bleat will show a bi-syllabic structure. This seems to occur when calves vocalize while in motion. Otherwise, all bleats and grunts are mono-syllables. Regarding the fundamental or base frequency of these two types of vocalizations we find some significant difference but, nevertheless, considerable overlap between bleats and grunt. Some bleats have relatively low fundamentals falling within the range of most of the grunts. The major difference between the two which I have been able to measure is in the harmonics or overtones. Almost all bleats have overtones of over 3,000 Hz and some go as high as 8,000. In contrast only one of the 14 grunts analyzed for the data in Table 2 had an overtone of over 3,000 and the means for the two types of vocalizations are different with a high degree of significance (Table 2). A further difference which is not illustrated in Table 2 is the

TABLE 2.--A comparison of bleats by caribou calves with grunts by adult females. All recorded July 3, 1971; Pitmegea R., Alaska.

	Duration (sec)			"Fundamental" (Hz)			Highest Overtone (Hz)		
	\bar{X}	sd	N	\bar{X}	sd	N	\bar{X}	sd	N
Bleats	0.196	0.04	60	1100	590	62	4300	2000	37
Grunts	0.203	0.06	17	630	480	12	2300	830	14
t=		0.63			2.58			3.56	
p=		>.50			<.02			<.01	

presence of a larger non-tonal or unstructured 'noise' component in grunts. That is, the tonality of the bleats is more marked. This lack of tonality becomes even more evident in the rutting grunts or panting sounds of bulls and I will be showing a sonogram later to illustrate this. I wish to leave the topic of maternal grunts and infant bleats now and will return to it later in a discussion of the use of acoustic signals for individual identification in *Rangifer tarandus*.

Going back to Table 1, I want to mention briefly the sesamoid click. The question mark which I have included in the table, under function, is to emphasize that there is really no strong evidence that this clicking sound, produced from the feet of reindeer and caribou, has a communication function. We only surmise at present that it does. Pages and pages have been written on the subject of this sound, and particularly on its anatomical derivation. This has been reviewed quite thoroughly in Jacobi's monograph in 1931, based primarily on the intensive work of Erna Mohr and others, and relatively little new information has been added since then. The consensus of opinion seems to be that the sound is produced by sesamoid cartilages. I have conjectured, as have others, that the sound aids in promoting group cohesion, which in turn is so important in response to predation, as I believe Dr. Cumming will be discussing in a later paper.

In Table 1, I list three acoustic signals associated with the rut. These are produced only by males, at least as far as I have observed with barren ground caribou and so far as I can determine from a literature review of material on other subspecies.

The first of these male rutting sounds is a very hoarse type of grunt (Fig. 1) made by short exhalations and produced in rapid succession. I have previously referred to this simply as the grunt (Lent, 1965). Bergerud (in press) refers to this as panting. He found that in Newfoundland panting was most frequent before the peak of breeding. It occurs in several different contexts involving both agonistic encounters between adult males and general 'chasing' of females. In the latter context the sound apparently attracts the attention of potentially receptive cows. The second male-produced sound is limited to male-female interactions and is associated with the 'tending' phase of courtship. Espmark (1964: 160) describes this as a "husky sound, audible at a distance of only a few metres, which appears to be made by smacking the slightly extended tongue against the palate." I have rarely heard this sound among barren ground caribou, presumably because most of my observations were made from too far away. I do not have a sonogram of this sound. Bergerud (in press) refers to this activity as tongue-licking and states it occurs along with the 'low-stretch' posture in a behavioral complex he calls 'slurping'. He suggests the overall effect is to demonstrate to a female being approached that attack is not intended. Finally in connection with rutting behavior, I want to mention the sound produced by antlers. While much has been written regarding antler function in *Rangifer*, the secondary role of hard antlers as organs of sound production has not been considered. It is a role even more developed in certain other

cervids, particularly moose. The sound of clashing antlers by two males is frequently sufficient stimulus to cause other mature males to move towards the combatants even though they are out of sight. Thus a mechanism exists which brings active rutting males together and presumably in contact with females in or entering estrus. Bergerud (in press) suggests that females are also attracted to the sounds of antlers striking one another. I have not observed this. Like most other cervids, *Rangifer* males spend time during the rutting season thrashing the vegetation with their antlers. This may have a similar acoustic effect especially when woody shrubs are involved. I have observed the attractive effect of such brush thrashing most clearly in moose (Lent, in press).

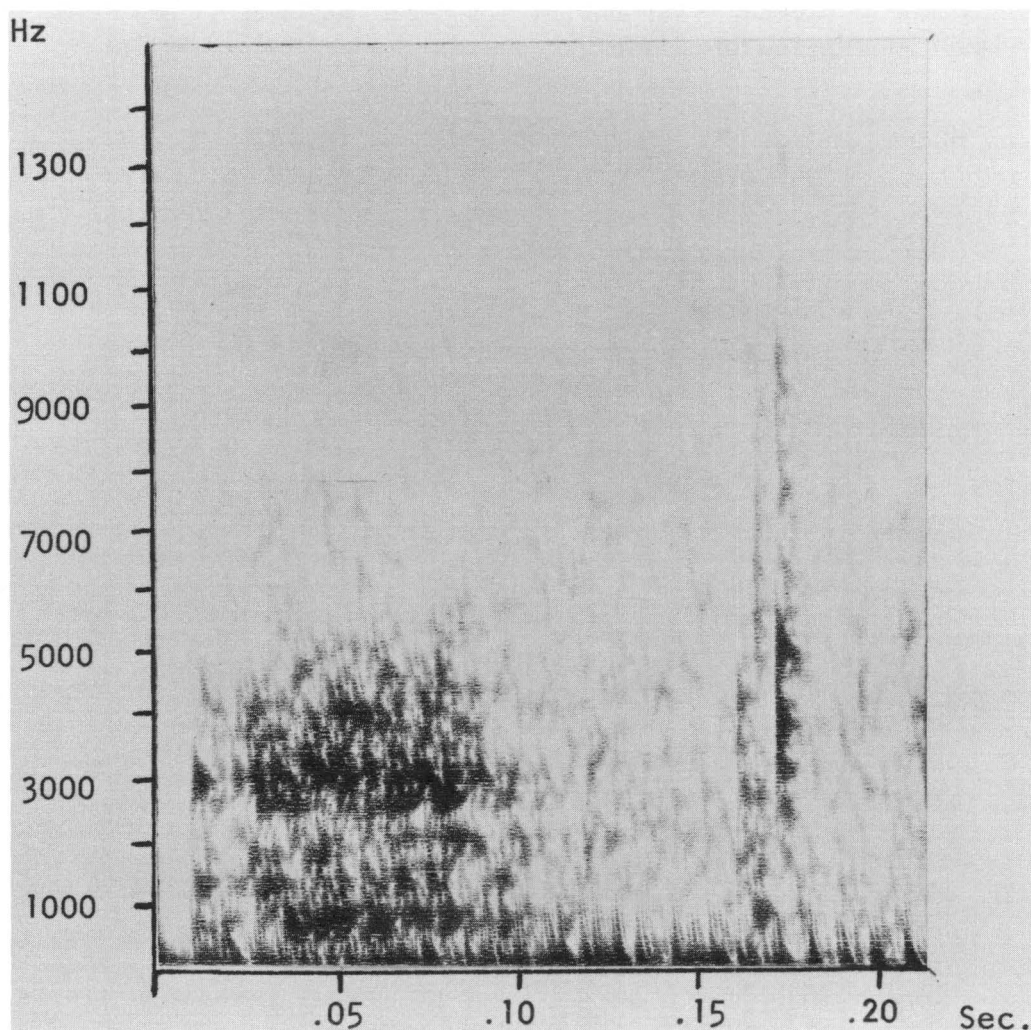


Fig. 1.—Rutting grunt (or 'pant') by male caribou followed by antler click.

What is lacking in the vocal repertoire of *Rangifer* compared to that of other ungulates? For one thing there are no long-duration vocalizations such as the bellows or roars so common among the Bovinae or the whistles and bugles characteristics of genus *Cervus* during the rut. Such long-duration calls are closely associated with long distance communication. Particularly in the case of rutting males, such long calls also show

great individual variability and may indeed function in individual recognition under conditions of wide spacing in forested habitat. Long duration calls would be better suited for compensating for information loss due to noise between signaler and recipient. Another gap in the repertoire is the lack of vocalizations by females during the rut, as I have previously mentioned. Also females do not employ specialized sounds associated with nursing such as occur frequently in the *Suidae* and in *Alces* for example. Finally, there is a poor development of acoustic alarm signals in *Rangifer* and a correspondingly greater dependence upon visual and olfactory signals for this function (Pruitt, 1960; Lent, 1966; Baskin, 1970). The snort is used in this context occasionally, particularly when the source of alarm is close by (Kelsall, 1968), and also as a threat signal (Fig. 2). It is clearly 'diffug' type, of short duration and formed rapidly.

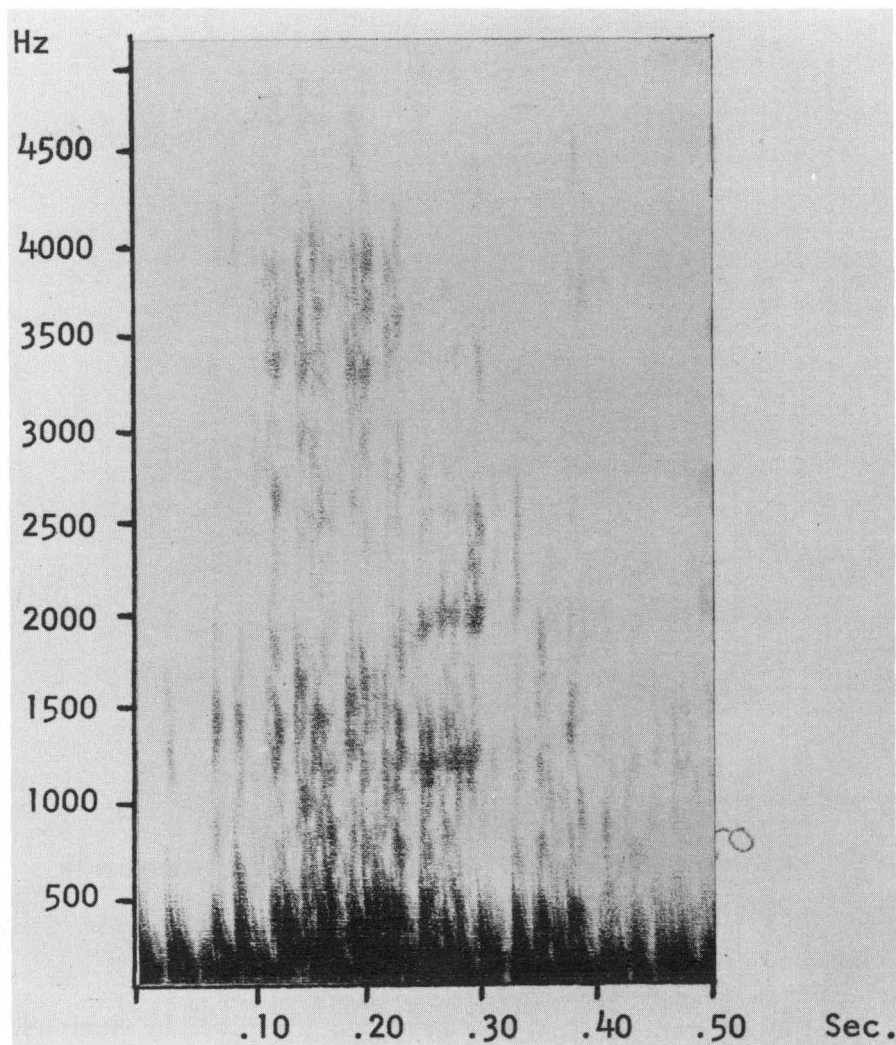


Fig. 2.—Threat snort by adult caribou cow.

The species *Rangifer tarandus* has evolved behavior to provide for efficient use of relatively open habitat. Its gregarious nature and generally open social structure permits populations to remain mobile and to converge at optimum times and places in great

concentrations (see Bergerud, 1971 for further discussion of this aspect). This lack of complex social structure is one of the reasons why the repertoire of acoustic signals is limited to relatively few simple messages. Essentially all these messages have a meaning of either 'come closer' or 'move away'. These are what Tembrock (1967) has referred to as the 'affin' type and 'diffug' type messages. Brereton (1971) in a comparative study of closely related parrot species found that the species with both intra- and inter-group hierarchies had the largest repertoire of auditory signals. The smallest repertoire was found in a highly gregarious arid-land species. I suggest that an analagous situation exists in the Cervidae.

Now I wish to turn to the subject of individual recognition by acoustic means. This discussion is limited solely to mother and infant relationships. It seems unlikely that acoustic individual recognition would occur in other relationships. Thorpe (1968) reviewed the evidence for acoustically based recognition in vertebrates. At that time the only experimental work with ungulates was that of Tschanz (1962) with moufflon and Smith (1965) with sheep. Since then Kurt (1968) has done some experimental work with roe deer and, most pertinent here, Espmark (1971) has done experimental work with Swedish reindeer. His work shows clearly that calves have the ability for individual recognition of their mothers based on recognition of vocalizations. Isolated calves were found to react fully only to playbacks of their own mother's vocalizations. Experimental evidence for maternal recognition of calf vocalizations is somewhat weaker since the procedure involved removing one calf from an otherwise intact group and then testing for a reaction by that calf's mother or by mothers of other calves whose calves were still present in the group. In this latter experimental series, Espmark did find that in almost all cases the mother of the calf removed from the group did react and that other mothers did not react.

I have attempted on two occasions to playback vocalizations of reindeer cows and calves to barren ground caribou during normal post-calving migration in the wild. Vocalizations attracted the attention of some individuals, particularly yearlings. The typical response consisted of an individual stopping, staring in the direction of the speakers, perhaps taking a few paces towards it, but never coming closer than about 40 m. After less than one minute the individual usually moved on in the direction which it had been traveling. A few individuals showed mild alarm responses. Generally, however, rapid habituation to the repetitive acoustic signal occurred. Unfortunately, there were no opportunities to test the reactions of cows and calves that had become separated from their respective partners to these playbacks.

Based on his many observations of reindeer in the USSR, both domestic and wild, Baskin (1970) believes that infants rapidly learn to identify the vocalizations of their mothers. He estimates that five to six hours post-partum are necessary for the development of this ability.

Many workers, including Preobrazhenskii (1961), Baskin (1970), Ericson (1972) and myself have observed that cows with young infants respond rather non-selectively to infant vocalizations and even to crude human imitations of these bleats, by becoming alerted and frequently searching for the vocalization source. Baskin (1970) suggests that there is selection in favor of this broader receptivity by mothers, since being the stronger of each pair they are best able to seek out and identify any uncertain signals. On the other hand, I have observed that they will rapidly habituate to strange infant's bleats and ignore them after initial investigation, even though their own infants may be missing.

One of the techniques used in the study of individual recognition in bird species has been the analysis of variance among successive calls. That is, measuring the positive correlation of certain variables between successive calls by the same individual and comparing these with the amount of variance between calls made by different individuals (Thorpe, 1968; Hutchinson *et al.*, 1968). This work has indeed shown highly significant

positive correlations between successive calls of individuals and significant differences between these correlation coefficients and those involving sequences of different individuals. I have under way similar analyses with caribou vocalizations, and Espmark is working on this with reindeer in Sweden. Some preliminary results of this work with caribou are shown in Tables 3 and 4. Of the three variables measured, it can be seen that the frequency of the

TABLE 3.--Correlation coefficients for selected variables from pairs of successive bleats by the same individuals.
Total sample 9 individuals.

Variable	r
Duration	.85
"Fundamental"	.87
Highest overtone	.99
P<.01 for all three	

TABLE 4.--Correlation coefficients for selected variables from 6 "randomly" paired bleats made by 12 different individuals.

Variable	r
Duration	.07
"Fundamental"	.49
Highest overtone	.44

highest overtone shows the highest correlation coefficient in the case of bleats by the same individual, duration shows the lowest coefficient. In the case of bleats selected randomly from different individuals, there is a relatively high correlation coefficient for the base tone or fundamental but none of these correlation coefficients are anywhere near as high as those existing between pairs of successive bleats by the same individual. Hutchinson *et al.* (1968), Thorpe (1968) and coworkers have used this type of analysis as supporting evidence for their belief that individual recognition by identification of vocalizations is important in many bird species. There are several weaknesses with this type of analysis, to be sure. One of these is that they are dealing only with vocalizations made in one series at a given moment, and have no data to compare vocalizations by the same individual made on different days. The work of Ericson (1972) with reindeer does indicate that the vocalizations change rapidly as the infants mature. This rapid change however, does not necessarily mean that the cow is unable to identify her own offspring's vocalizations, since one only has to assume a continual feedback process which permits the cow to continue recognizing the bleat of her own offspring as the individual matures. Another major weakness to this approach is that there are certain variables in the vocalizations which are easily measured and others which are not. Obviously, one tends to select for statistical analyses those qualities which are easily measured. These may not be the ones which are of any significance to the animals involved. For example, I selected the duration of the signal, the fundamental frequency and the mean frequency of the highest overtone. However, the shape of the fundamental and its overtones appear highly characteristic. We have no way of treating this statistically at present, even though it is a visually obvious phenomenon, as may be seen in Figure 3. In this figure I have

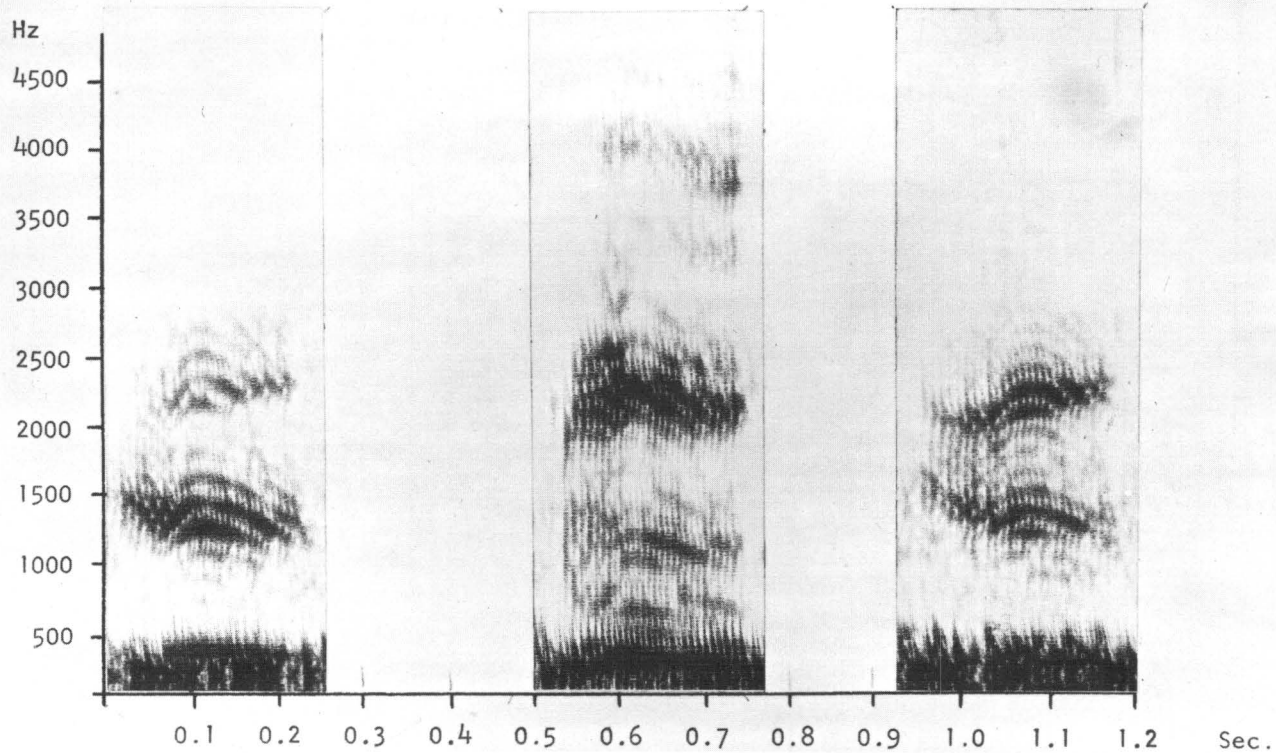
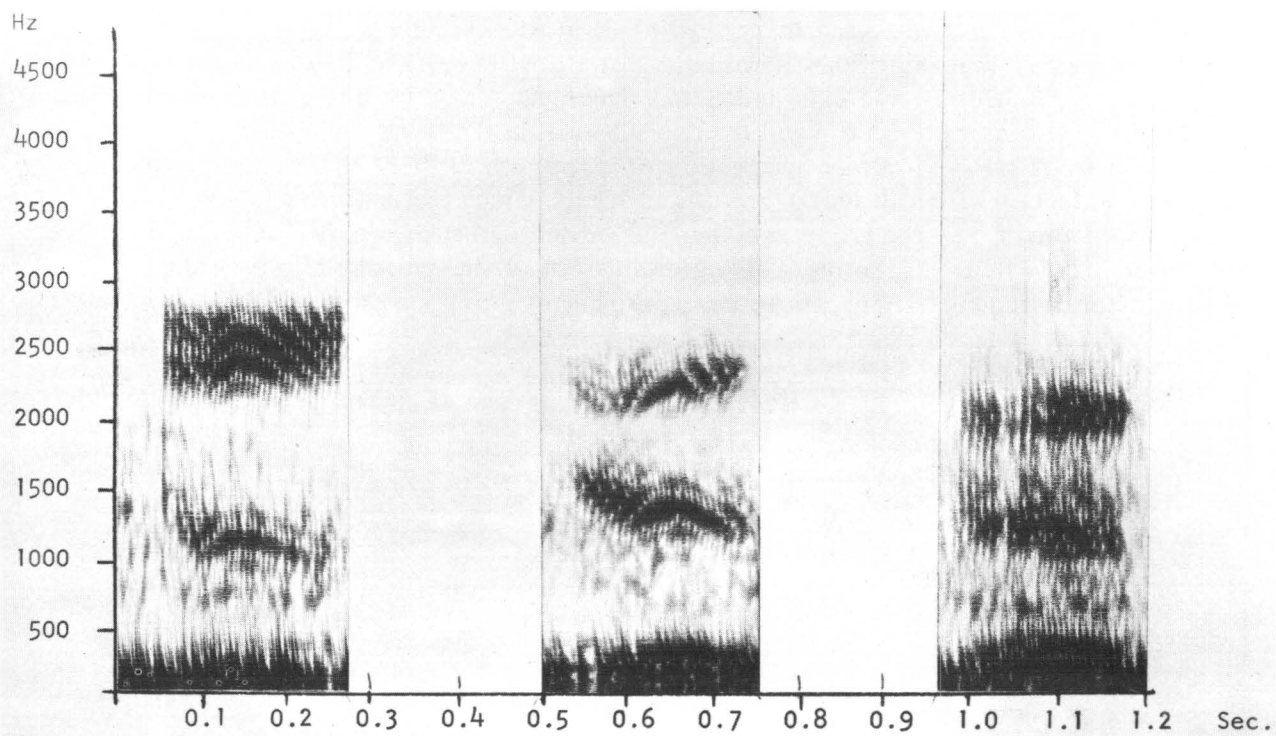


Fig. 3.—Six bleats by caribou calves. Three of these were successive bleats by the same individual. They are scattered randomly (see text).

selected three successive bleats made by the same individual calf and mixed them randomly with three bleats by other individuals. I would ask you now to see if you can visually pick out the three bleats made by the same individual. The bleats made by the same individual are B, D and F, the center one on top and the two side ones in the lower row.

In a dense, active post-calving aggregation of migratory caribou, there is an almost continuous production of vocal signals, grunts and bleats, which increases to a babble with any form of disturbance to the group, whether this be an event such as a river crossing or a rainstorm or even a flock of ptarmigan flying up in front of the animals. This continuous acoustic environment (Fig. 4) appears to promote general group cohesion and behavioral

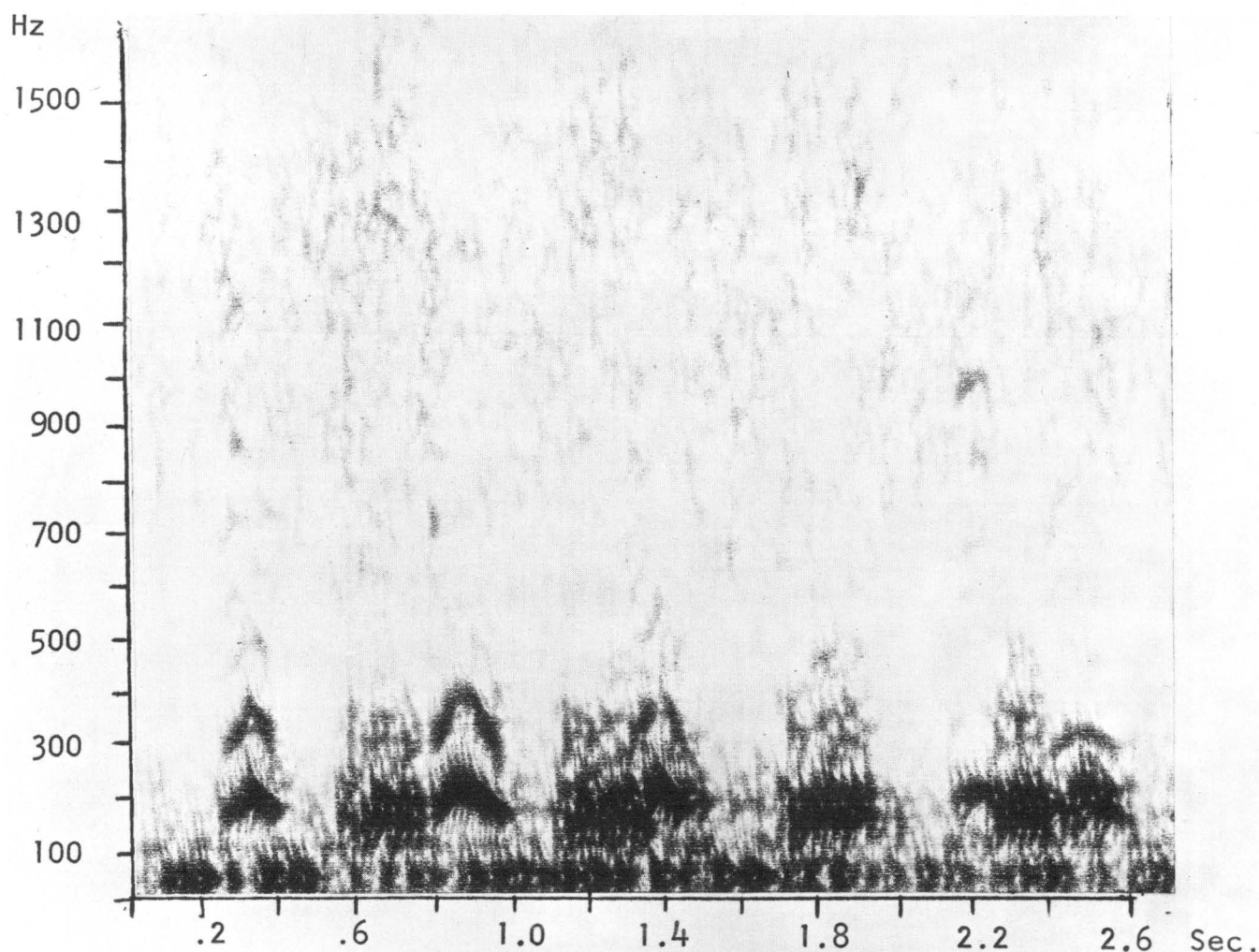


Fig. 4.—Noise associated with disturbed caribou group during post-calving period.

synchrony. If a cow has been separated from her infant she may move through such a group, or in a reverse direction from the migratory movement, ignoring this acoustic bombardment, and reacting only when the familiar signal of her own infant is heard. The similarity between this situation and the so called cocktail party effect described by Cherry (1957), in which humans are able to filter out a babble of noise to pick out and understand a familiar voice, is quite striking. Of course, the caribou mother always confirms her acoustically based

identification with visual and, probably more importantly, olfactory cues after she and her infant come together again. My own observations suggest that as the time post-partum progresses, mothers become less and less susceptible to excitation by any calf bleat and more and more selective in responding only to their own infants' bleats. Thus as one would expect in such a precocial species in which ontogenetic events occur very rapidly, the age of the calf is an important and critical variable to be considered in any further experimental work on individual identification. Obviously the results which are attained by the calves of say one week of age may be very different from those attained with calves of five weeks of age.

Because of their relatively small vocal repertoire, and the simple nature of the vocalizations produced by reindeer and caribou, they provide excellent subjects for further experimental work in the field of animal communications, ontogeny of behavior and information theory.

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MOTHER-YEARLING RELATIONSHIPS IN REINDEER AT BIRTH OF THE NEW CALF

Yngve Espmark
Department of Zoology
University of Stockholm
Stockholm, Sweden

ABSTRACT—The behavior involved in breaking up of the social bonds between the reindeer mother and her yearling when the new calf is born was studied. Social affinity was quantified by recording occurrence of agonistic behavior between mother and yearling and estimated average distance between them when resting. No agonistic behavior was observed during the pre-calving period and the average resting distance was estimated to be significantly shorter than between any two randomly chosen individuals in the herd. At parturition the mother became very aggressive towards her yearling, who was actively driven off, and consequently the resting distance between them increased to what was considered to be at least the average distance between randomly chosen animals in the group. No difference in social relationship between mother and yearling related to the sex of the yearling was found. Presumably due to strong general social affinity between the individuals in a reindeer herd the sudden breaking-up of the mother-yearling bonds appears to be less traumatic for the reindeer yearling than for yearlings in more solitary cervids.

The behavioral interactions between the mother and her yearling at the birth of the new calf and the period thereafter have been considered, although briefly, in a number of papers dealing exclusively or in part with behavior of the genus *Rangifer* (e.g., Kelsall, 1957; Lent, 1966; Espmark, 1971a). Convincing evidence is given that mother and yearling separate around the time of birth of the new calf, but it is not satisfactorily clarified whether the separation is caused by the yearling being driven off by its mother or if the yearling simply leaves its mother by choice when the new calf is coming (deVos, 1960; Lent, 1966). Although not supported by satisfactory evidences some authors (deVos, 1960; Kuhmunen, 1968) indicate that the social mother-yearling bonds break up some time before the actual calving time and that if the bonds do last until the mother's parturition, the yearling is most likely to be a female. It is also suggested that the yearling, after a period of separation, may rejoin the cow in late summer or autumn (Banfield, 1951).

The present paper is an attempt to bring some clarity to the understanding of the underlying processes leading to the definite separation between the reindeer mother and her yearling.

MATERIAL AND METHODS

In conjunction with behavioral studies on the mother-infant relationship at the National Reindeer Research Station Kuolpavare in northern Sweden in 1968, observations were also made on the relationship between mother and yearling. Some of these data are presented in a previous paper (Espmark, 1971a). As this material suffered from incompleteness a more detailed investigation was undertaken at the Reindeer Station in the

spring and summer of 1972. All the herd, consisting of about 150 animals, constituted the study group although most of the quantitative data were based on eight cows and their yearlings, all of them marked for individual recognition. The sex composition of the marked yearlings was four females and four males. In 1968 the study started on May 17, which was about the peak of the calving season, and ended on August 24. The observations in 1972 covered about one month before and one month after calving.

Social relationship was quantified by recording the number of aggressive acts from the mother towards her yearling and by estimating the distance between mother and yearling when resting. This measurement was chosen because it was considered to be more standardized than the individual distance in the moving group.

Most of the yearlings in the 1972 study, including all those individually marked, had been separated from their mothers for nutritive studies during the period November 25 to April 6. The separation distance was about 100 m thus excluding any contact. When reunited with the rest of the herd, the yearlings almost immediately joined their respective mothers and the relationship between them appeared as firm as between unseparated pairs.

RESULTS

Pre-calving Period

The yearlings were closely associated with their mothers during the whole period. The average resting separation was less than 5 m although in two out of 109 cases it reached as much as 100 m (Fig. 1). Aggressive behavior was often seen in pregnant cows although it was never observed to be directed towards their own yearlings but only towards other cows and strange yearlings. The aggressive displays in the herd during this period were considered to be normal expressions of dominance orders (Espmark, 1964). When mother and yearling became spontaneously separated, which often happened during foraging, all efforts to reestablish contact originated on the part of the yearling. This has been reported to be the case also in the genus *Odocoileus* (deVos *et al.*, 1967). Grunting calls were rarely heard from the yearlings searching for their mother. Mothers were never heard to call for the yearlings. Although communications were obviously not based on vocalization, the yearlings never failed to find their mothers without much hesitation. This might indicate that older calves recognize their mothers primarily by sight, while vocalization is more important in young calves (Espmark, 1971b).

It has been suggested (Lent, 1966; Kuhmunen, 1968) that male yearlings would display an earlier independence in their relation to their mothers than the females. Although based on a small material no such sex differences have been revealed in the present study.

Calving Period

Some time before parturition, in most cases around 24 hours, the pregnant cows began to display restless behavior, manifested in a gradual separation from the main herd, nervous trotting in the surroundings, sporadic and unconcentrated grazing, occasional grunting and an increasing intolerance towards herd members including their own yearlings. The time from the start of these first signs of the forthcoming parturition until the parturition is finished might be defined as the calving period proper. During this time the first aggressive attacks towards their own yearling were observed, although the yearling did not immediately respond to this increased intolerance by increasing the distance to the mother (Fig. 1). On the contrary, the yearling usually persisted in its attempts to maintain close contact with the mother leading to still more frequent and more vigorous rejections. As soon as the 'rest-

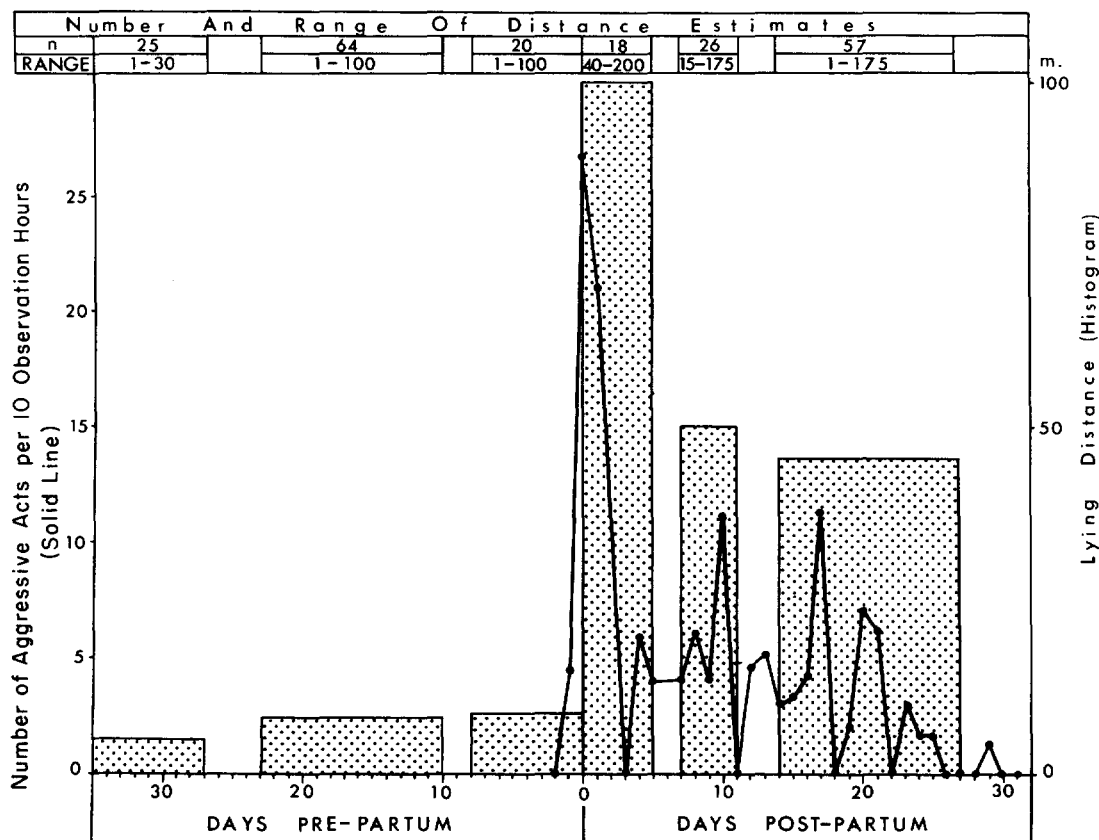


Fig. 1.—Frequency of aggressive behavior of the reindeer cows towards their yearlings and estimated lying distance between mother and yearling.

less' behavior of the cow ceased she became stationary in a small area where the calf was dropped. At this time there was a pronounced increase in the mother's aggressive activity and as a consequence the yearling began to bed at a considerable distance from the mother, a distance which was estimated to be greater than the resting distance separating two randomly chosen individuals in the herd. At parturition the yearling as well as other herd members were very curious and paid particular interest to the new-born calf and this resulted in a pronounced aggression from the mother.

Post-calving Period

The sudden change in resting distance between mother and yearling at parturition was obviously a result of the increased aggressive level in the mother. The considerable resting distance was maintained for the first five days post-partum although there was a pronounced reduction in the frequency of aggression. The yearling seemed to stay away from the mother by choice, probably as a result of associative learning.

The decreasing frequency of aggression might indicate an actual decrease of the aggressive level in the mother with a consequent increased tolerance towards the yearling. Linsdale and Tomich (1953) reported a similar development in the mule deer, *Odocoileus hemionus*. In addition, the reindeer yearling lost more and more interest in the mother and joined other yearlings and adult males, which constituted a separate group, often spatially

separated from that part of the herd consisting of mothers with new-born calves ('nursery band'; Pruitt, 1960). This spatial separation resulted in reduced possibilities for the mothers to interact with the yearlings.

During the first days following parturition the yearlings were driven off whenever they appeared in the vicinity of their mothers but most attacks were thereafter delivered when the nursery group prepared to rest. At such times the yearlings often became very persistent in their efforts to bed close to their mothers. If some of the yearlings succeeded to bed down they were then usually left without receiving any further attention from the mother. It might be suggested that an active and in particular an approaching yearling is more likely to evoke hostile responses from the mother than a passive yearling, even if it happens to be at a proximate distance.

Although the resting distance as well as the mother's aggressive behavior decreased gradually, there were no indications that the social bonds between mothers and yearlings were reestablished in late summer. The yearlings were more and more tolerated by their mothers, however, and after about three months the yearlings appeared to be well integrated into the mother group, even though they were still recipients of more attacks than other herd members.

Some of the cows lost their calves some days or weeks after parturition. After some 24 hours of 'mourning' (described by Espmark, 1971a) the cows resumed normal behavior and lost all hostility towards their yearlings, which successfully reestablished the association with their mothers.

DISCUSSION

The observations indicate that the social bonds between the reindeer mother and her calf weaken gradually from shortly after birth until the yearling's independence is completed some time after the birth of the new calf.

It might be assumed that the yearling makes efforts to maintain a two-sided social association. It tries to maintain contact with the mother, who before parturition tolerates the yearling but takes no obviously active part in maintaining the association. As a gregarious animal the reindeer yearling also tries to maintain contact with other herd members. When the new calf is born the efforts of the yearling to maintain contact with the mother will not be rewarded by acceptance but by hostility. In less gregarious cervids, for example moose, this might result in a social crisis for the yearling (Altmann, 1958) but such a crisis is not evident in the reindeer yearling and is presumably not occurring as it is able to satisfy its need for social contact by associating other herd members.

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WEATHER AND ITS EFFECT ON CARIBOU BEHAVIOR PATTERNS AND MIGRATION

Angus Gavin
Environmental Consultant
Atlantic Richfield Company

ABSTRACT—Studies on caribou movements on the North Slope of Alaska indicate that weather and snowfall have a decided bearing on range use and migration patterns. In the fall, high pressure systems apparently will trigger a steady movement and immediately after these the pace of migration slows considerably. Spring migrations to the calving grounds can be completely disrupted by weather and snow cover along their route. Strong winds and drifting snow will turn a whole migration around or delay it for many days since caribou are adverse to facing storms.

While considerable study and research on the caribou herds in the northern part of Alaska had been done prior to the major oil discovery on the North Slope in 1968, the advent of this discovery and all its related activity triggered an extensive research program. This program was designed to measure the effects this activity might have on the caribou frequenting this particular part of the Slope.

The writer, starting in 1969, has spent the last four summers on a study of the wildlife on that part of the North Slope affected by oil developments. Caribou migrations, numbers and patterns have received particular attention. Continual observations were carried out on practically a daily basis depending on weather conditions. Helicopters were used during the study.

DESCRIPTION OF AREA

The portion of the Alaskan North Slope under study consists of approximately 41,500 km² (16,000 mi²) of coastal plain. The major part of this is comparatively smooth, rising imperceptibly from the Arctic Ocean to a maximum altitude of 150 to 180 m.

Pingos break the flat monotony and produce an undulating skyline. Generally, the shore is quite flat, broken only by sand dunes near some of the river deltas and much of it is only about 1 m above the ocean level.

The whole area is very poorly drained and consequently quite marshy. Much of this part of the coastal plain is covered by elongated thaw lakes ranging in size from only a few m to over 2 km in length. All are quite shallow, varying from less than 1 m to a maximum of 4 m in depth. The entire area is underlain by permafrost which reaches a depth of over 300 m. Ice wedge polygons cover the entire plains. Several rivers and streams intersect our study area, the major ones being the Colville, Canning and Sagavanirktok. All are heavily braided and contain large quantities of gravel.

Surface vegetation throughout the coastal plains is typical tundra type, with mosses, lichens, grasses and sedges being most dominant. Throughout the numerous valley and river courses extensive stands of willow and dwarf birch prevail.

Since the entire area is poorly drained, sedge-grass marshes vary greatly, but the dominant plants are various species of *Carex* and grass interspersed with sedge, sphagnum

moss and bog-type plants.

NORTH SLOPE CARIBOU POPULATIONS

While portions of two major caribou herds frequent areas of the North Slope, the maximum numbers counted within our study area were in 1969 when some 26,000 animals were recorded during our fall survey. Hemming (1971) gives a fine history of the caribou populations using the North Slope. He indicates that the Arctic herd has a population of some 242,000 animals and in the main frequents that part of the Arctic Slope lying west of the Colville River during the summer months. From the same publication the size of the Porcupine herd population are given as some 142,000. This herd winters mainly in Canada and moves into Alaska during the spring and summer season. Much of the area used by the Porcupine herd lies within the Arctic National Wildlife Range which stretches from the Canada-Alaska border to the Canning River. Offshoots from both these herds comprise the total numbers of animals under study in the area lying between the Canning and Colville rivers and between the Beaufort Sea and the Brooks Range.

During spring migration there are several points of entrance from the Brooks Range to the study area (Fig. 1). The major ones are: (1) from Anaktuvuk Pass thence up the east side of the Colville River, (2) from the Dietrich and Atigun areas up the Itkillik and Sagavanirktok Rivers, (3) from the east fork of the Chandalar across to the Canning River thence northeast and northwest from this source. In 1969 total caribou in the area taken from summer counts by Sage and Gavin (unpub.) were roughly 26,000. In 1970 the count was about the same. Surveys in 1971 gave us a total of about 15,000, and in 1972 the number in the study area, as counted at the end of June, was only 2,000 animals.

WEATHER AS AN INFLUENCE ON PATTERNS AND MIGRATION

While it is well known that caribou have traditional calving grounds which they try to reach each spring, observations indicate that snow and other weather factors often prevent them from doing so. Our observations in 1971 bear this out quite clearly. Studies of fairly large herds, 6,000 to 10,000 animals, also suggest that high pressure systems and imminent storms will trigger migrations in late summer and fall.

Pruitt (1959), Banfield (1954), Kelsall (1960) all make reference to wind and snow conditions having an effect on caribou patterns and migrations. Our own observations indicate that snow conditions and wind coupled with low temperatures can change completely the traditional or normal pattern of spring migrations. In 1969 and 1970 the spring migration of caribou into our study area followed a pattern that was undisturbed either by deep snow or adverse weather conditions. Numbers were, as indicated earlier in this paper, around 26,000. These animals migrated in from the Anaktuvuk Pass area, from the Atigun-Dietrich area and up the Canning River. Calving in both 1969 and 1970 was well distributed along the coastal plain and the majority of animals stayed in these areas during much of the summer. Migrations in 1971 were entirely different. Deep snow in the mountains and over all of the coastal plain slowed the spring migration to such an extent that few animals reached the coastal areas by calving time. Much of the calving took place within the Brooks Range itself, and although some post calving movement into the area was noted, very few animals reached the coastal zone and only about half the usual numbers of animals came into the area under study. Most of the post calving movement in 1971 was on the east side of the Sagavanirktok River with the largest concentration of animals being in the Kavik area. Fall migrations were also entirely different. Few animals migrated west along the coast as in 1969 and 1970, most used the Sagavanirktok River, Dietrich-Atigun route.



Fig. 1.—Spring migration routes observed in study area.

Migrations in 1972 were also different from those of the past if we consider 1969 and 1970 as normal. In those two years conditions were excellent. Thawing temperatures by early May left open grazing along much of the higher ground. Caribou were over much of the coastal plain by the middle of May. In 1971 and again in 1972 snowcover over all of the coastal plain and into the foothill area was continuous with little or no thawing up to near the end of May. Temperatures at Prudhoe Bay rarely reached the thawing point over much of the month.

Surveys of the caribou population within our study area in 1972 commenced in early May and have been fairly continuous up to the end of June. At that time some 2,000 animals were estimated to be in the area, which is a tremendous drop from previous years. Heavy snow and extremely adverse weather conditions undoubtedly played a major part in keeping the normal quota of animals off this particular part of the Slope.

So far, I have dealt only with weather and deep snow as a factor in spring migration patterns. I also believe that weather, particularly high and low pressure systems, have a decided effect on fall migration movements. Like waterfowl, these systems affect the keen senses of caribou and warn them in advance of pending storms much the same as with waterfowl. On several different occasions I have witnessed a marked disturbance among caribou just prior to a storm. The most recent occurrence was in 1969. On the eastern part of our study area during the early and middle part of August there was a herd of about 6,000 caribou, composed of a mixture of cows, calves, yearlings and bulls. They were in close proximity to a very large pingo which served as an excellent observation point. Commencing on August 16 a close check was kept on this herd for several hours each day. Weather for the first two days was good with only some light clouds. Little movement was noticed in the herd during these two days other than a normal grazing pattern. On August 18, however, with bright clear weather there was a distinct milling and running around with no definite direction. Bunches of up to 100 animals would take off from the herd at a crisp gallop for several hundred meters and then turn around and race back towards the main herd. This continued at intervals during the several hours we spent watching from our observation point on the pingo. On August 19 the herd had moved about 16 km north but was still within glassing range of the observation point. Milling was much more evident during this period of observation. The whole herd was in motion during much of the time with no definite direction of movement being evident. Weather was extremely hazy to the northeast but still clear. On August 20 a snowstorm with strong northeast wind hit the base and continued all day clearing in late evening. We went east after the storm to observe the herd but it had completely disappeared. We covered the area by helicopter and finally located the herd far to the west near Ugnu. These animals had traveled some 100 km during the night of August 19 and presumably had done so ahead of the storm (Fig. 2). They remained in this area for nearly a week before moving down the east side of the Colville River towards Anaktuvuk Pass.

There are several questions one has to ask in connection with this particular movement. (1) Was the milling of the herd due to a high pressure system? (2) Did these animals sense that a storm was coming and move out ahead of it? (3) Could they just have been moving from one grazing area to another with the storm having nothing to do with their rapid movement? (4) Was the milling observed just prior to the move from one area to another part of normal fall migration patterns? In order to move the distance they did, they must have traveled at a rapid pace without stopping to graze which is not usual during fall migration.

I observed the same situation in 1938 at Bathurst Inlet off Coronation Gulf. We had been caught in late fall by freezing conditions and had to winter our small schooner in near the midway point of Bathurst Inlet. Soon after reaching there, we observed a herd of some

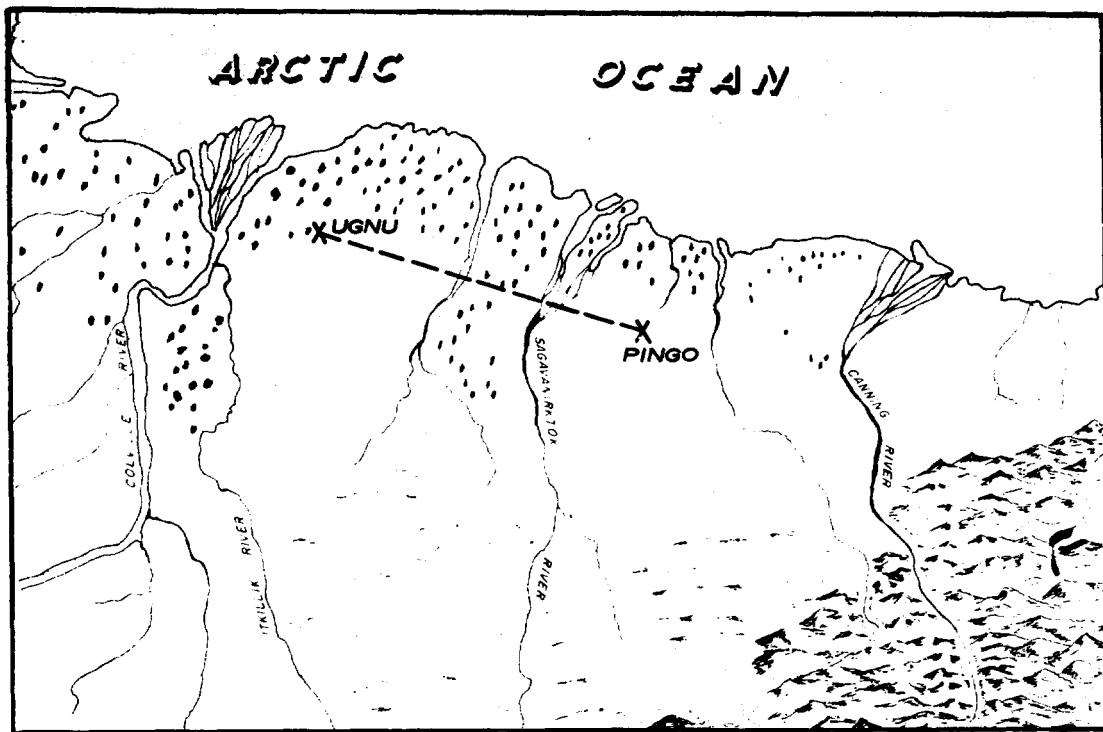


Fig. 2.—Movement of caribou occurring on August 19-20, 1969.

10,000 caribou along the east shore. They were less than one km from our boat and clearly visible at all times. Practically the same movements and milling were observed as near Pingo. In the Bathurst Inlet situation, however, we were able to observe the migration leaving. Weather was bright and clear when the movement took place but was followed the next day by a raging blizzard that continued for two days. Not having a helicopter available to follow up this movement as we had in 1969, we were unable to ascertain the exact distance this herd moved on this particular migration, however, we later talked to Eskimos who had contact with this herd. They reported that the caribou apparently moved well south of the bottom of the inlet before stopping for any length of time to graze. This was a distance of over 120 km. Here again, questions have to be answered as to whether this movement was prompted by a normal migration urge and the blizzard which followed was only a coincidence or whether these animals sensed a storm coming and moved out ahead of it. Further study may provide some of the answers to these questions.

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REVIEW TO RECENT REINDEER STUDIES IN FINLAND
BY STATE GAME AND FISHERIES RESEARCH INSTITUTE
AND UNIVERSITY OF HELSINKI

Leo J. Salo
Department of Agricultural and Forest Zoology
University of Helsinki

ABSTRACT—During the last few years reindeer studies carried out in Finland by the Division of Game Research, State Game and Fisheries Research Institute and the Department of Agricultural and Forest Zoology, University of Helsinki have centered in three major areas: (1) *nutrition of reindeer* including nutritive value and annual crop of lichen, the role of arboreal lichens as winter food, possibilities and methods of applying emergency winter feeding and the use of artificial mineral licks; (2) *effects of intensive forestry* including mortality of reindeer in connection with logging operations, probable poisonous effects of forest fertilizers and the ways and means to avoid these effects; (3) *various aspects of predation*, mainly the role of the golden eagle *Aquila chrysaetos* as a predator of reindeer fawns.

NUTRITION OF REINDEER

In northeastern Finnish Lapland die-offs due to starvation are of considerable importance especially during winters of deep snow. Nutritive values of lichens used by reindeer have been studied by Pulliainen (1971) and another project dealing with lichen crops in this area was initiated in summer 1971.

The study by Pulliainen (*op. cit.*) was based on the fact that the winter diet of reindeer consists of both ground and arboreal lichens but snow often restricts the use of ground lichens. Samples of several species were collected in wintertime and analyzed by a commercial laboratory (Peat Research Institute of Oy Satoturve). The results showed that arboreal lichens should not be considered an 'emergency food' as they are even more nutritious than *Cladonia* species. On the other hand, arboreal lichens are available in small amounts and the bitter taste of some species may reduce palatability.

The lichen crop study was initiated in summer 1971 and will probably continue for two-three years. The main aspect of this study is on the production rate and chemical composition, protein and minerals, of the lichen biomass.

Logging operations provide some 'artificial' winter feeding of reindeer by making available additional arboreal lichens. It has been stated that logging provides a continuous and regularly distributed winter feeding regime for reindeer that congregate in the logging areas. Rajala (1967) has discussed various positive and negative aspects of this phenomenon in detail. He came to the conclusion that in spite of death losses caused by logging, there is a real advantage to reindeer from feeding in the area. The close proximity to man also gives reindeer protection against predators, saving the lives of some 100-200 animals per year. In addition, ranges (ground lichens) have time to regenerate or are saved for later use. It has been reported that reindeer hear the 'call' of the chainsaw from the distance of about 10 kilometers. During winters of difficult snow conditions this behavior can be used in making winter feeding more feasible and beneficial. Hay may be provided in portable feed shelters

especially when the felling phase is in process in the logging area.

Several Swedish scientists (Skuncke, Nordfelt, Steen) have shown that in spite of good availability of lichen in the winter range of reindeer, their nitrogen balance is negative, and there is also an apparent deficiency of minerals during wintertime.

In order to see how eagerly reindeer would use artificial mineral licks, an experiment was set up near the Värriö Subarctic Research Station in 1971-72 (Pulliainen and Jaakkola, 1972). The licks weighing 10 kg each were placed in the area on May 11, 1971. Their average weight were 6 kg on September 15, and about 1.9 kg on December 30, 1971. In spring of 1971 reindeer left the Värriötunturi fell without touching the factory fresh licks placed there. In July several hundred cows with fawns appeared in muskeg along the Nuorttijoki River and were observed to use the licks placed there earlier. In July-August 20-30 animals still remained in the area and used the licks regularly. In winter 1971-72, several licks in the immediate vicinity of the Värriö Station were used daily. The reindeer ate also man's urine frozen in the snow. The following conclusions were drawn from this experiment:

At least in some circumstances reindeer will use artificial mineral licks.

Factory fresh licks are not especially attractive; urination on the licks by man improves the attractiveness and the use of them by reindeer.

Artificial mineral licks are apparently not a method to keep reindeer in some specific area but it is an easy and inexpensive method for improving the physical condition of local herds.

The licks should be placed about 1 m from the ground/snow surface.

Licks are most easily distributed on reindeer range in late winter when snow supports a snowmachine.

The best locations are along established reindeer trails and around corrals.

EFFECTS OF INTENSIVE FORESTRY

Rajala (1965) studied the importance of accidental losses of reindeer in logging areas. Results from 124 areas showed that 104 reindeer were killed during winter 1963-64. There was a great variation from year to year depending on the range and snow conditions and also on the number of reindeer in the area. The peak of accidental losses occurred in February-March (50 per cent in February alone!). This correlates with the congregation of reindeer in logging areas and with the maximum depth of snow. The study also showed the losses were proportionally greater in the smaller herding districts, apparently due to overgrazing of normal winter range. According to Rajala (1965), these losses can be controlled to some extent by herding reindeer away from the lots where timber is being cut and by providing hay in feed shelters far from the dangerous areas. When cutting and felling of trees stops, the shelters may be closed and reindeer allowed to graze the abundant supply of arboreal lichens now available.

Several dead moose and reindeer were found in Pudasjärvi commune, northern Finland, in winter 1969-70 and it was claimed that forest fertilizers used in the region had caused this die-off. Therefore an experiment was conducted at the Meltaus Game Research Station in late winter 1970 (Rajala, 1970) to detect possible poisonous effects of the commonly used fertilizers and also to see if wild ungulates actually eat these fertilizers at such high concentrations. The fertilizers were commonly used brands, 10 reindeer were used as experimental animals. The fertilizers contained phosphorus, potassium and nitrogen. Fertilizers were offered on snow, in buckets, distributed on the lichen mat and mixed with lichen. In experiments where normal fodder was provided as a control, the animals would not eat the fertilizers, however some individuals ate fertilizers thrown on the lichen mat.

Fertilizers added to lichen and urea (500 g urea/300 g lichen) were readily consumed by two reindeer following which the reindeer were quiet and sleepy for several hours. However no acute symptoms of poisoning were observed.

These results show that when fertilizers are distributed properly on the forest, no harmful effects will be noted with the reindeer.

GOLDEN EAGLE, *AQUILA CHRYSAETOS*, AS A PREDATOR OF REINDEER FAWNS

There are contradicting opinions about the role of the golden eagle as a predator of reindeer fawns in northern Finland. Since there is an urgent need to protect the few eagles still remaining in Finland, several studies have been made on the diet of this raptor in the reindeer grazing area and in other parts of Finland. Sulkava and Rajala (1966) studied the diet of the golden eagle in the reindeer husbandry region in 1957-65 by collecting 1,336 samples of prey animals from 27 nest sites in this region. Reindeer accounted for 9.1 per cent of the samples, tetraonids 51 per cent and the snow hare (*Lepus timidus*) 25 per cent.

This study showed without doubt that eagles eat newly born reindeer fawns. There is, however, no evidence that the eagle itself kills all the fawns it brings to the nest, even though small fawns, 4-8 kg body weight, fit well within the prey range of the golden eagle. There are great variations from year to year, 14.1 per cent in 1964 — 6.6 per cent in 1965, and also between various nest sites. It is probable that individual eagles specialize in preying upon reindeer fawns. In general, however, the losses caused by the golden eagle within the reindeer husbandry region are so small that the bird should be completely protected and losses to herders compensated from general funds.

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**DISTRIBUTION, MOVEMENTS AND SOCIALIZATION OF BARREN GROUND
CARIBOU RADIO-TRACKED ON THEIR CALVING AND POST-CALVING AREAS**

Frank L. Miller
Canadian Wildlife Service
Eastern Region
2721 Highway 31
Ottawa, Ontario, Canada

Fred W. Anderka
Canadian Wildlife Service
Bio-Electronics Section,
6, Beechwood Avenue
Ottawa, Ontario, Canada

Chitra Vithayasai and R. Lyn McClure
Biometrics and Computer Science Branch
Department of the Environment
161 Laurier Avenue, West
Ottawa, Ontario, Canada

ABSTRACT—Eighty barren ground caribou (*Rangifer tarandus groenlandicus*) were captured in northern Manitoba in April 1970. Twenty-seven were fitted with radio-transmitter collars and were later found on their calving ground in the District of Keewatin, Northwest Territories. They were radio-tracked about 150 km west of the calving ground, then during their midsummer migrations south-southwest, south and south-southeast for about 375 km to the McConnell River drainage at the northeastern edge of the taiga. A total of 246 contacts were made with radio-equipped caribou; 109 radio detections and 47 visual observations in June, 137 radio detections and 86 visual observations in July. The greatest number of observations for one animal was 27, and 11 radioed caribou were contacted more than 10 times each. The migrating caribou occurred in three distinct aggregations each of which included many small cohesive groups. Eighteen of the 23 radioed caribou observed during July were in association with other such caribou. Statistical analyses of the data demonstrated the following: (1) certain animals were usually seen on the same day, (2) certain animals were usually in the same groups and (3) animals returned to the same groups after being separated for hours or days. The non-random association of the radio-equipped caribou is believed to be a result of social cohesion.

The Kaminuriak population of barren ground caribou ranges over northern Manitoba, northeastern Saskatchewan and southeastern District of Keewatin, Northwest Territories, an area of about 282,310 km². Because of their migratory habits the caribou of the Kaminuriak population are subjected to the different harvest regulations of Manitoba, Saskatchewan and the Northwest Territories. The results of the Canadian Wildlife Service's three-year (1966-1968) intensive study of the Kaminuriak caribou suggest that the current principal limiting factor is the low rate of annual increment, as a result of high losses in the

calf crops during the first month of life. On the basis of the 1966-68 findings, a one-year study of calf mortality on the calving ground of the Kaminuriak population was carried out during the 1970 calving (June) and post-calving (July) periods.

STUDY AREA

The study area encompasses the calving ground and summer range of the caribou of the Kaminuriak population, about 160,500 km² (Fig. 1), District of Keewatin, Northwest Territories. Geographically, the study area is divided into the coastal plain extending inland about 130 km from the west side of Hudson Bay and the interior plateau west of the lowlands grading into the hill and mountain region (Robinson, 1968). The geology of the study area has been described by Wright (1955). Floristically, the study area includes both Tundra and Forest-Tundra (Rowe, 1959). Weather is characterized by cool wet springs and relatively dry moderate summers. Mean annual precipitation is 15 to 30 cm (Kelsall, 1968). Maximum precipitation occurs in July and August (Kendrew and Currie, 1955).

METHODS

Barren ground caribou were live-captured in tangle nets in northern Manitoba in April, 1970 (Miller *et al.*, 1971). Groups of animals were located on frozen lakes by aerial reconnaissance and nets set on their back trails in the adjacent forest. The caribou were then herded into the nets by taxiing aircraft. Eighty caribou were captured in seven days: 27 were equipped with radio transmitters.

The radio transmitter and collar plus snaps weighed 270 g. The radio transmitters were similar in electrical design to that described by Cochrane and Lord (1963), but with 60 cm whip antennae. The transmitter frequencies ranged from 40.590 to 40.770 megahertz at 10 kilohertz intervals.

The radio collars were made from 10 X 91 cm (4 X 36 inch) strips of high-gloss pink 'Saflag' material from the Safety Flag Company of America, Pawtucket, Rhode Island. One end of the 'Saflag' strip was folded back 3.8 cm and sewn in place. The opposite end was folded back 33 cm and sewn along the edges to form a pocket. Two metal gromets 1.3 cm inside diameter were set at the top and bottom of each end with a 51 cm spread on center from end to end. The batteries were put in the bottom of the pocket and the transmitter was placed in the pocket 2.5 cm (1 inch) off the center of the collar. The pocket was then sewn closed above the batteries and beyond the transmitters. A 0.317 cm metal eyelet was set above the transmitter to pass the whip antenna through to prevent lateral wear on the collar. The power lead was left disconnected and protruding from the back of the collar so that the ends could be connected when the collar was put on a caribou. Black identification numbers were painted on each side of the top of each collar with RamCote flexible finish paint (RamCote Products Inc., Chicago, Illinois).

When two or more transmitters were on the same channel differing pulse rates were used for identification, these ranged from two pulses per second (pps) to four pps. To conserve power the pulse widths were maintained between 50 milliseconds (msec) and 25 msec. The average power drain of 2 milliwatts (mw), (0.75 milliamperes at 2.7 volts) was supplied by two RM1450R mercury batteries in series. With a nominal capacity of 4500 milliampere-hours, a transmitter life of between seven and nine months was obtained.

As extreme miniaturization was not of utmost importance, the transmitter was built around a 0.5 cm (0.2 inch) diameter ceramic coil form (Cambion No. 1532-3-2). This coil form with its four soldering lugs provided support for most of the components, leaving only one 'floating' connection. In addition the panel mount feature of the coil form provided a

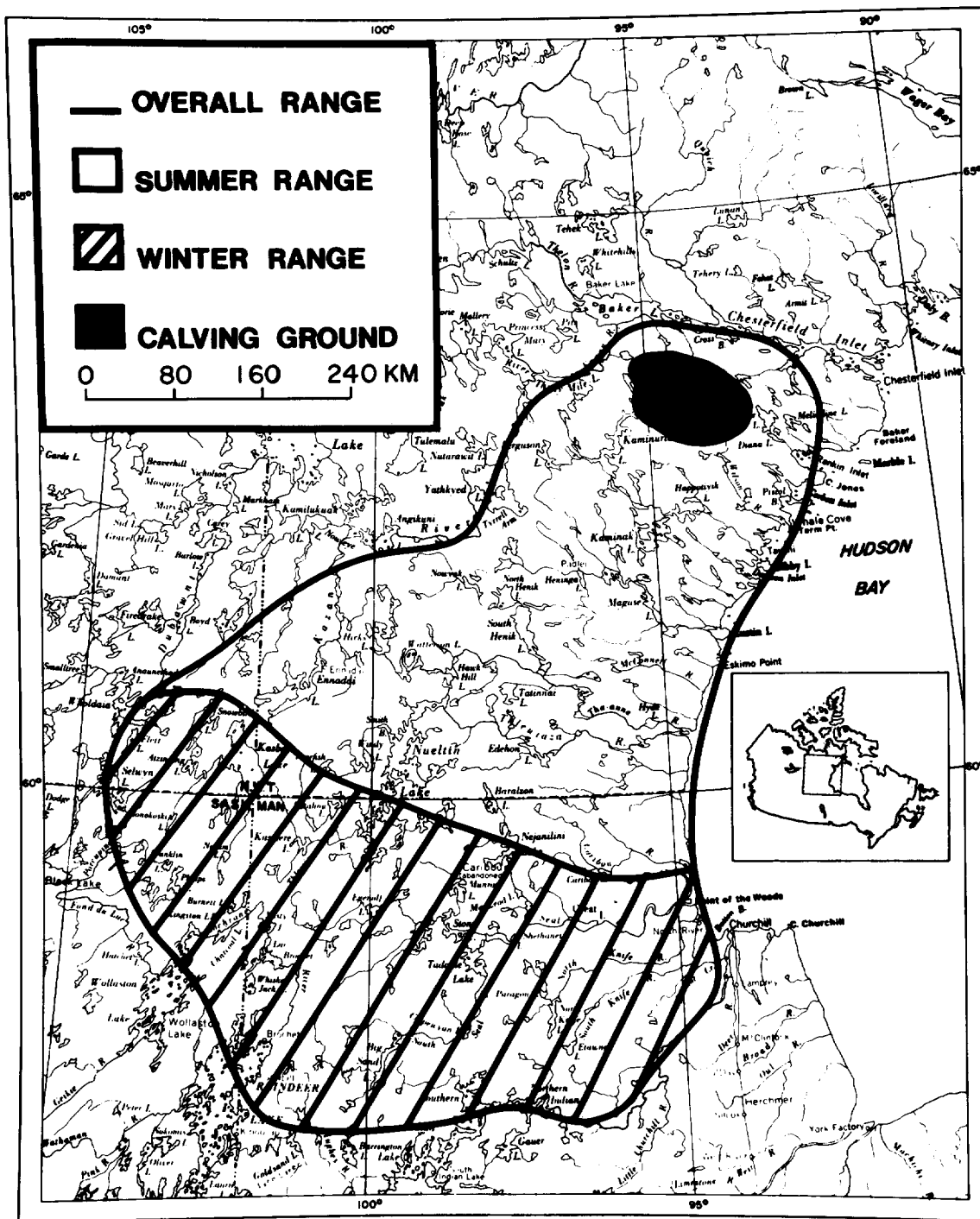


Fig. 1.

sturdy anchor point for the antenna. The 61 cm antenna consisted of four pieces of 0.064 cm piano wire 61 cm, 46 cm, 30 cm and 15 cm soldered into a 1.3 cm long piece of thinwall brass tubing and covered with a continuous piece of shrinkable tubing. The assembled antenna was then soldered to a small piece of copper which was in turn fastened to the coil form.

After assembly and preliminary tuning the transmitter was first dip coated with Canlab M7370 Paraplast (paraffin or beeswax is also suitable) and then covered with dental acrylic. A 1.6 mm hole was left in the dental acrylic for access to the coil form slug (the brass screw must be slotted) with a jewelers screwdriver. Final tuning was performed at that time and the hole sealed. The potted transmitter was approximately 2.5 X 3.6 X 2.0 cm with a remote tape and shrinkable tubing covered battery pack 3.8 X 8.1 X 1.5 cm.

To maintain the antenna in an upright position on the back of the animal's neck the battery pack was placed remote from the transmitter and connected with a 30 cm piece of miniature coaxial cable (RG-174/U). With the battery pack attached at the break in the collar and the transmitter just short of the midpoint, the combined weight of the battery pack and the steel snaps maintained the antenna in the desired position most of the time. Several animals were observed with the antenna between their front legs. In all cases, when next observed, the collar had righted itself.

The receivers used had been previously designed for a polar bear study conducted under very similar tracking conditions. Both projects required a high gain portable receiver with 22 tuneable channels spaced at 10 KHz intervals from 40.570 to 40.780 MHz capable of operating at low temperatures.

To reduce development time, the receiver employed a modified citizen band receiver board. This board contained a dual conversion receiver with one Radio frequency (RF), two converter and three Intermediate frequency (IF) stages, a mechanical filter, a detector, an audio noise filter and several voltage regulators. To increase the gain and operating frequency, a high gain RF amplifier and converter were added. The use of 22 switch selected crystals in the first converter oscillator of the receiver board eliminated severe temperature drift problems and provided the discrete 10 KHz spaced channels. To provide variable tuning across each channel, the crystal controlled second converter oscillator was replaced with a temperature compensated varactor tuned oscillator. The addition of a saw tooth generator to this oscillator provided an automatic sweep tuning feature. Detection of the unmodulated carrier from the transmitter was improved by the addition of a beat frequency oscillator. An integrated circuit audio amplifier provided approximately 0.25 watts of power to an integral speaker or auxilliary earphones. Power to operate the receiver for approximately 12 hours was obtained from a 1.0 ampere-hour 12.5 volt nickel cadmium battery. All the components of the receiver including the battery were housed in a weatherproof aluminum case 17.8 X 12.7 X 12.7 cm (7 X 5 X 5 inches) (Zero Manufacturing No. ZE-7030).

The minimum detectable signal was 0.03 microvolts under ideal conditions. Due to atmospheric noise and the RF noise generated by corona discharge and ancilliary equipment on both the Cessna 180 and the Hiller 12E it was often impossible to use the sensitivity available. Under unfavorable listening conditions the RF gain of the receiver had to be reduced to a point below saturation where the minimum detectable signal was between 0.1 and 0.5 microvolts.

Since yagi antennae at 40 MHz are unwieldy on the ground and impossible to install on a small aircraft, the receiving antenna was reduced to a simple dipole. But even a dipole at that frequency was somewhat large for a small aircraft. The design that was finally used with good success was a center loaded dipole 208 cm long. Automotive antenna staffs were used as the dipole elements thus providing the added benefit of being collapsible. Although they

were subjected to speeds in excess of 225 kmph (140 mph) with no damage, they were occasionally damaged by chunks of ice and snow during takeoff and landing. The identical antennae were used on helicopters where the damage was usually produced by the sympathetic vibrations of the elements, or by people walking into them. With both types of aircraft the antenna elements were pointed in the direction of flight. By mounting the dipole on a hardwood dowel, the antenna was maintained at least 1.1 m (3.5 feet) away from major metal surfaces. When mounted in this manner the null in the antenna pattern was approximately in the direction of the flight path, with the major lobes 90° to the flight path. As with all loop and dipole antennae there was a 180° ambiguity. Due to the rate of travel, this was not a great inconvenience in the aircraft.

The cost of aircraft charter and the time required in searching for dead calves did not allow us to carry out systematic patterns of radio tracking. Caribou were radio-tracked from a Cessna-180 in association with other survey work. Most flying was done between 150 and 300 m altitude, with brief periods at 600 and 900 m to check for radio signals. Radio tracking was also done from a Hiller 12E helicopter during low level (30-90 m) flights while searching for dead calves and from high level (150-300 m) flights while observing large aggregations of caribou.

To locate radio-equipped caribou with the helicopter a diminishing box search pattern was used. The pattern is a series of 90-degree right or left turns initiated when the received signal strength starts to decrease after reaching a peak. A similar technique was used with the fixed-wing aircraft, but the inability to turn quickly and the effects of wind drift made it difficult to place the animal accurately.

Extensive searches for post-calving aggregations and dead calves were made throughout June and July (Miller and Broughton, 1972). The searches were non-random and unsystematic procedures. We returned as often as possible to the areas where caribou had been located and followed their fresh trails to their new locations when possible. Ground observations were usually brief and sporadic.

RESULTS AND DISCUSSION

Twenty-four of the 27 caribou fitted with radio transmitter collars in April 1970 were located on the calving ground. Two of the remaining three radio-collared caribou had been killed by Eskimo hunters during mid-May. Only one radioed animal was not found during the study period.

A total of 246 contacts were made with 24 radio-collared caribou: 109 radio detections and 47 visual observations in June, 137 radio detections and 86 visual observations in July 1970. Unless otherwise stated all observations and data reported in this paper refer to these 246 contacts with radio-equipped caribou. The greatest number of observations of one animal was 27, and 11 caribou were contacted more than 10 times each.

Of the 21 radio-collared caribou seen after the peak of calving (12 June), 81 per cent (17) had produced calves. Subsequent observations of the 17 radio-collared maternal cows indicated that 35 per cent had lost their calves by 15 July.

The distribution and movements of caribou on their calving ground were determined by aerial surveys and radio tracking. The locations of caribou on 8 and 9 June 1970 were used to estimate the size of the calving ground by the perimeter-point method (Odum and Kuenzler, 1955). We judged 8 and 9 June to be the mid-period of maximum calf production in 1970 (Miller and Broughton, 1972). On 9 June, the calving ground was delineated by an aerial survey of adult females (Fig. 2). It was estimated to be about 4,000 km² (1,544 mi²) by use of radioed caribou and 3,800 km² (1,467 mi²) by aerial survey.

When we arrived on the calving ground on 1 June, several cows with newborn calves

were observed. The incidence of cows with calves increased each day until 10 June. Caribou were forming post-calving groups by 11 June. On 4 June about 10 per cent ($n=1,805$) had newborn calves and by 8 June, 55 per cent ($n=2,117$) were with calves. Eighty per cent of the cows ($n=1,148$) segregated by aerial photography on 12 and 13 June were with young.

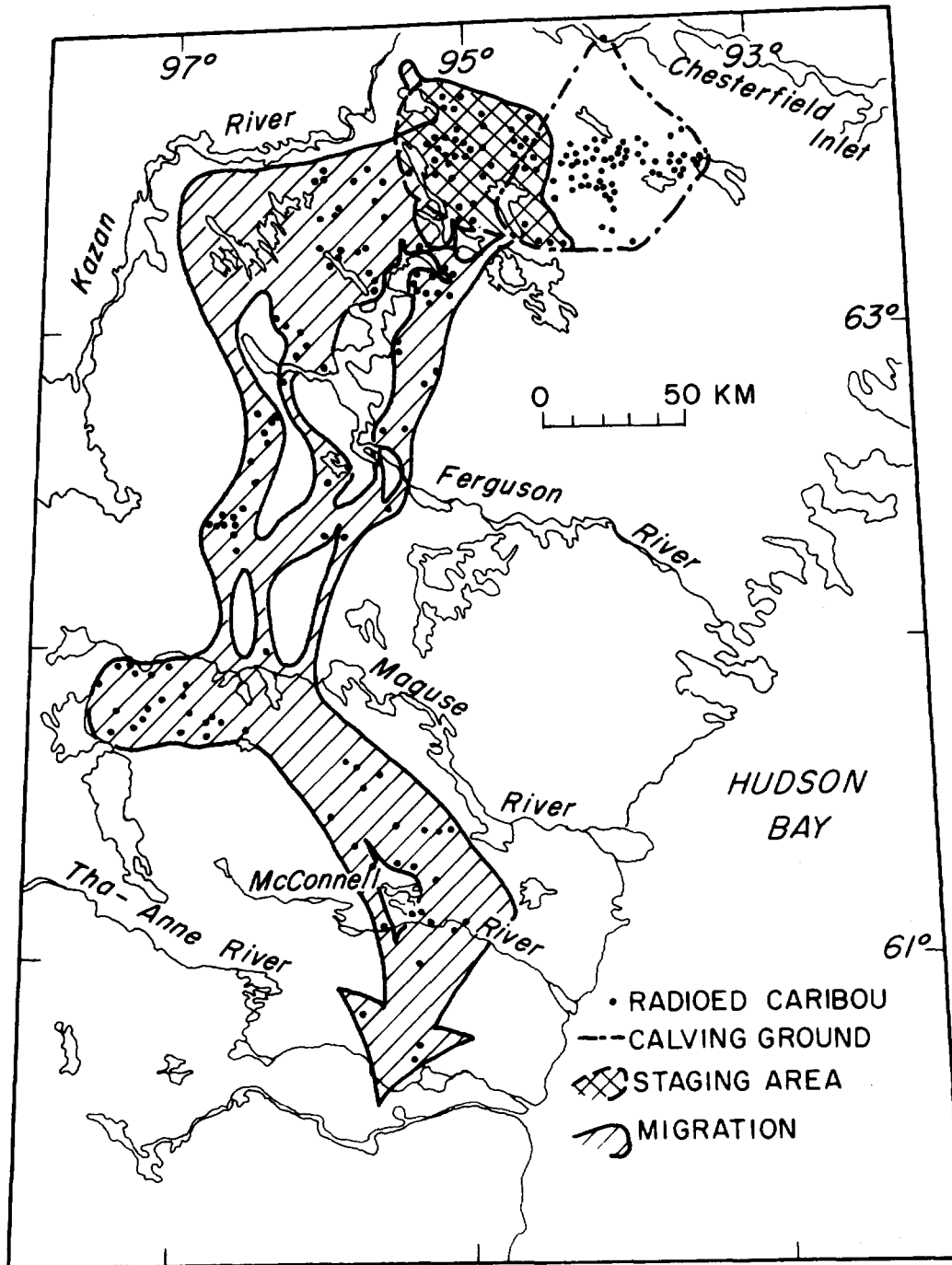


Fig. 2.

On 12 June, about 12,000 caribou were concentrated on several square kilometers at 63°30'N, 94°10'W. They were beginning a slow northwest movement. By 14 June a second aggregation of several thousand caribou was concentrated about 15 km north of the caribou in the first movement. The caribou in the first movement traveled about 78 km west and entered the area north of Parker Lake, while the animals from the second movement traveled about 64 kilometers westward and concentrated in the area north of MacQuoid Lake. Those two general areas were occupied by the caribou until approximately 27 June 1970. There was much local movement and fragmentation of large concentrations and regrouping for a 10- to 12-day period.

The post-calving migratory period began 28 June with the general southwest movement of caribou around Parker Lake (Fig. 2). The caribou divided into three groups. One group moved almost due west to the south shore of the Kazan River. The second movement from the Parker Lake area went west of the north end of Parker Lake and took a sharp southerly course to the east of the first movement. The third movement from the Parker Lake area moved down the east side of Parker Lake and crossed the narrows at the south end of Parker Lake.

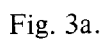
The caribou from north of MacQuoid Lake moved westward to the area just east of Bissett Lake. Those caribou returned on a more northerly course to an area above the west end of MacQuoid Lake. They then traveled southeast about halfway down the east side of MacQuoid Lake. A segment of the movement, however, turned at the north end of MacQuoid Lake and came around the west side of MacQuoid Lake and continued down the west side to the east side of Parker Lake and then down the east side of Kaminuriak Lake.

The caribou continued south on three wide fronts. During several periods of inclement weather the movements fragmented into many small sub-units which foraged and moved about the countryside. As the weather cleared, the caribou regrouped and continued their travel southward. It is likely that the fragmentation represents the breakdown of the larger post-calving movements, that in themselves are relatively weak social units, into the smaller sub-units which are the more persistent or binding social groups. The cores of these sub-units are most likely composed of the remnants of previous winter bands. Even though marked caribou from the Egenolf and Nuelin spring movements were observed in the large post-calving aggregations, fragmentation of the aggregations resulted in those animals always separating and traveling with different smaller groups. This suggests that caribou have a tie to their population or movement, but maintain a stronger bond of socialization with the basic social unit — the band (Miller, in press).

The 12 caribou, each of which was detected 10 or more times, traveled minimal distances that ranged from 286 km to 597 km and averaged 447 km. The individual movements of the 12 caribou are shown in Figures 3a and 3b. The differences in activity of the 12 caribou during the pre-migratory and migratory periods are reflected in Table 1. Average values in column five (Table 1) are minimal and do not reflect all the wanderings but serve to indicate the relative amount of travel during each period.

Caribou were observed to travel 0-55 km/24 hr (n=24) at a maximal rate of 8.7 km/hr for 3 hr during the premigratory period and 2-64 km/24 hr (n=39) at a maximal rate of 16 km/hr for 2 hr during the migratory period. Of the caribou seen twice within 24 hr periods during the premigratory and migratory periods 25 per cent and 40 per cent, respectively, were traveling at average rates in excess of 1 km/hr. Overall average rates, however, are misleading because of the individual variations in daily activities. One caribou traveled 103 km in 41 hr (2.5 km/hr).

Eighteen of the 23 caribou tracked during the migratory period were detected in discrete groups with other radio-equipped caribou. Individual caribou were detected with from one to nine other radio-equipped caribou at different times. The total number of

[illegible]

430

the measure was tested by methods given in Robson's appendix (Pielou, 1972). The calculations gave a chi-square value of 88.3 on 21 degrees of freedom, $P < 0.005$. The results indicate that there was association among these caribou.

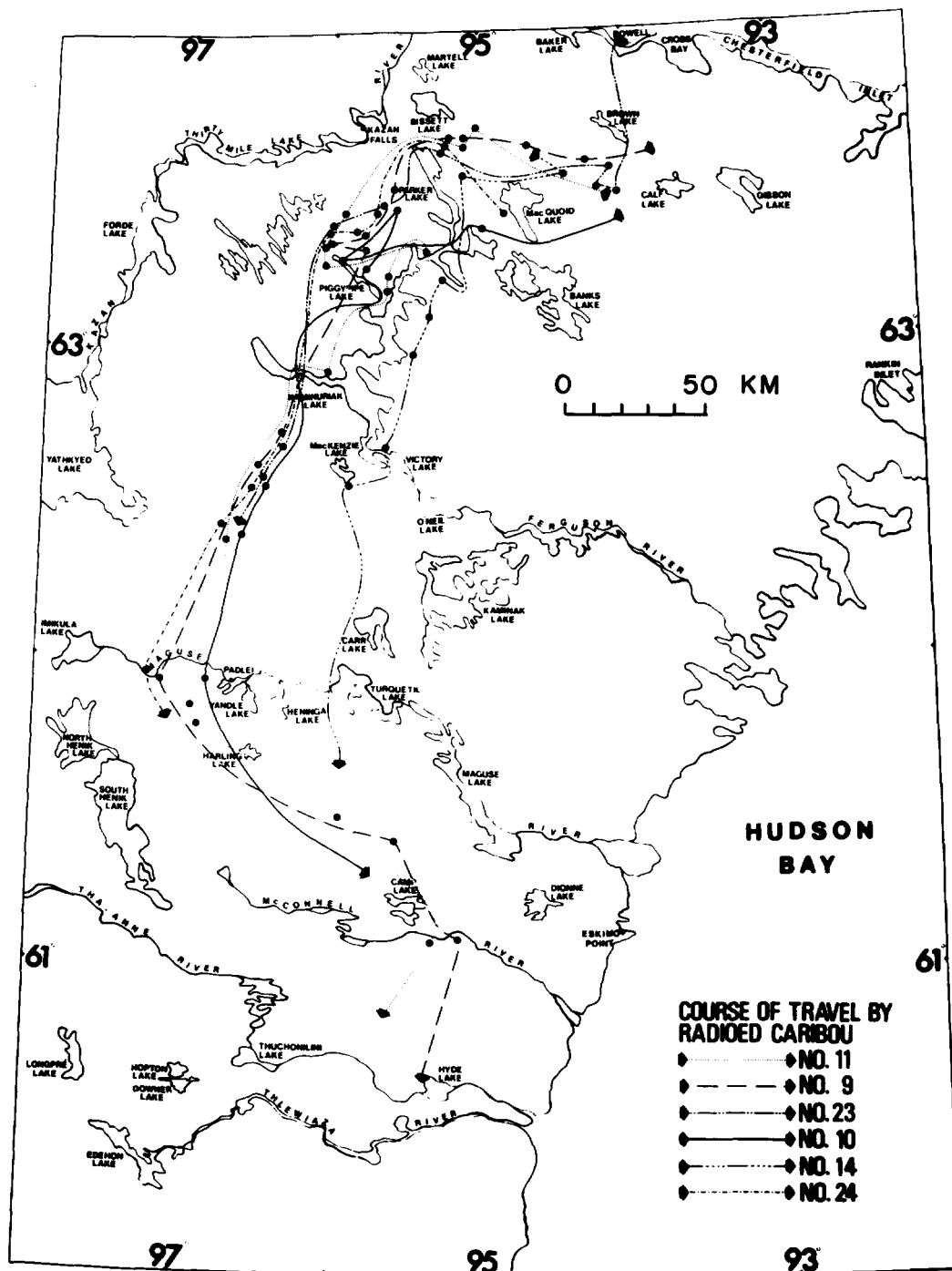


Fig. 3b.

TABLE 1.--Minimum distances traveled by the 12 caribou detected most frequently during June and July 1970.

Radioed caribou number	Number of detections	Time lapsed from first to last detection (days)	Minimal distances traveled (km)	Average distances traveled per day (km)
Pre-migratory period (1-28 June)				
6	12	20	88	4.4
9	6	20	104	5.2
10	3	20	54	2.7
11	5	19	128	6.7
14	3	20	45	2.3
15	7	20	191	9.6
18	7	20	139	7.0
20	7	20	83	4.2
21	6	20	155	7.8
23	8	19	132	6.9
24	3	19	74	3.9
26	10	8	71	8.9
Migratory period (28 June-29 July)				
6	15	28	484	17.3
9	9	26	418	16.1
10	8	28	380	13.6
11	12	26	420	16.2
14	8	17	241	14.2
15	6	5	137	27.4
18	5	24	349	14.5
20	13	25	514	20.6
21	13	24	359	15.0
23	4	7	164	23.4
24	7	14	215	15.4
26	7	22	415	18.9

Are certain animals usually seen on the same day?

We can study association by testing for patterns of caribou usually seen on the same days, as all animals were not sighted on every day. To test association among the four most frequently detected caribou (Nos. 6, 11, 20 and 21) we examined days on which either two or three of them were seen. For two of the animals there were nine occasions and six possible combinations (which are equally probable if there is no association): [see next pg] Because the sample is so small, we cannot use X^2 to test whether the distribution is unusual. Therefore, we generated by computer a large number of random samples and the probability of a distribution as extreme as the observed was estimated to be 0.00011 (we used 300,000 samples of nine days evenly distributed over the six possibilities). We conclude that because this probability is very small ($P < 0.0005$) there is association among these four animals.

Possible combinations	Predicted no. days	Observed no. days
Animals No. 6,11	9/6	0
6,20	9/6	7
6,21	9/6	0
11,20	9/6	0
11,21	9/6	2
20,21	9/6	0
	9	9

Are certain animals usually seen in the same group?

We can attempt to test for association using the same four most frequently sighted animals. If we have grouping information on three of the animals, then we know that the one animal not sighted was in a separate group, so we can use the nine days when at least

TABLE 2.--Detection of radioed caribou from the Kaminuriak population during the post-calving migratory period, 1970.

Date June-July 1970	Radioed caribou in migratory groups		Daily total
	Together	Alone	
28	(6,20) (11,21) (14,15) (23,24)	9,10,18,19	12
30		6,10,20	3
3	(20,21) (9,18,24)	6,11	7
4	(6,9,18,23,24) (8,19,20)	22,26	10
5	(1,8,10,25) (6,7) (11,21)	9	9
6	(6,14,20)	15	4
7	(6,14,15,20)	12	5
8	(6,14,15,20)		4
9	(1,10,23,24) (6,14,15,20) (11,21)	5,8,9,12	14
10	(1,10,18,23,24,26) (11,21)	5,8,9	11
11	(1,10,23,24) (6,14,15,20) (8,18,19) (21,27)	5	14
16	(6,20,24,26) (11,21)	5	7
18		1,3,6,9,20,24	6
21	(6,8,20,26)		4
22		26	1
23	(5,14,25) (11,21)	10,20	7
24	(6,9,20,26) (11,21)	3	7
25	(11,21)		2
26		21	1
27		6,9,10,11,18, 21,26,27	8
28		11	1
29		9,11	2

three of the four animals were sighted.

<u>Grouping possibilities</u>		<u>Days occurring (observed)</u>
1 group	(6,11,20,21)	0
2 group (2-2)	(6,11) (20,21)	0
	(6,20) (11,21)	4 28 June, 9,16,24 July
	(6,21) (11,20)	0
	(3-1) (6,11,20) 21	0
	(6,11,21) 20	0
	(6,20,21) 11	0
	(11,20,21) 6	0
	3 group (2-1-1) (6,11) 20 21	0
	(6,20) 11 21	1,11 July
	(6,21) 11 20	0
3 group (2-1-1)	(11,20) 6 21	0
	(11,21) 6 20	2,5,23 July
	4 group	1,27 July
	6 11 20 21	9

If we assume that 'no association' means that there is random mixing between successive days of observation, we expect that, for the same size groups, the various possibilities are equally probable. In these data, we see this means the possibilities for *two groups with two* of these selected animals should be evenly distributed and they are not.

<u>2 groups of 2</u>	<u>Expected days</u>	<u>Observed days</u>
(6,11) (20,21)	4/3	0
(6,20) (11,21)	4/3	4
(6,21) (11,20)	4/3	0
	4	4

Because only one category was observed, the proportion of four out of four observations was tested against the binomial distribution of four events with an expected probability of 0.33. The resultant probability was 0.012. Therefore we conclude that there *is* association of animals with certain groups.

Do animals return to the same group after being separated?

There are four times during the observations when we know animals No. 6, No. 11 and No. 20 were in separate groups: 30 June to 5 July, 18 July, 23 July and 27 July. If there is no association the pairing of No. 6 and No. 11 should be just as frequent as No. 6 and No. 20 before and after these 'mixups'.

<u>Grouping</u>	<u>Expected days</u>	<u>Observed days</u>
(6,11) 20	4/3	0
(6,20) 11	4/3	4
(11,20) 6	4/3	0
	4	4

The four occasions of grouping are 28 June, 6 July, 21 July and 24 July. As in the above test, the probability of a distribution as extreme as this by chance alone is small ($P < 0.05$).

Therefore we conclude that animals returned to the same group.

CONCLUSIONS

Our preliminary work with radio tracking caribou indicates that the technique is a workable method for obtaining more detailed information on caribou movements and migrations. The use of high frequency radio transmitters would increase the area of detection and possibly reduce the cost of radio tracking.

The conclusions resulting from the analyses of these data are consistent with the supposition put forth by Miller (in press), that one of the primary functions of post-calving migratory movements among caribou of the Kaminuriak population is socialization by creating a favorable situation for regrouping or previous social groups with minimal social strife.

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SIGNIFICANCE OF ANTLERS IN THE SOCIAL LIFE OF BARREN GROUND CARIBOU

A. B. Bubenik
Research Branch, Wildlife Section
Ministry of Natural Resources
Maple, Ontario

ABSTRACT—This study has been made by direct observations of antler use among caribou in northern and central Alaska and the responses of free-ranging caribou to artificial caribou heads carried by a man. Caribou antlers are dominant releasers from 'short' distances for estimating the sex and social class, but not the individual rank of conspecifics. It is interesting that willow ptarmigan perceive a caribou dummy as a caribou. Caribou antlers overshadow all other releasers including human scent. Gestures expressed through antlers are an important code in the ikonographic language of this species. The construction pattern of caribou antlers seems to be influenced by three different selective mechanisms: protection by providing an effective shield against facial injuries due to special architecture of bez tine, inner tines and dorsal tined or dichotomous branched upper zone of the antlers; the social effect of enforcing threat displays by presenting palmated brow tine and the length of beams and tines; the aerodynamic shape of forward bent beams which allows easy movement with or against the wind but impedes movement in a crosswind. This could be a factor holding caribou in herds and on the same migration routes.

By perceiving or presenting specific signals or stimuli, animals not only obtain or exchange information involving sex, age, physiological status or momentary mood of conspecifics but also of other species within their social environment. Factors which release responding behavior are called *key stimuli* or *social releasers* (Lorenz, 1935). The action involved is either one of innate releasing mechanisms (IRM) or of acquired conditioned responses. Special morphological structures, odorous substances, sounds and/or conspicuous movements and posture have been evolved for these purposes or have become adapted for them (Lorenz, 1943, 1965). Occasionally, distinct single cues are used in relationship and constitute a *configurational stimulus*, also called *search-image*. The components of a search-image reinforce the effect of the information or channel it in one direction on the basis of *heterogeneous summation* (Seitz, 1940). This stimulus-summation-phenomenon was long accepted as a criterion for innate releasing situations as opposed to the *gestalt principle* which was a criterion for acquired releasing situations. But Baerends *et al.* (1965) have shown that such differentiation is not always valid.

The readiness of IRM for responses to key stimuli or search-images is so rigid and intensive that if they are abstracted from the animal they still operate in the same way (Franck, 1966; Lack, 1943; Noble and Curtis, 1939; Tinbergen, 1948, 1951; Tinbergen and Kuenen, 1939; and many others). The key stimuli and search images as models or dummies could be recognized and differentiated from *gestalt* by the Lorenz's rule of thumb (1954): "Where an animal can be 'tricked' into responding to simple models, we have a response by an innate releasing mechanism; where it cannot be thus confused, we have an acquired recognition of a *gestalt*" (in translation from German by E. Klinghammer in Eibl-Eibesfeldt,

1970).

Occasionally there are peculiar and remarkable situations in which artificial stimuli have better releasing effects than the normal ones. Koehler and Zagarus (1937) were the first to discover this effect in ringed plover (*Charadrius hiaticula*) which prefers black spotted and up to four times larger eggs over its own eggs with dark brown spots. Tinbergen *et al.* (1943) found that the males of grayling butterfly (*Eumenis semele*) are more attracted to black models than to those with natural colors, etc. The fact that such artificial cues operate with the same attractiveness in all individuals led Portmann (1960) to the conclusion that they could represent genetically fixed *dormant cues*.

Some of the cues can serve different communication purposes depending upon situation, age, physiological or social status of animals as is the case for example, with morphological structures like feathers and hairs, antlers or skins with rich patterns of pigmentation, odorous substances and/or sounds (Eibl-Eibesfeldt, 1970; Tembrock, 1965; Tinbergen, 1953; Wickler, 1970). The readiness of IRM to respond to a distinct cue also depends on the mood of the perceptor which can change with its physiological processes and/or with its appetitive behavior (Craig, 1918). Many examples about motivation to respond can be found in the monographs of Eibl-Eibesfeldt, 1970; Hinde, 1953, 1966; Marler and Hamilton, 1966; Tembrock, 1964; and others.

A distinct releaser can therefore change its rank order among stimuli. Therefore we have to speak about hierarchy of releasers in a similar way as has been postulated for instincts by Tinbergen (1951). The hierarchy of stimuli can be related to the releaser of one perception system or to all releasers in general. There is also a distinct range of variance for the cues within which they operate, as it is well known for coloration, sounds and especially pheromones (Müller-Schwarze, 1969). The limits of tolerance predetermine whether or not they are important barriers for social contact and hybridization between races and/or subspecies. The top rank in this regard should be awarded to those cues which inhibit any panmixy even with sympatric populations. In this view the theory of Geist (1971) is open to question. His comments about the spontaneous hybridization between the Sika deer (*Sika dybowski*) and Izubra deer (*C. canadensis xanthopygus*) in Manchuria are based on a confused reference (Heptner *et al.*, 1961). Up to now there is no evidence for such spontaneous hybridization neither in the Far East between the red deer (*C. elaphus*), nor in Scotland or New Zealand (Bubenik, 1971; Delap, 1968; Kiddie, 1962; MacNally, 1969).

The evolutionary history of optical releasers is closely connected with optical perception in the biomes where the species have evolved. Therefore the visual capacity of the species and the features of their releasers complement each other. The simplest and most easily perceived releasers have been developed in densest cover. The most complicated and intricate releasers are to be found in species adapted to life in open country.

Antlers of cervids belong among the morphological structures operating as cues. Their explosive evolution in the Pliocene-Pleistocene period could be explained first by their significance as social releasers and important accent of the 'head pole' of these species (Portmann, 1960; Bubenik, 1962, 1966, 1968). While they represent a very important element in optical communication system (Altmann, 1965; Darling, 1937; Gossow, 1971; Hediger, 1946), they are also releasers which can occasionally operate as acoustic, olfactory and touch stimuli as well. They can dominate over the head pole of the body in such a way that they belong to the search-image of the species concerned and to the gestalt as well.

ANTLERS AS ORGANS

Antlers have a long and little known history which goes back far into the Miocene and Oligocene of Eurasia and North America (Bubenik, 1962, 1966). From the microstructure

of vellericorn eoantlers we have to conclude that they have not been developed as weapons (Darwin, 1859; Beninde, 1937b; Lettow-Vorbeck and Rieck, 1956) but as organs reinforcing the search-image for social status (Bubenik, 1966; Darling, 1937; Hediger, 1946, 1966; Severcov, S. A., 1951). Much later during their evolution they acquired properties which allowed them to be also used as weapons. But there is no evidence to suggest that this trend has predominated. All known patterns of antler construction and the use of antlers in recent cervids show clearly that they are an organ of display which have a prevalent defensive character.

The 'flowering time' for antler development is closely connected with great changes in the environment toward the end of the Miocene and in the Pliocene period, when the bush biomes were being replaced by more open country. I agree with Beninde (1937a,b), Darwin (1859), Müller-Using and Schloeth (1967), Sewertzoff, A. (1931) and Severcov, S. (1951) that the selective forces stimulating the morphogenesis of antlers were not the increased size of the deer (Huxley, 1931), but the physical structure of open habitats and the social significance of antlers (Bubenik, 1968). In more open biomes the antlers were perceived better and could attain higher rank as cues. To substantiate this hypothesis, I have used dummies as a method for testing the releasing properties of the antlers.

METHODS

Previous to my studies with the red deer dummies some 12 years ago I had not found any ethological records concerning the testing of antlers as behavioral cues.

This, of course, does not mean that antlers could not have been used by hunters for approaching game. I suggest from pictographs in caves left by Magdalénienne hunters about 20,000 to 10,000 years ago (Ucko and Rosenfeld, 1967) that the men with antlers were not shaman but camouflaged hunters (Fig. 1).

My studies with cervid dummies were based on the results of the classic studies upon key stimuli from Noble and Curtis, 1939; Franck, 1966; Lack, 1943; Tinbergen, 1951; and Wickler, 1962, 1965. Also I have used Portmann's (1969) theory concerning the morphological accentuation of the head and anal 'poles' of animals. The information transmitted by cues originates in this way and the attention of the perceptor is focused to the body poles. The spots or stripes between these poles are then of reduced importance as species-specific releasers (Fig. 2).

Antlers are only part of the head pole which represents the species specific search-image. Therefore a cervid dummy must have the proper form, the essential color patterns and must be used in the species-specific manner. If these important components are not respected, the responses to the dummy could be halted, interrupted or the dummy will change to a flight releaser. This is necessary to know not only to avoid such negative situations but also to use them for avoiding a dangerous attack.

The rank of antlers in the hierarchy of releasers can be deduced from: (1) their attractiveness for the conspecifics, (2) the critical distance of approach and (3) its dominance in relation to other releasers. Antlers as part of the head reach the highest rank among releasers when both sexes respond to the dummy with the same readiness and when the human scent of the dummy carrier is not important. Among cervids it is the Alaska moose (*Alces alces gigas*) whose antlers have reached such a rank. The aim of this paper is to describe the rank of antlers among the optical cues and responses and in the hierarchy of all releasers in barren ground caribou of western and central Alaska (*Rangifer tarandus granti*).

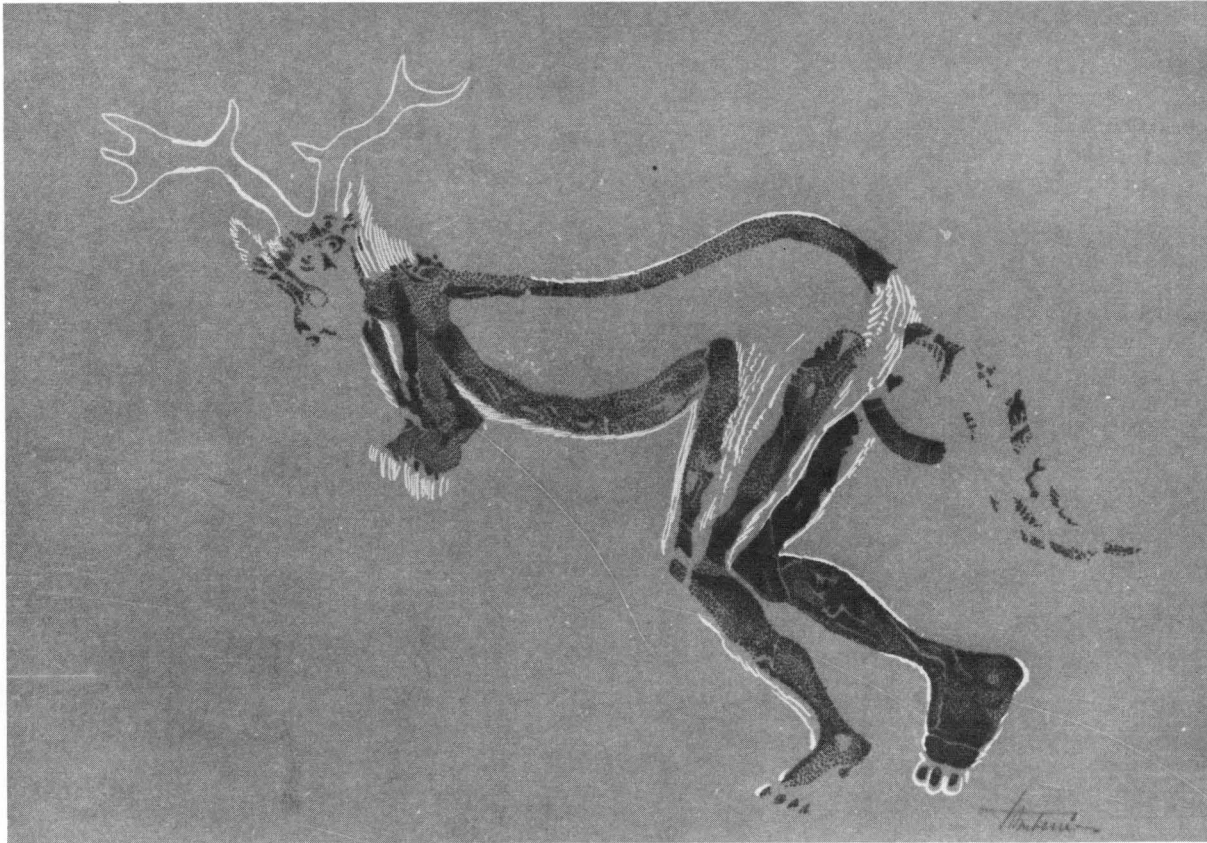


Fig. 1.—A pictograph of 'shaman' in the cave 'Les Trois Freres', France.

The Study Areas and the Behavior of Caribou towards Human Image:

I studied the use of antlers and their social significance in the barren grounds of Alaska during two consecutive years 1968 and 1969. In late summer I was in contact with herds of the Arctic population in the Endicott Mountains. During the rut I operated in the Lake District southwest from Selawik. The herds of the Nelchina population were studied at the beginning of the rut in the valleys of Little Nelchina and Little Oshetna Rivers.

The behavior towards man of these two populations was quite different. In the Selawik area the caribou did not show any particular fear towards moving man. They maintained a critical distance of 150, seldom over 300 m, i.e., similar to that of a wolf. In the Endicott Mountains the flight distances were greater — 200 to 400 m. In the heavily hunted Nelchina population it was rare to approach the herds in the open closer than 400 m. Generally the flight distances were between 600 and 800 m. Therefore it was possible to get good close-up pictures and movies only from Selawik River. This is unfortunate because the bulls of the Nelchina herd were quite interesting. First, the great flight distances toward the human, *gestalt*, and the easy approach with the dummy clearly testified to the high rank of the dummy as a releaser. Secondly, the bulls of the Nelchina herd were more aggressive and encounters with them produced more behavioral responses.

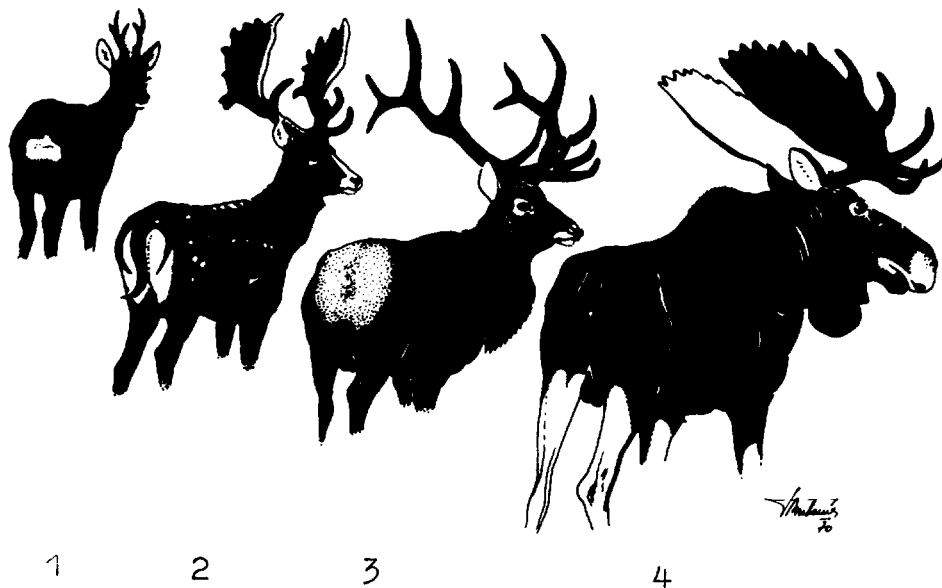


Fig. 2.—Evolution of antlers as key-stimuli in cervids: roe deer (*Capreolus capreolus*) (1), fallow deer (*C. dama*) (2), wapiti (*C. canadensis*) (3), moose (*Alces alces*) (4). (Bubenik, 1971.)

TECHNICAL EQUIPMENT

The caribou dummies were self-made heads from styrofoam or PVC-foam, partly covered by nylon fur. The heads had moveable ears, eyes and neck; the antlers could be replaced with others of various sizes and shapes. I operated with the following sets of antlers: one each of a female, a yearling and a 'teenager' male, a 'prime' male of good size and an over-sized male.

Still photographs were made from the dummy by the carrier with a Nikormat camera and 55 mm lens plus 2 x convertor and by an observer using a Hasselblad camera with 500 mm telelens. Movies were made with a 16 mm Beaulieu Electronic and a Super 8 mm Nizo ST 80. Ektachrome HS film was used except for the Nizo ST 80. The dummy operator recorded information on a Phillips pocket tape recorder.

THE USE AND SIGNIFICANCE OF ANTLERS IN *RANGIFER*

My observations and conclusions upon the significance of antlers in reindeer differ from other records (Dugmore, 1913; Espmark, 1964a,b; Henshaw, 1968; Lent, 1965b, 1966; Pruitt, 1960, 1965) in the following ways:

- (1) I refer to the differences in shape, use and significance of antlers in males and females to their different evolutionary stages.

- (2) Greater attention is paid to the use of antlers as threat releasers and/or components of agonistic behavior.

The Differences in Use of Antlers in Females and Males

For better understanding the dissimilarity in use of antlers in both sexes it is necessary to deal briefly with the sexually dimorphic character of *Rangifer* antlers. As I have stressed in another paper (Bubenik, 1972) it is my opinion that antlers in female reindeer did not develop additionally as an advantageous organ but rather they retained them for two reasons:

- (1) The antlers are not restricted to the males due to the special pattern of hormonal regulation of pedicle and antler growth.
- (2) The retaining of antlers was preferable for social reasons as described by Pruitt (1960, 1966) and Lent (1966).

We can conclude that female antlers represent one of the earliest stages of morphogenesis of this organ in *Rangifer*. This view is supported by the first stages of organogenesis in male antlers which are similar to those of females. Up to now it is not possible to say which evolutionary step in *Rangifer* the female antlers represent. Why they did not develop farther can only be suggested.

The amount of nutrients needed for the development of large male antlers cannot be wasted in female antlers as these are necessary for the growth of fetuses and for the production of milk. I assume that further development of female antlers was not advantageous for these reasons. As has been proved by the authors mentioned above, the female antlers grow to social significance only when the males are antlerless. Therefore female antlers did not compete in development with male antlers. Should it occur that a female must attack an antlered male, then it is more advantageous for her to use her forelegs, as females of other cervids do (Bubenik, 1968; Müller-Using and Schloeth, 1967). I have no personal experiences involving the use of antlers in social encounters between females. From the descriptions of Lent (1966) and those of Pruitt (1960, 1966) I have concluded that the primitive structure of their antlers represents such an offensive stimulus that they are used predominately for threat. Unfortunately the records are not adequately detailed and have not been extended to all possible situations. More attention to use of antlers in females could give us a better basis for understanding of the evolutionary significance in reindeer antlers in both sexes.

The male antlers in reindeer despite their primitive ontogenesis (Bubenik, 1956, 1959) have one of the most developed antler structures in Cervidae (Bubenik, 1966; Pocock, 1933). This is recognized from the following characteristics:

The male antlers have nearly lost their offensive features as weapons, but the shape and size in prime males have gained such a releasing effect that they rank over other optical stimuli and can overshadow the olfactory cues. The optical releasing power is partly due to the antlers hypertelic upper zone. Despite the great variability in structural pattern, they have lost the property of a personal symbol. They are chiefly the sign of a distinct social class and condition.

Such development is not surprising. The absolute open type of social relationships with continual fluctuation of herd members does not allow or makes it difficult for a single animal to be well-known among a long-term circle of acquaintances.

The low rank of antlers as symbols of personality could be the reason for a very simple peck order. I never observed bulls in velvet to establish any pronounced and permanent rank-relationships. In communities of rutting bulls the peck order was nearly always related to the 'Alpha' and 'Beta' bulls. This is in accordance with the detailed studies of Espmark

(1964a, b). Like other gregarious cervids the 'A' males are rarely involved in fights. The most violent combats which they have to undergo are with the 'B' males. The 'Beta'-bull or a newcomer as a potential 'Alpha'-male are the only challengers of 'Alpha'. Towards all other inferior males the 'Alpha'-bulls behave altruistically as long as they are ready to keep the necessary personal distance. They guard their top rank dominantly by threat. The highest social temperature and velocity (Calhoun, 1965) occurs in 'B' bulls attained by unsuccessful attempts to dominate the 'A'-bull. The excitement of 'B'-bulls is then redirected towards the lower-ranked animals, which are terrorized by them. Among the inferior bulls the rank order fluctuates steadily (Bubenik, 1968).

This general pattern of rank order and social behavior of barren ground caribou does not differ from that in woodland populations (Banfield, 1961; pers. comm., 1969; Bergerud, 1971; Dugmore, 1913; Espmark, 1964a, 1971; Murie, 1935; Pruitt, 1960). Even though they are more sedentary, they live in small herds with harem formation that affects their social temperature and velocity (Calhoun, 1965; Lorenz, 1957) but their peck order is still limited to two males (Espmark, 1964b). This could be evidence for the rigid social behavior in *Rangifer* which the taiga habitat is not capable of modifying to a closed social type similar to that of red deer (*Cervus elaphus*).

This statement gives evidence for the assumption that *Rangifer* is a very young genus with a primitive social behavior which is not related to the antler structure. The absence of ritualized threats and fights in which antlers are used indicates a low level of social development.

The Use of Antlers in Courtship and Fight

The really few gestures in which antlers play a role have been described in different manners many times (Dugmore, 1913; Espmark, 1964a; Henshaw, 1968; Lent, 1966; Pruitt, 1960). It is my opinion that two of these have not had enough attention paid for proper understanding. *The tilted-head*: Dugmore (1913) mentioned this in connection with behavior of bulls towards females. Espmark (1964a) reports about an 'awry' position of the bull's head without describing correctly what he meant by this term. The tilted-head is described by Lent (1965b) and only Pruitt (1960: 9) stressed its importance with these words: "...I received the distinct impression that he [the bull which charged Pruitt] was 'presenting' the tines or shovels of his antlers as an integral part of the display." Pruitt then referred to the paper of Moynihan and Hall (1955). These students described the tilted-head as a part of the courtship in spice finches (*Lonchura punctata*). They should have explained this posture as conflicts between the drives for attack and for fight.

The tilted head is very common in many ungulates and is universal in the horned ones. It is also used by canids as well. Of course, in all these species the head is postured frontally and the attitude is used when a foreign object is optically explored. I shall explain the tilted-head posture in reindeer as typical for an offensive-defensive threat. Its origin could be in the lateral blow (see below). It could be used as a single element with the neck in line with the body or turned to the side. It is used also as a reinforcing or a completing element in other search-images like in 'horse-shoe' posture (Fig. 3). This display is common among Odocoileninae. It shows slight specific variance from that in *O. virginianus*, where it is performed in both sexes, to the moose (*Alces alces*) in which it is limited only to the male and only when incited. In general the hind-legs are close to the forelegs, back is arched, penis erected or hanging down, tarsal glands thrown together and (not always) moistened by urine. It is performed fully by alpha or solitary bulls.

Occasionally the signal of white-of-eyes and husky sounds can be mixed in the display of tilted-head. Such code then represents an optimum offensive threat which should

intimidate. The tilted-head is therefore a very important part of the repertoire of behavioral patterns. Its study is easy by using dummies as the following comments from my records testify: *October 10, 1969 — 12:35 h*: On the bed of a braided section of Little Nelchina River. Cloudy weather, west-wind, grade 2, -4 C. I am standing with two yearlings about 10 to 12 m from the creek behind a curve. A small herd of caribou is appearing below the 3 m high bank opposite me. They walk down along the stream bed. Leader is a Senior doe with her fawn. I count 24 animals, two of them are yearling males. The leading doe is now right in front of me. She stops and watches me for 30 to 40 seconds. I imitate 'feeding' and doe continues on followed by the herd. A mature buck in his first prime year trundles along at the rear of the herd. He stops on the same location as the leading doe did. He also turns frontally towards me and we watch each other. He investigates by *head-bobbing* and intimidates me with a few husky sounds. I am also answering with head-bobbing and then I display *tilted-head* with my prime-sized antlers. The bull responds immediately. He is approaching with stiff legs up to the edge of the creek only 3 to 4 m from me. The wind is blowing downstream.

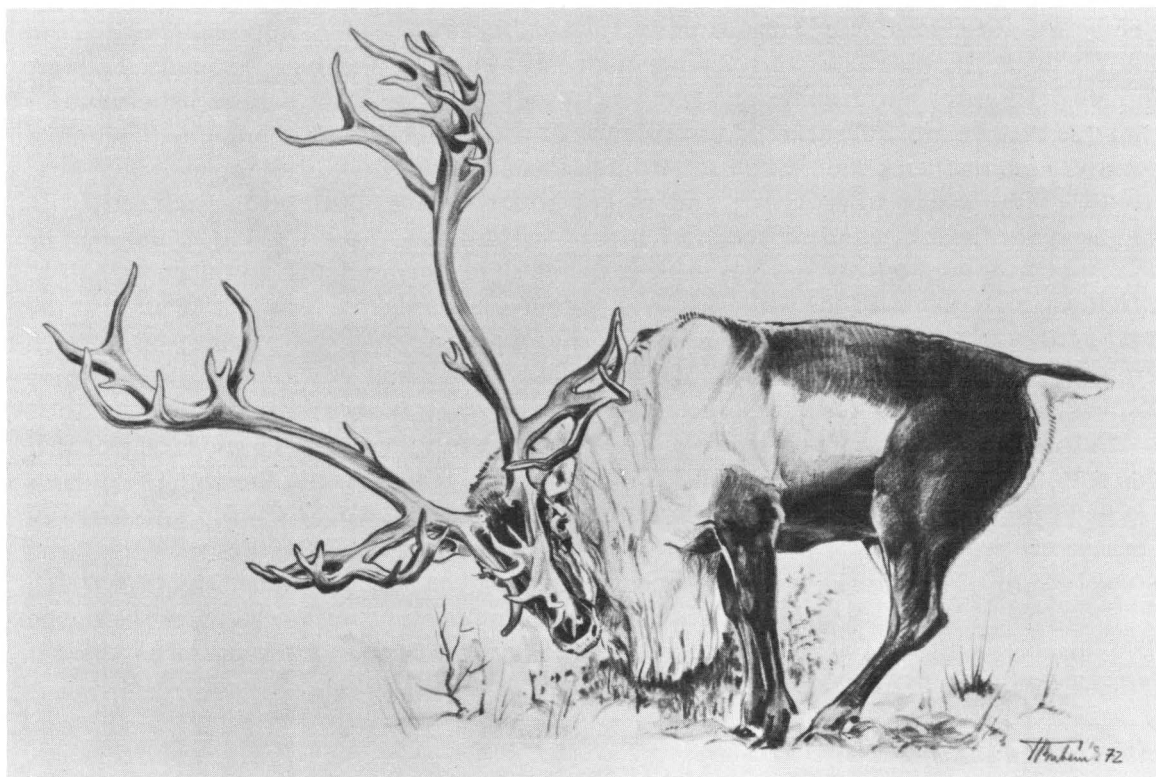


Fig. 3.—'Horse-shoe' posture with tilted head in barren ground caribou.

Now he lowers the head and presents the top of his antlers. I am responding with tilted-head. My gesture is answered with the intention to jump over the creek. At this moment I lower my antlers with a rush and make a red deer call and he rises on his hind-legs but my nonspecific behavior turns him back in mid-air. After 3 or 4 jumps he stops and watches me from about 12 to 15 m, the body lateral, downstream and head frontal. I am now displaying a tilted-head. The bull responds with 'horse-shoe' posture erects his penis and moistens his tarsal glands. Thereafter he follows the herd, now 50 to 70 m downstream.

He uses the long steps of prancing as master bulls do, head in upward-threat. Only the 'white-of-eye' is displayed backwards, i.e., towards me. He is about 50 m away as I cross the creek. He stops and turns. When he sees that I am following him he moves very fast, head slightly down, tail half up, ears forward, straight toward me. Halfway to me he stops and intimidates me with 'horse-shoe' posture combined with husky sounds. When I display the head-up laterally he gives up and follows the herd. They are now climbing the creek bank and at 12:43 h all animals disappeared from my view.

12:45 h: I am following the herd up the bank and see that the two yearling bulls in the creek's bed did not follow the herd. They are feeding about 20 m downstream and do not pay any attention to me even though they can smell me. As soon as the head of the dummy is over the edge of the bank the bull which is watching the feeding herd charges me. But he stops about 30 m from the bank, when I turned back down the bank to rest.

12:58 h: Now I climb the bank again and see that the tail of the herd is disappearing over the bank at the other side of the loop of this creek. The bull still follows behind. He sees me, turns back and intimidates frontally. His head is tilted laterally with body in a horse-shoe posture and moistens his tarsal glands. I am answering with lateral presentation of body and tilted-head. He starts to move towards me. His head is only slightly tilted but relatively high. He alternates this gesture with head-bobbing and husky sounds. Ears are alternately forwards and backwards. The herd trundles in phalanx formation with him. It is an unique picture and adventure. At a distance of 7 to 8 m he stops, scratching the ground violently. I see the black soil flying back from both sides of his body. He displays tilted-head with the white-in-eye towards me and makes husky sounds. I am also responding with tilted-head and husky sounds. Thereafter I offer the antlers for sparring. In this moment he turns and drives the herd away. He is using prancing steps, the body half to the cows, half to me in low-stretch, but with the white-in-eye threatening towards me. Now it is 13:08 h as the whole herd with the bull have disappeared. If my impression of his departure was correct, then the bull pranced away in amble, with tail raised and his rump patch flashing conspicuously from one side to the other.

Unfortunately the age at which the tilted-head gesture begins to be used, and/or if it belongs to the common repertory in antlered or antlerless females is not known. The records of Lent (1966: 723, Fig. 5) are ambiguous. This knowledge could be a very important key in behavioral research of caribou. It is of interest that the courting male uses the tilted-head gesture toward the female in heat (Dugmore, 1913: 58) (for possible explanations see later).

The gaps in knowledge about the use of antlers in females force me to focus the theme of this paper on the use of antlers in males. Beginning with the ontogeny of antlers our attention should be focused on the first and second set of antlers.

Antlers of 'Pre-teens'

The great similarity in size and shape between antlers of females and those of the first and second antlers of males and the similar coat have a peculiar social effect. The antlered calves or generally yearlings and some of the two-year old males with retarded antler development are difficult to distinguish by sight from antlered females. It is this group that I refer to as 'Pre-teens'. In this way these males form a special sexually camouflaged group (Bubenik, 1971; Wickler, 1968). By this way the social pressure of prime bulls is chiefly redirected to 'Teens'. Simultaneously, the presence of the pre-teen-class diminishes the number of 'Teens', who in other species recruit directly from Kids (Bubenik, 1971). Such social differentiation enables caribou 'Primes' to maintain a majority or at least parity with 'Teens' despite heavy natural losses (Bubenik, 1971).

Unfortunately, records of the use of antlers in 'Pre-teens', including my own, are insufficient for any valid conclusion concerning development of antler use in reindeer.

Antler Use in 'Teens'

The available data about sexual and social maturation in caribou are not uniform (Bergerud, 1971; Pruitt, 1966). The discrepancy between the authors could be partly due to the lack of quantitative analyses regarding these processes (Bubenik, 1971) and/or that there was a very different status of social organization in the studied herds. This, of course, could be the source of different rates of sexual maturation (Bubenik, 1971). A similar discrepancy could be found in my own records also. In the Arctic herd the prime-age seems to begin in the fifth year of life. But in the socially disorganized Nelchina herds it probably begins one year earlier. In accordance with some observations of Bergerud (1971) I will put the 'Teen-age' in male caribou between the fourth and fifth year. When the age of 'Primes' ends and that of 'Seniors' begins is not easy to establish. Bergerud (1971) believes that the upper age of 'Primes' is in the eighth year. He made this conclusion based on two bucks with antlers in regression, aged by tooth-wear between seven and 10 years. Compared with ageing in other large cervids like wapiti (*Cervus canadensis*), red (*C. elaphus*) and fallow deer (*C. dama*) the age range of 'Prime' caribou bulls seems to be too narrow. We now know that in these species the 'Prime-age' ends between 10 to 12 years. But between the sixth and 10th year of life nearly every antlered male has 'regressed' antlers once or twice. This is probably the effect of great exhaustion during the rut. The most stable and best developed antlers are found (in the mentioned species) always near the age when 'Prime' status ends and that of 'Seniors' begins (Bubenik, 1966, 1971).

The remark of Pruitt (1966) that the brow tine is not fully developed "until a buck is about four or five years old" testifies that in this age the bulls start to become 'Primes'.

The morphological differences between 'Teens' and 'Primes' and those between 'Primes' and 'Seniors' are not well described. The most pronounced differences concern body size and coloration pattern. The white pattern, i.e. neck with mane and conical flank strip changes in shape. Together with the degree of darkness of face and body hairs this color pattern gives the best evidence for class membership (Fig. 4). It is my impression only that the optimum color pattern is not developed before the bulls are five to six years old.

I have not found adequate detailed descriptions about the use of antlers in 'Teens' and mine are not complete. I cannot find in my own records any comments about the use of the lateral blow with antlers towards the rival's beam or threatening with tilted-head. Both of these gestures belong to the normal behavioral repertoire of 'Primes'. My records of 'Teens' refer to frontal sparring or frontal thrusts to any part of the body. These are primitive fighting techniques of which only the lateral blow shows any ritualization.

Antler Use in 'Primes' and 'Seniors'

Both classes encompass mature animals. This means that their behavior is completely ritualized. The high sexual potency of Primes is one characteristic of this class. Referring to antler use, the tilted head and the lateral blow with antler is *Rangifer*-specific. The lateral blow characterizes the *Rangifer* fighting technique.

Severcov (1951) was probably the first to recognize the high specificity and importance of this fighting technique in reindeer. In his book he reports: "...*Rangifer tarandus* in which a new fighting technique has been developed — the sideward blow with the first and the second tine towards the beam of the rival." (In free translation from Russian.) This blow which could be made also by the upper part of the beam is immediately

parried by tilting the head and catching the blow with the tines or palms of the upper part of the antlers.

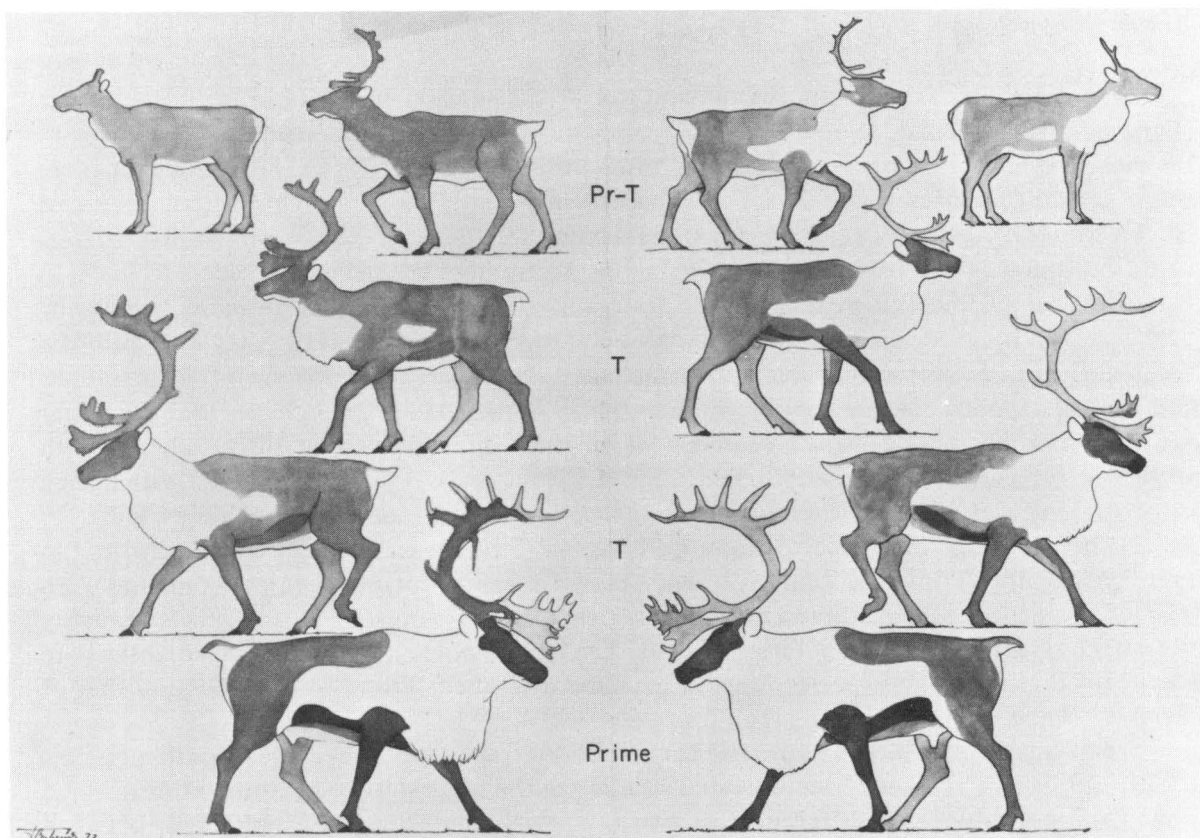


Fig. 4.—Changes in coloration pattern of male barren ground caribou: A — in late August and beginning of September, B — in mid-October. Pr-T = Pre-teens, T = Teens, Pr = Primes. In woodland caribou the white conical stripes on the flanks are not developed.

Searching for the explanation of the significance of tilted-head in courtship it could be said that this posture is a gesture ritualized from the intention to parry or to perform a blow.

The frequency of broken tines and ends in the upper zone of reindeer antlers indicates how often and with what vigor the blow is used. Similar fighting behavior is known in Eld's deer and Barasingha (*Rucervus eldi* and *R. duvauceli*) and in European fallow deer (*Cervus dama*). These species have antler ramifications analogous to *Rangifer* (Fig. 5) but inhabit quite different biomes (Grzimek, 1968). There is only enough information from fallow deer about its fighting techniques to compare it with reindeer (Müller, 1970; Ueckermann and Hansen, 1968). In summary it could be concluded that, despite differences in social organization and evolutionary ages, both species use antlers in poorly ritualized manner. In fallow deer antler structure has remained at a more primitive level; i.e., it represents a more offensive stage than in reindeer. Heavy injuries in fallow deer caused by lateral blows on ribs, legs and belly give evidence for the offensive use of antlers in that species. In reindeer the evolution of antlers is more progressive. The antlers developed structures with apparently defensive characteristics. A brief ethological analysis of reindeer antlers should

show if these conclusions are correct.



Fig. 5.—Antler structures in Cervinae similar to that in *Rangifer*: (1) Eld's deer (*R. eldi*), (2) Barasingha (*R. duvauceli*), (3) fallow deer (*C. dama*).

The Functional Elements of Reindeer Antlers

The basic structural pattern of *Rangifer* antlers is a monopodium (Beninde, 1937) from which the tines branch first anteriorly and then posteriorly. The beam is 'C' shaped in a manner similar to white-tailed deer (*Odocoileus virginianus*). In all populations we will find also individuals with other complicated patterns. The upper part of the beam may bifurcate in two equivalent branches which can ramificate farther. There is a third type of branching which is exceedingly rare: an anteriorly tined beam, which I call 'eucladocerine' (Bubenik,

1975). I found it only in three specimens of European reindeer (*R. t. tarandus*) but it should also occur in woodland caribou of eastern Canada. The evolutionary relationships among these three structures cannot presently be evaluated.

The First Tine

As I have pointed out (Bubenik, 1975) this first tine is homologous with the brow tine of Cervinae. Its direction is modified in *Rangifer*-specific manner. The tine extends forward or is bent over the nose. In well nourished bulls it is vertically palmated, otherwise it is only forked. In the majority of antlers only one palm is well developed. The ends of the brow palm are pointing straight ahead. They form a blade which can inflict injuries on the face. It is my opinion that the brow tine is the most dangerous part of reindeer antlers. A direct hit with the brow tine can tear the skin and even perforate the forehead bones (Fig. 6). In huge brow palms some of the ends are alternately directed slightly to the left and to the right. It



Fig. 6.—Ontogeny of brow tine and alternating bending of points in well developed palm.

could be that by such architectural modification of the palm reduces the danger to the face (see Fig. 10; Bubenik, 1975). These conclusions are contradictory to those of Pruitt (1966) who assumes that the function of the brow tine is only protective, i.e., to avoid an injury to the eyes when bulls are thrashing antlers in epigamic display. My thesis is that the brow tine is offensive and by tilting the head it is presented to frighten the rival.

The Second Tine

As I proved in another paper (Bubenik, 1975) this tine is homologous with the trez tine of other cervids (Fig. 7). It is located very low on the beam and is modified in an



Fig. 7.—The shield of face and eyes formed by second tines.

intricate manner to provide an excellent shield of the face. The second tines protect the eyes in any head position. It would be of great importance to obtain significant morphometric data concerning the extent of the variability of the second tine in tundra and taiga reindeer populations in relation to the assumed difference in social temperament.

The Third Tine

It is presumed that this tine is in regression (see Fig. 3; Bubenik, 1975). In a few specimens it is quite long. I assume that it was formed to protect the neck and parietal region. This idea is deduced from observations on fighting in fallow and axis deer (*Axis axis*). Also in their antlers is a medio-posterior directed tine serving the same purpose (Fig. 8). Causes of its regression in reindeer are not yet known. The third tine can occur only on

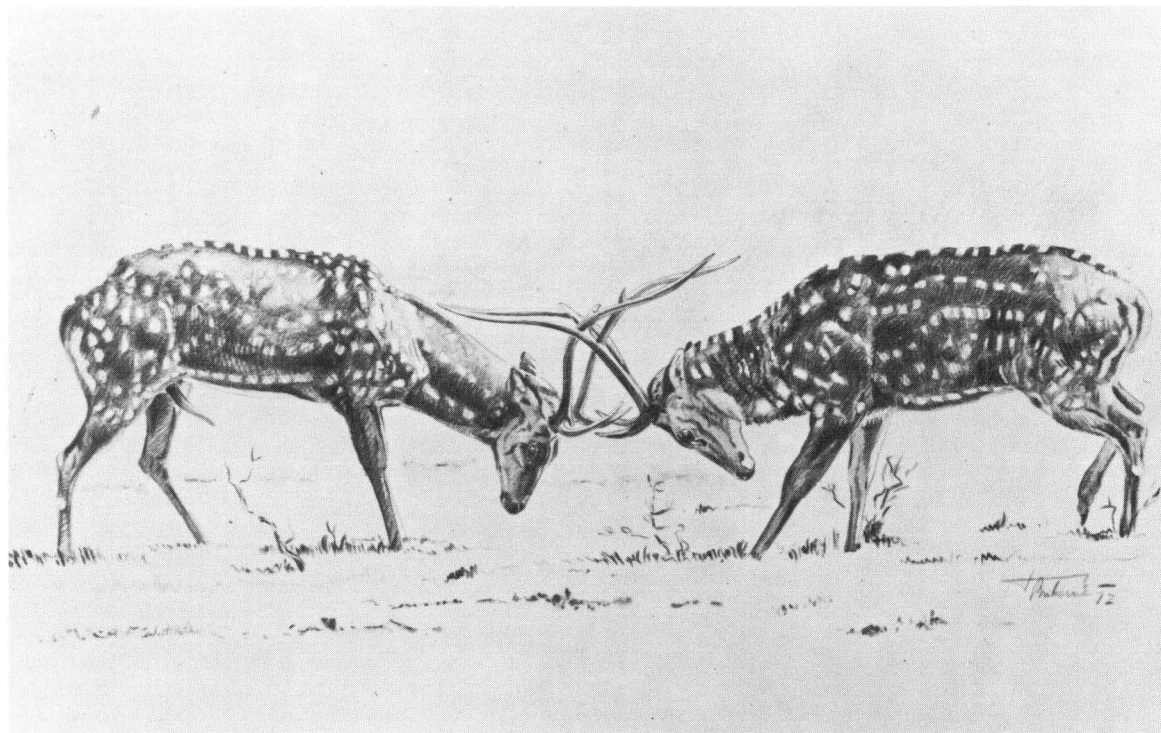


Fig. 8.—The role of antero-posterior tines in fight of chitals (*Axis axis*).

one beam or it could be entirely absent. In this regard it behaves similarly to the bez tines in red deer. I assume that in this species its significance declined when the so-called 'royal' or 'cup' appeared on the top of the beam. The great catching capability of this feature makes it easy to hold the rival's antlers away from the face, especially from the eyes (Fig. 9). In antlers with 'royals' the bez tine loses its function of eye protector and could regress. The numerous tines on the posterior edge of reindeer antlers or highly bifurcated beams behave in a manner similar to 'royals'. It may be that their hypertelic character and advantage in fighting were the main causes for regression of the third tine.

The Upper Zone of Antlers

As mentioned above the upper zone of reindeer antlers is hypertelic or has the inclination for hypertely. It represents the youngest zone of antler structure. This might explain its large variance in structure and architecture (Bubenik, 1975) (Fig. 10). From available data it is not possible for me to decide whether this hypertelic growth was selected

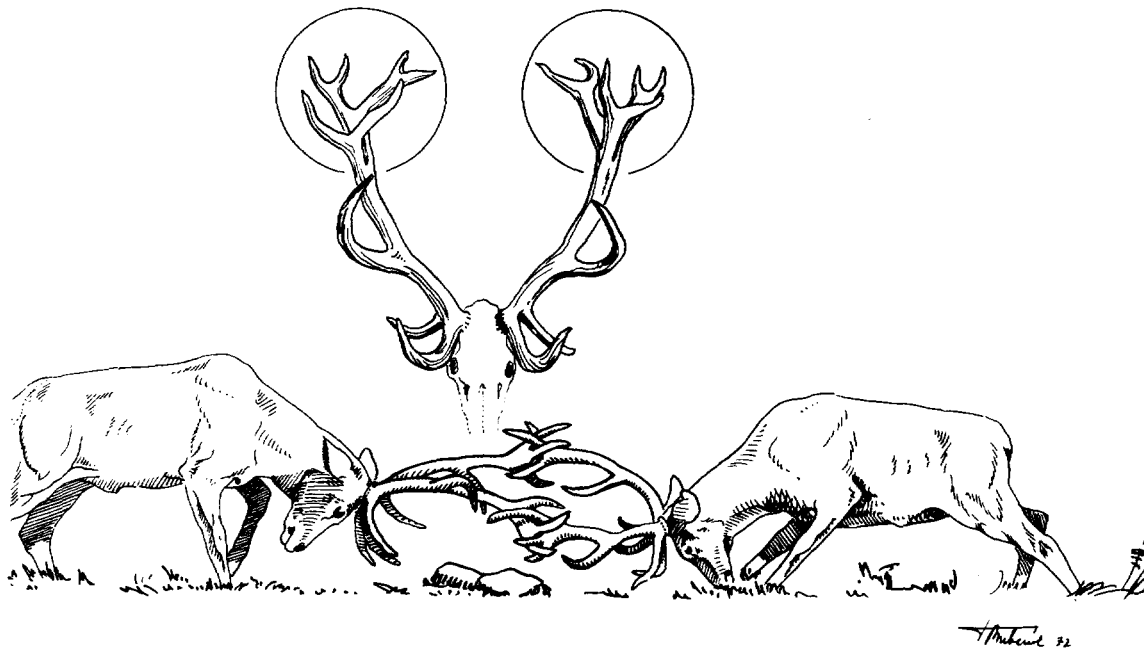


Fig. 9.—The role of 'royals' in fight of red deer stags (*C. elaphus*).

to perform and to parry the lateral blow; or for catching the frontal thrust of antlers and hold the rival's brow tine far apart from the face.

Due to the great variability in spread and beam architecture it is rare that both rivals have antlers so similar that the upper zones of both can fit into each other. The common case is that only one beam from each animal can clinch (Fig. 11). If this does not happen the third or second tines are then the last defending zone of the face. These observations could support the assumption that the major creative and selective process in reindeer antlers was the lateral blow with its method of use and resulting effect.

All these impressions and conclusions refer to the viewpoint of several observers. From the dummy operator's view the antlers achieve additional significance.

The Responses of Caribou to Antler Dummy

The responses to the dummy were different in the late summer and in the rut. In both cases the dummy had the winter hair pattern. But the winter pelage of the caribou in the Endicott Mountains only began to appear in late August. At this time there were only a few prime bulls with white necks, their dewlaps were short and the conical strips on the flanks were small. Also the brown of the hair was not dark. Therefore my dummy ranked over all animals that I encountered. No bulls had shed velvet and many of them had antlers still growing. The high rank of my dummy could be responsible for the low success of responses to my approach. Of course, it is generally known (Banfield and J. Kelsall, pers. comm.) that there is certain avoidance of contact among groups and individuals of barren ground caribou in this time. Generally a distance of 50 to 70 m is held between groups. A foreign individual or a foreign group can join only after a long chase. Everyone who has had experiences with

the speed of moving caribous will agree that it is impossible for man to follow them. All my attempts to approach the dummy closer than 50 to 150 m were fruitless. This, of course, is a much shorter distance than could be attained without the dummy. But it was not short enough to allow experiments, close-up observations and primarily to be significant because the investigative behavior of caribou is well developed and foreign subjects could be very attractive (Pruitt, 1965).



Fig. 10.—Different kinds of upper zone ramification in *Rangifer*.

In the rut the responses to dummies of both sexes were much better. The dummies operated as species-specific releasers and in the case of male dummies with appropriately large antlers it was not difficult to join the herds on the tail or on the flank. Dr. David Klein, who was with me at Selawik River came one day camouflaged by dummy through a rutting herd of about 30 caribou and then pushed them towards my camera. My main observations were focused on the question of the antlers as a search-image. Therefore I searched for encounters with 'Primes', i.e., animals with fully developed courtship behavior. The tilted-head was then my main study object.

From the high number of successful encounters I would like to pick out only two which should illustrate my conclusions.

Prime bulls were always willing to attack me. The type of antler structure and/or antler size of the dummy was not important (Fig. 12). 'Teens' and 'Pre-teens' maintained different distances to the dummy. When I was alone they would approach the dummy from over 500

m and then followed 30 to 50 m behind. They were ready to lie down when the dummy was 'feeding' or bedded. Bachelor 'Teens' were often much closer, sometimes 15 to 20 m. When a 'Teen-bull' possessed a harem he first tried to intimidate me with a 'horse-shoe' posture and then gave up the harem. He then stood close to the herd and behaved like a bachelor.

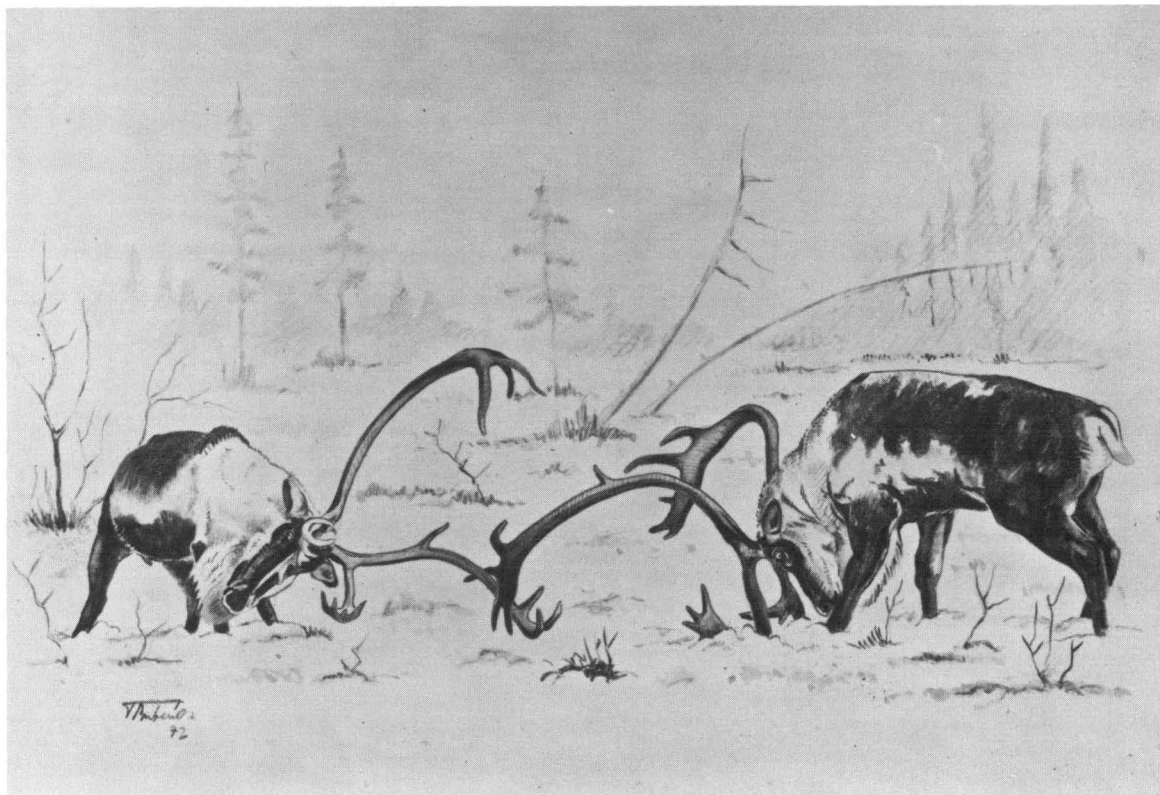


Fig. 11.—Fighting technique in barren ground caribou. Note the significance of upper and third tines in holding the rival's antlers away from the face (after a picture in Hemming, 1971).

When the females were alone or the harem was spread apart, the females responded to the dummy by approaching. Their reactions could be intensified by the size of the dummy. I have observed the same responses to size of antlers on the dummy in females of red deer, wapiti and moose also.

Females who were guarded by a master bull were only interested in the victor of our encounter. In one of such cases a cow was bedded about 10 m from me and ruminated even though I was charged three times by her bull.

On a few occasions when close approach was not possible due to the rough terrain, the herds with the bulls were ready to follow me when the antlers were over-sized.

In all my approaches with the wind the caribou were not afraid. They only moved to one side of the wind and were searching olfactorily and optically far behind me for the releaser of the human-scent.

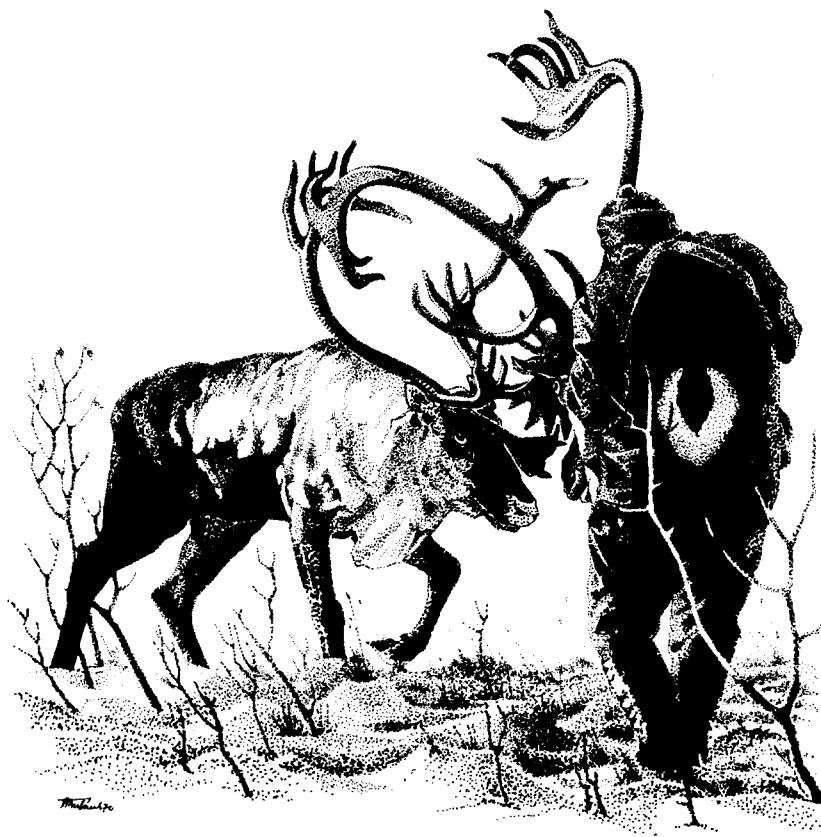


Fig. 12.—Dummy attacked by caribou bull (after a slide by D. Klein).

Antlered Dummy and Wind

As only an observer of caribou without dummy, I underestimated the effect of wind. With female and small Teen's antlers on the dummy I had no problems with the wind. But beginning with medium-sized antlers the movement in crosswind was impossible when its velocity was grade 2 or more (branches of trees and shrubs moving). I then investigated the relationships between wind and movement directions of caribou in the rutting season. Under entirely different wind directions I recorded that: in 13 cases the herds were moving with the wind, in 10 cases towards the wind and in one case in side-wind (October 9, 1968, 14:00 h, wind velocity grade 1½).

My experiences are, of course, quite subjective. But I find them interesting enough to recommend further study. It could be that the shape of male antlers could be also selected by the wind (Fig. 13). If the wind resistance for antlers and dummy are the same for caribou, then the wind can influence their behavior. Under such conditions the wind direction could be a major factor in holding the bulls together, and in determining the migration routes of herds in addition to the effect of wolves as argued by Bergerud (1972).

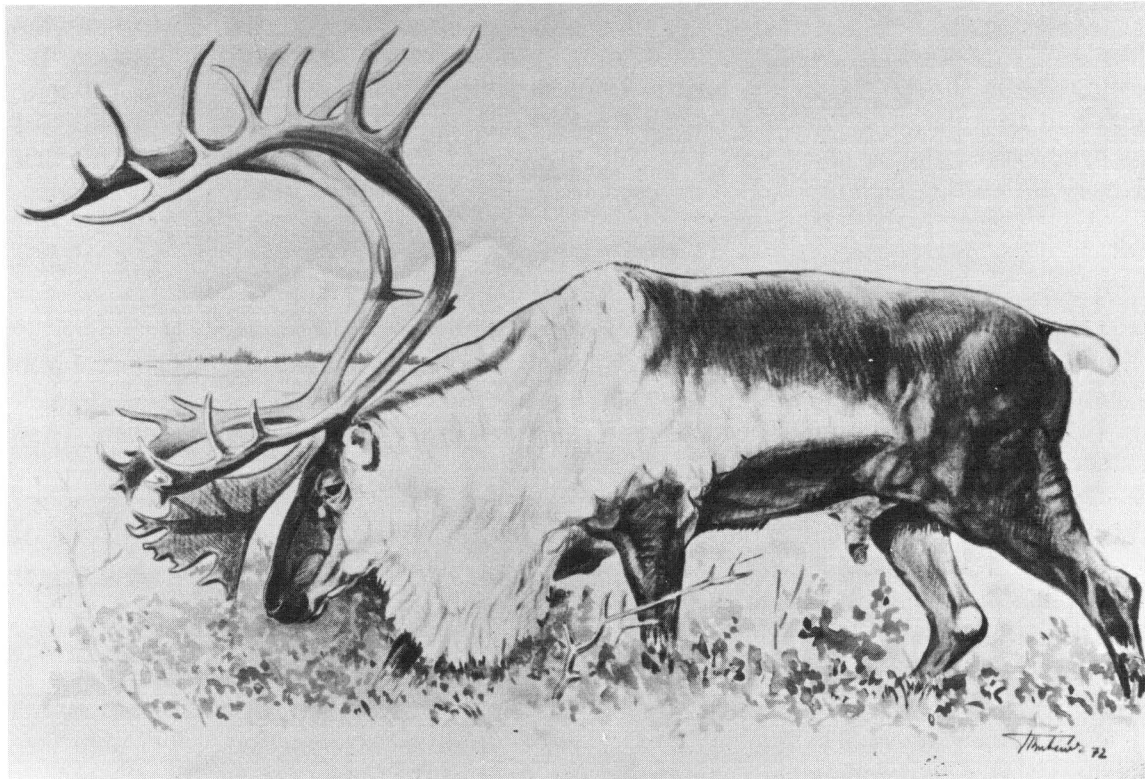


Fig. 13.—Huge antlers of barren ground caribou with 'aerodynamic' shape, offering less resistance to the pressure of cross-wind.

In the first case it has protective effect against insects and wolves (Murie, 1935; Bergerud, 1971). In the other it facilitates the social contact and might influence the direction of migration during the rut. When the antlers are shed or not too large the animals can move in any wind directions. In taiga or in high mountains where always lee-sites are easy to be found the wind direction cannot influence the movement so much as it does in the barren grounds. It is also generally known that woodland populations possess antlers with a higher grade of ramification or palmation than the barren grounds populations.

Responses of Animals and Man to Caribou Dummy

Autumn 1969 was an extraordinarily good year for willow ptarmigan (*Lagopus l. alascensis*) in the Alaska Mountain Range, west of Tahneta Lake. Their flocks did not show any fear of moving or grazing caribous. My previous experiences with positive responses of wild boar (*Sus scrofa*) and pheasant (*Phasianus mongolicus*) to red deer dummies as well as horses to a moose dummy led me to also study the responses of ptarmigan. I found that the caribou dummy released in ptarmigan identical responses as toward caribou. I could move through the flocks without them being afraid. Only when I drove them too long did they fly 30 to 40 m away. Acoustic signals released by ptarmigan which remain behind me and focused on those ahead of me were the same as I heard when caribou were moving through the flocks.

These observations show how the use of dummies could be harmful for these species when used by hunters or poachers. But it could also be harmful for the carrier if used in the hunting season. In the wide valley of the Little Nelchina River I was twice investigated by hunters in two planes, in one of these two cases the man held his rifle ready to shoot. This experience and a similar one I have had with moose and red deer dummies taught me that this very interesting technique must be used with all possible precaution in the study area.

DISCUSSION

On the basis of these findings the following recapitulation can be made:

- (1) The antlers in male caribou are a dominant search-image at short distances. From antlers the sex and class rank of the animal can be determined.
- (2) In social encounters the individual rank of antlers inside a class is less important. They seem not to have the characteristics of a *gestalt*.
- (3) Ontogenetic stages of antler structure allow differentiation of the following social classes: Pre-Teens, Teens, Primes and Seniors. The difference in coloration of the social classes should provide possibilities of making structural analyses of herds and populations from aerial pictures.
- (4) The antlers represent a configurational stimulus which in its releasing capacity is not separable from the key releaser 'head-pole'.
- (5) The different shape of female and male antlers represents at least two different evolutionary stages. The female's antlers are of primitive stage due to the fact that they do not need to compete with and evolve like those of the bulls.
- (6) The structure in female antlers is developed for more offensive threat than in males.
- (7) Male antlers represent a more highly developed structure with dominantly protective characteristics which is very well adapted to the primitive fighting techniques in male caribou.

All these results offer two interesting themes for discussion:

The evolutionary aspects: In the evolution of behavior and antlers of *Rangifer* there is something contradictory. From the time of McDougall's "Psychology of Animals" (1952) up to now (Wickler, 1968, 1970) it has been generally recognized that the pace-maker of evolutionary processes is the evolution of behavior. This means that new morphological characteristics are selected by new elements in behavioral patterns. In evolution of antlers and behavior in reindeer this rule seems to fail. We have sufficient evidence to believe that reindeer antlers are the most developed form in all cervids. But we have also enough facts at hand to believe that the use of antlers is a very primitive one. This contradiction is only apparent. We suggest that the dynamic evolution of construction and architecture of male antlers in *Rangifer* was permanently controlled by its primitive and poorly ritualized use, e.g., their development to higher construction patterns was under the selective pressure of this primitive behavior. Only more defensive elements were preferred. In this way the male antlers could make the head-pole to be a key releaser without fundamental changes in behavior pattern.

The perception in animals: The antlers of caribou and other large cervids are the main components in the search-image 'head-pole' which is the cue of the whole animal when the 'rear-pole' is not seen. Of course, on the head there are many elements which can transmit information such as eyes, ears, lips, coloration patterns, olfactory signals and head gestures. It seems likely that for any given endo- or exogenous situation and for any exchange of information the structure and/or sequence of these elements have a programmed pattern which is perceived as one single code.

Maybe it is my own defect in optical perception that, despite more than 12 years of

training and studies with antlered dummies, I am not able to read these codes at one look, like the cervids do. It may be, of course, that my perception is quite normal and that between man and all other animals a difference in perception exists. Human beings, due to a highly developed abstractive imagination, are not capable of filtering out details which are not important. Therefore, the perception of such complicated codes is relatively slow. Man's vision centers have to analyze signal after signal. This requires more time than the duration of the coded information. Therefore, the reading and immediate comprehension of animal expressions is nearly impossible for man.

The search-images as dominant releasers give animals a much faster communication than man's language does. But for the ethologist they represent a key for successful communication between man and animal.

Special importance should be given to the fact the species can correctly understand search images of those foreign species which are a permanent member of their social environment (Mitwelt).

CONCLUSIONS

Due to observations of caribou and their response to the antlered dummy I have to conclude that the short distance releaser 'antlers' as a part of the 'head-pole' attained a rank of importance among cervids which is higher only in moose (Bubenik, in prep.).

Despite the evolutionary discrepancy between the primitive system of social organization and poor ritualization in behavior in caribou on the one hand and the highly developed structure of antlers on the other, the social pressure on the antlers seems to be so large that it is chiefly responsible for their structure and architecture.

It could be that the other formative power might be the wind and its direction. But this possibility must undergo further study.

The antlers in *Rangifer* have a high social significance. The fact that they occur also in females is more due to the influence of social advantages of an organ which was always present than as a new acquisition for better social advantages.

The evidence for this conclusion is not only in the probably quite different hormonal regulation of antler cycle but also in the more primitive and offensive pattern of female antlers.

Through this study the problem of significance of antlers to reindeer is not satisfactorily solved. It seems to me that I have shown that what we know or believe to know about the reindeer antlers is less than what should be known for better understanding of this unique species.

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LEADERSHIP IN WILD REINDEER IN NORWAY

Brian R. Thomson
Department of Forestry and Natural Resources
Edinburgh University
Scotland

ABSTRACT—The social behavior of wild mountain reindeer in southern Norway was studied from 1969 to 1971. Herd leadership was recorded frequently, once every six hours on average, most often in winter, and most typically in critical situations. Moving ahead of the herd, the leader dictates the pace and direction of travel to suit each situation. Eighty per cent of single leaders were adult females, 13 per cent were adult males in spring and summer and only five per cent were juveniles. Leading the herd was one of several roles which promoted herd security; others were alerting the herd, standing as look-outs and aggressively approaching small predators. The maternal experience of mature females suits them for these roles. The capabilities of experienced leaders makes leadership in reindeer a highly adaptive group process.

In traditional ethology the social organization of an animal species has been represented by describing the type and frequency of behavioral interactions between the individuals in a population. However recent work on a range of higher animals from birds to ungulates to primates suggests two main inadequacies in this approach (reviewed by Crook, 1970).

Firstly, social organization is not a static attribute peculiar to a species, but is molded and influenced by the environment and dynamics of the particular population studied. The explanation of variation in behavior and social structure between different reindeer or caribou populations should be sought in local differences in the ecology of the populations, before genetic differences are assumed.

The second criticism of the traditional approach to behavior is that classification of reciprocal behavior patterns and signals may give an imbalanced view of the social structure by stressing one aspect such as reciprocal dominance relationships, at the expense of other group phenomena such as spacing, cooperation or leadership.

A leader has been defined as an individual who frequently is at the head of a moving column and often seems to initiate a new activity (in cattle; Hafez *et al.*, 1969). In reindeer the communication that one sees between leader and followers identifies leadership as a group process, one aspect of social organization.

In the course of a field study of a wild reindeer population in Norway an attempt was made to observe group processes as a whole. Instances of leadership were recognized and recorded with a view to assessing their importance in group movement and security.

METHODS

The behavior of wild reindeer herds in mountain areas of southern Norway was studied from September 1969 to September 1971. Direct observation of herds by spotting scope (X 25) and binoculars (10 X 50) allowed recording of group activity, size, composition and dispersion at different times of the year. This study formed part of the Norwegian IBP

Tundra Biome and Statens Viltundersøkelser investigation into the role of wild reindeer in the arctic-alpine ecosystem. The total population of wild reindeer in Norway is around 30,000 distributed in five or six mountain areas in the south of Norway. Research was concentrated on the Hardangervidda mountain plateau (7,500 km²) with a population of 14,600 in 1970.

A complete report on the behavior of these reindeer is in preparation. Many aspects of behavior are similar to those recorded for other reindeer and caribou populations (Espmark, 1964, 1971; Pruitt, 1960; Lent, 1966; and others). Herd activity on Hardangervidda has been described in separate reports (Gaare, Skogland and Thomson, 1970; Thomson, 1971).

RESULTS

The emergence of a leader does not occur in all situations involving movement but rather is most typical of reindeer groups or herds in a potentially hazardous situation. When an individual takes up position ahead of the herd, it dictates the route and rate of travel away from a source of disturbance, or leads the herd in swimming across a river, or leads through a narrow mountain pass, or leads across a frozen lake in winter. Leadership may also occur in situations less obviously hazardous, such as moving between winter grazing areas, and trekking in long columns in the April migratory movement.

Hafez, Schein and Ewbank (1969) emphasize the importance of 'followership' in the leader-follower relationship of cattle. In reindeer, too, a single animal at the front of a steadily moving group can be simply characterized as the animal which first moves in the direction which most of the deer want to go. This passive leadership is the only type so far recorded for semi-domestic reindeer in north Norway (Skjenneberg and Slagsvold, 1968). However two types of active leadership occurred in wild reindeer, whereby the leader functions as an action model for the remaining deer.

The most common type is where the leader functions as an instantaneous action model. This is particularly a feature of disturbed reindeer: the herd bunch together, run off a bit and stop to look back; then a leader emerges. When the leader, who may be 10 to 50 m in advance of the herd, starts trotting so the herd behind trots; when the leader stops so the herd stops behind; when the leader walks the herd walks; and so on (Fig. 1). The direct visual control of activity between leader and followers continues until the leader returns to normal activity, such as grazing or lying, and is re-integrated into the herd.

The other type of active leadership is where the leader functions as a delayed action model. Here the herd copies the leader's movements over the same piece of ground. This is frequent in winter herds, disturbed or undisturbed, moving over untraversed snow. Again the leader is ahead of the herd: when the leader starts trotting so the herd trots on reaching the same place; when the leader stops to look around so the herd stops at that place also; and so on (Fig. 2). Animals behind the leader frequently dip their muzzles down to the leader's track they are following and this apparently enables them to assess and copy the same activity over that piece of ground. In long, walking columns of undisturbed reindeer in winter, an individual, by sniffing in the tracks of those ahead, copies their activities over the same route, even when the animals ahead are out of sight (Fig. 3). This olfactory communication is apparently achieved through a response to trail scent from the interdigital glands of the deer ahead. It is known that the interdigital glands of caribou leave scent on the ground following an excitation jump from an alarmed deer, and that the deer following will themselves react with fright on reaching this spot (Pruitt, 1960). It would appear that the type or quantity of exudate deposited on the ground from walking, standing, trotting and running can be distinguished.

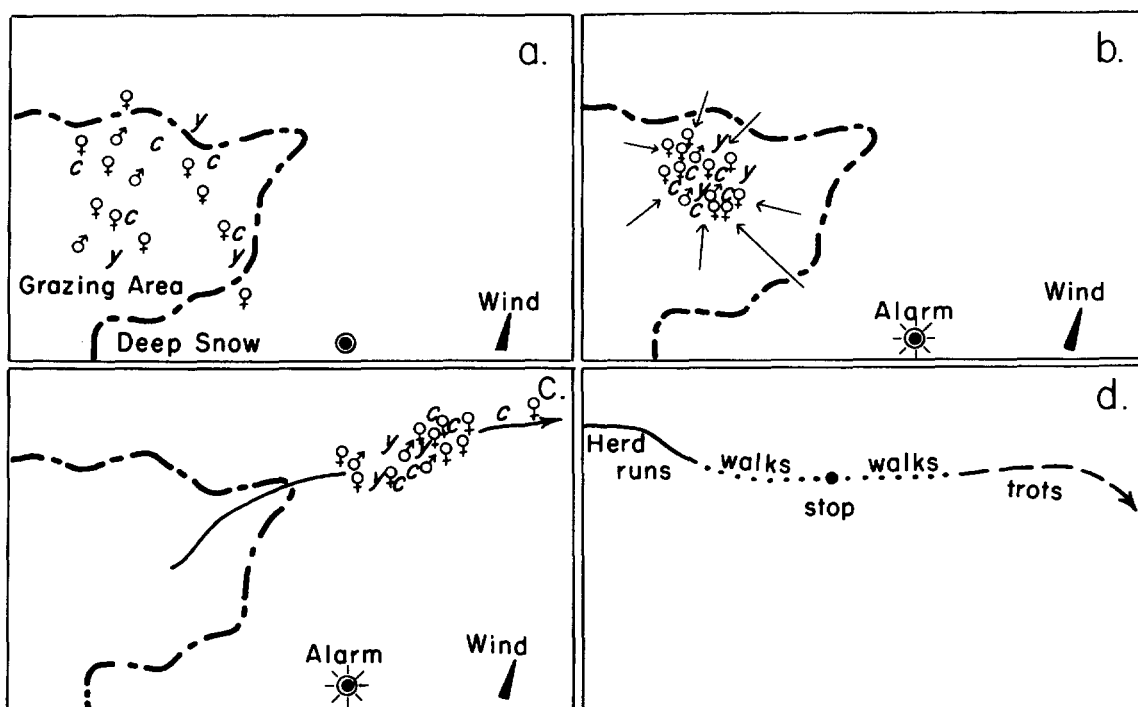


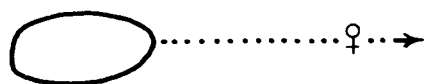
Fig. 1.—Schematic example of the leader as an instantaneous action model. A herd of 21 reindeer at Hardangervidda on 28th January 1970. (a) The group is spread out grazing peacefully. (b) The reindeer react to the alarm source by bunching together. (c) As the group runs off an adult female (with calf following) emerges as leader. (d) The leader determines the rate and route of travel of the group.

Frequency of Leadership

Herd leadership, either of the active or passive type, was observed on 140 separate occasions in the course of 855 hours when the groups or herds were in view. Leadership was most frequent in winter: one leadership bout every five hours compared with one bout every seven to nine hours in spring, summer and autumn (Table 1).

TABLE 1.—The frequency of leadership events.

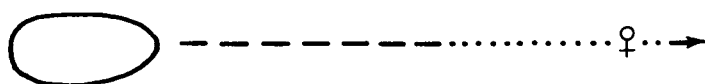
Season	Leadership	No. of events	Hours of observation	Average frequency
Winter	(Nov.-Apr.)	70	336	1 event/4.8 hours
Calving	(May-June)	32	222	1 event/7.0 hours
Summer	(July-Aug.)	23	161	1 event/7.0 hours
Autumn	(Sept.-Oct.)	15	136	1 event/9.1 hours
All seasons		140	855	1 event/6.1 hours



Leader walks; herd is stationary.



Leader stops; herd walks up and stops.



Leader trots on then walks.



Herd trots over same ground then walks, etc.

Fig. 2.—Schematic example of the leader as a delayed action model. A herd of 264 at Hardangervidda on 25th January 1971.

Out of these 140 leadership bouts at least 40 were a direct consequence of herd disturbance. Of all recorded disturbances causing flight, 25 per cent resulted in leadership (36 per cent of the winter disturbances but only 17 per cent in summer, Table 2). Herds in

TABLE 2.—Proportion of disturbances resulting in leadership.

Season		No. of disturbances	No. with leadership	% disturbances with leadership
Winter	(Nov.—Apr.)	53	19	36
Calving	(May—June)	25	5	20
Summer	(July—Aug.)	48	8	17
Autumn	(Sept.—Oct.)	31	8	26
All seasons		157	40	25

summer are less readily disturbed than in winter (Thomson, 1971), and when they are disturbed they more often move off in a mass without a recognizable leader.

The Role of Leader

On most occasions it was possible to classify, according to sex or age, the individual performing the role of leader. If the leader changed within a bout of leadership, the new leader was similarly classified. For mixed herds and groups containing females, males,

TABLE 3.--The role of leader in mixed groups.

Season	Leader	♀	♂ hard antler	♂ shed or velvet	Yearling	Calf	Unclassified	All leaders
Winter	(Nov.-Apr.)	31	1	3	0	1	26	62
Calving	(May-June)	22	-	5	4	0	2	32
Summer	(July-Aug.)	15	-	5	0	0	3	23
Autumn	(Sept.-Oct.)	10	1	-	0	0	4	15
All seasons		78	2	13	4	1	34	132
Expected incidence of leadership*		45%	14%		19%	22%		100%
Observed incidence of leadership		80%	15%		4%	1%		100%
$\chi^2 = 37.8$ at 3 degrees freedom. $P < 0.001$								

*Estimated herd proportions after calving, 1971.

leaders of mixed herds in summer (when all deer are growing their antlers) they are nevertheless dominant on account of superior body size. In winter and spring the rank of an animal, and thus its ability to defend or procure feeding and lying sites, is largely predictable on the basis of antler size. With regard to leadership, females of all ranks from well-antlered dominant females to poor-antlered or unantlered subordinate females voluntarily take on the role of leader.

This lack of relationship between dominance and leadership has also been found in domestic goats (Stewart and Scott, 1947), sheep (Scott, 1945) and cattle (Kilgour and Scott, 1959). The distinction between dominance and leadership is not always clearly made in some deer studies (e.g., Darling, 1937).

Other Roles which Promote Herd Security

The direction and activities of a leader, particularly after a disturbance, is one of the least predictable aspects of reindeer behavior. The rate of travel and the route taken by the leader is highly variable and appears adapted to the actual situation. Whether the leader is eluding a predator, or choosing a crossing place for swimming a river, or guiding across an ice-covered lake, the capabilities and experience of the leader automatically becomes the 'common property' of the group.

Directing the herd movement is not, however, the only role which contributes towards the control of a potentially hazardous situation. The responses of a herd in winter to a potential danger will include all or most of the following elements: this scheme illustrates that it is the actions of a few reindeer in the herd (i.e., those marked by an *asterisk) which promote the herd safety.

- (1) The most alert reindeer* see, smell or hear potential danger. They cease grazing or get up from lying and face the disturbing factor. Behavior indicating alarm includes a prolonged urination stance, a high-stepping gait with tail up and an alarm bark.*
- (2) The reindeer run together into a bunched herd. Reindeer at the edges* of the herd are most alert. More alarm signals are used.
- (3) a. If the cause of the alarm is a small predator on the ground, such as a fox (*Vulpes vulpes*), raven (*Corvus corax*) or gull (*Larus canus*), the nearest reindeer* walk forward together and a single reindeer* charges at the predator. The herd returns to normal activity, some reindeer* remaining alert longer than most.
or b. If danger is confirmed, the herd runs a short way off and stops to look back. More alarm signals. A single reindeer* leads the herd away with stops to look back and to survey the way ahead.
- (4) Before finally passing out of sight those reindeer at the rear* of the herd stop to look back at the source of disturbance, or having already passed out of sight temporarily return to look back.
- (5) The herd gradually returns to normal activity when the leader* does, some reindeer* remaining alert longer than others.

The reindeer which are most alert, which act as look-outs at the edges and rear of the herd, and which approach and charge potential predators, tend to be the adult females, i.e., the typical leader animals. The role of 'look-out', the role of 'defender' and the role of leader are taken by adult females, and all have the same function, that of herd security.

The concept of a look-out animal is not a new one. Among reindeer-owning Lapps it is commonly believed that a single female, the 'varsimla', stands guard while the rest of the herd peacefully graze or lie. Indeed Sdobnikov (1935) recorded this for reindeer in Russia. However the 'varsimla' has not been found in semi-domestic reindeer in Norway (Skjenneberg and Slagsvold, 1968), nor was it found for wild reindeer in this study.

Nevertheless the alertness and wariness of the reindeer is greatly increased on suspicion of danger, or in disturbed herds, and it is then that some animals show a degree of alertness and attention to danger in excess of others, and function as temporary 'look-outs'. The responses of these ultra-alert animals determines the herd pattern: in turning to flight, or advancing towards a small predator. Subsequently the leader out in front is most attentive and alert with supporting adult females at the edges and rear of the herd.

While flight is the usual form of defense, a more active defense is made by approaching and charging towards small predators on the ground. This aggressive approach was seen on six occasions, each time involving females, and directed towards fox, gull and eagle (*Aquila chrysaëtos*) (Table 4). This behavior was similar to that of isolated mother females in the calving season who on nine occasions were seen to actively defend their calves against ravens, gulls and eagle. Caribou females in Alaska have been known to charge aggressively at humans who handle their newborn calves (Lent, 1966).

Out of thousands of antagonistic threats and retreats seen in winter connected with feeding and lying spots, 20 acts were recorded which had an apparent connection with leader or look-out roles. Fourteen of these antagonistic acts (usually antler threat) were directed from an animal behind to the leader of a movement, usually when it hesitated or stopped. Although dominant over the leader the instigator would choose not to take over the role of leader but rather it appeared that the animal in front was being forced into continuing its leadership. It appeared particularly true of an unantlered male leader in an all-male group in winter that if it hesitated to lead it might receive an antler in the rear from the dominant antlered male behind it. With females too, threats towards a leader were apparently not aimed at usurping its role. In the other six cases however, there was positive competition to be in a look-out position nearest to the source of alarm. The dominant (five times a female, once a velvet-antlered male) would procure a frontal look-out position, to the exclusion of a sub-dominant or juvenile. This suggests that reindeer in the role of look-out and defender may tend to be more dominant than those who typically adopt the role of leader.

DISCUSSION

In this field study it was found that the reindeer involved in leadership and its associated roles were typically adult females, often breeders of the current year with a calf to heel, and of all dominance ranks from dominant to subordinate. It was not possible to test whether all adult female reindeer were equally capable of leadership, but there is evidence to suggest that age and maternal experience are important.

As a mother, the female reindeer performs many of the actions of herd leadership. The mother is wary at all times and when disturbed it leads its young calf away, stopping frequently to check the progress of the calf and to survey the source of danger. It also actively defends its calf by chasing off gulls and ravens from the ground nearby. These aspects of maternal behavior are paralleled in the roles of herd leader, look-out and defender. For red deer in Scotland it has even been suggested that a female which ceases to be a regular breeder soon ceases to be a leader (Darling, 1937).

Juvenile reindeer were seen to be followers rather than leaders (Table 3). The mother-infant relationship builds up rapidly through visual, olfactory and auditory communication and from the first day of birth the calf builds up a habit of following the action model, at this stage the mother. In sheep, as in reindeer, the earliest and strongest social relationship is developed with the mother and forms the foundation for leadership in the flock. As the lamb becomes more independent some of its following tendency is transferred to adults in general (Scott, 1945). Leadership in sheep may be traced to the

TABLE 4.--Incidence of active defense against small predators.

Date	Size of group	Type of defender	Type of defense	Type of predator
18/10/70	80	1 ♀	10-12 bunch; approach and 1♀ charges	fox
23/01/70	347	1 ♀	30 bunch and 1♀ approaches	fox
03/03/71	100	6	6 bunch and approach	fox
04/03/71	133	1 ♀	1♀ stands alert	fox
08/05/71	320	1 ♀	1♀ rears up on hind legs	eagle (flying)
25/05/71	50	1 ♀	20 bunch, approach and 1♀ charges	gull (on ground)
Calving (end May-begin June)	♀ & calf	mother ♀	Gets up and stands over calf	eagle (flying)
Calving	♀ & calf	mother ♀	Approach and charge	raven (on ground) 3 EVENTS
Calving	♀ & calf	mother ♀	Approach and charge	gull (on ground) 5 EVENTS
Calving	♀ & calf	mother ♀	Approach and charge	human (Lent, 1966)

continued association of related ewes in overlapping generations. With domestic reindeer in Russia it has been claimed that discernible family groupings of up to 30 individuals exist in the herds with the oldest female as the leader of each group (Sdobnikov, 1935). With wild reindeer however, the frequent splitting and coalescing of groups and herds throughout the year make permanent kinship bonds unlikely, except for the association of mother and her calf of that year. Thereafter the yearling transfers its following habit to adults in general.

Although there is no proven association between successive generations it is probable that the oldest of the female reindeer tend to predominate in leadership roles. This is thought to be the case in several wild deer populations, e.g., black-tail, white-tail and mule deer (in Taylor, 1956), and moose (Altmann, 1956a) in North America; and red deer (Darling, 1937) and Soay sheep (Grubb and Jewell, 1966) in Scotland. With domestic reindeer in Russia, Naumov and Baskin (1969) found that in critical situations the deer were led off by experienced females of five to six years, or castrated sled males of seven to eight years.

Adult males, while having had the universal experience of following as young animals, lack the experience of leading and defending the calves. Nevertheless it was seen that males with shed antlers or in velvet occasionally acted as satisfactory leaders of mixed herds in spring and summer, and of all-male groups in winter. This contrasts with red deer in Scotland where there is no apparent leadership by males, and all-male groups in winter are loose aggregations which readily split up when disturbed (Darling, 1937).

The control and regulation of herd behavior which is achieved through the actions of a few reindeer in leading, defending and watching for danger has not been well documented in most other *Rangifer* population studies. However, Naumov and Baskin (1969) stressed that the leader that emerged in critical situations was usually an older female and that on account of her experience the herd was led off away from the source of alarm in the most tactical direction. Reindeer herds containing a large number of potential leaders were disciplined and adaptable when disturbed, whereas herds with few potential leaders tended to run wildly on disturbance or mill together in a mass. The importance of leadership in the social organization has not so far been documented for caribou. Indeed, in comparison with other cervids, it has been suggested that caribou have no social organization or leadership (deVos, Brokx and Geist, 1967). DeVos (1960) found an absence of leadership among groups of Canadian barren ground caribou at calving time, as shown by a lack of organization when alarmed, and an indecision when changing direction or about to swim. Leaders at the front of the groups changed frequently without regard to sex or age. Banfield (1954) found that caribou groups are usually led by an adult female, but sometimes by younger animals or even calves. However observations by Kenneth Child (pers. comm.) on the reaction of caribou to pipeline simulations on the Alaskan North Slope and by Frank Miller (pers. comm.) on movement in Canadian caribou, suggest that leadership is indeed an important part of caribou group behavior. Continuing work on group processes and behavior should show the extent of behavioral differences between *Rangifer* populations and relate them to ecological differences in the population structure and availability of food and shelter in the habitat.

The roles of leader, look-out and defender described in this study are similar to some of the leadership behavior described for red deer in Scotland and for elk in North America. Darling (1937) describes the leading females in red deer groups as being constantly anxious for the herd welfare: they are alert for signs of danger and exert clear-cut leadership. As with reindeer, a female at the rear of a moving red deer group often stops to look back for danger. Altmann (1952, 1956b) too found that leadership by mature elk females is the rule and describes their actions in choosing river crossing sites, shielding their calves by swimming downstream of them, approaching a human while the rest of the group are

retreating and defending the calves against coyotes.

It is clear that the role of leader in deer cannot be adequately defined in terms of an allelomimetic leader-follower relationship whereby animals are unequally stimulated so that one tends to lead and the other to follow (Scott, 1956). Rather, leadership and its associated roles place deer in the realms of decision-making and problem-solving in the psychological sense. The unstereotyped actions of experienced animals in guiding, protecting and directing the movement of others increases each individual's chances of survival. As such, leadership is an important process within the socially adaptive behavior of reindeer.

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CLUMPING BEHAVIOR AND PREDATION WITH SPECIAL REFERENCE TO CARIBOU

H. G. Cumming
Wildlife Branch
Ministry of Natural Resources
Parliament Buildings
Toronto, Ontario, Canada

ABSTRACT—A question concerning the effect of clumped distributions on the vulnerability of caribou (*Rangifer* spp.) to predators led to a review of literature on clumping and predation among invertebrates, fishes, birds and mammals. Many prey species reduce their vulnerability to predation through anti-predator behavior associated with clumping, such as active defense and confusion due to swarming. However, where clumps of prey become large, they may attract additional predators which specialize on these prey and nullify any benefits from the clumping. Since behavior by prey and predator obscured the effects of clumping itself, a simulated predation experiment was necessary to isolate these effects. It showed that clumping tends to increase the average distance from predator to nearest prey unless the predators are similarly clumped. Presumably this would make predation more difficult. The spacing behavior of predators frequently prevents them from exploiting such clumped prey. I concluded that clumping by prey tends to decrease their vulnerability to predation unless predators react by (1) changing their catching methods or (2) clumping in response. Although this conclusion runs counter to some opinion concerning caribou, it can be reconciled with most studies and it helps to explain some previously paradoxical observations, such as the differing effects of spring caribou aggregations on predation by wolves (*Canis lupus*) and lynx (*Lynx canadensis*).

Bergerud (1971:51) generalized from his study of Newfoundland caribou (*Rangifer tarandus terranovae*) that a dispersed distribution of prey is more effective against predators than a clumped distribution, unless cooperation among members of clumps is sufficiently effective to overcome the disadvantages of concentration. Tostowaryk (1972) came to similar conclusions concerning sawfly larvae (*Neodiprion* spp.). Holling (1961:179) agreed, but then commented that if the increased vulnerability arising from such behavior is so important, it seems paradoxical that colonial behavior has evolved. Patterson (1965) came to an entirely different view. Presenting good evidence that black-headed gulls (*Larus ridibundus*) reduced, rather than increased, predation on their eggs by nesting in colonies, he concluded that colonial behavior acted as a defense against predators. These apparently contradictory conclusions raised the question, "Does clumping behavior by prey increase, decrease or leave unchanged predation rates?"

The importance of this question for caribou is obvious since caribou characteristically form groups and aggregations (Lent, 1965). I hope to show that it is also an important question for many other species. Nevertheless, I found that clumping has not generally been recognized as an important component of the predation equation. Holling (1961:164), for example, mentions only a swarm effect for prey and a group stimulation for predators. Only

Ivlev (1961) has attempted to include clumping in general equations. In view of this discovery, the only way to answer the question seemed to be to examine the literature for evidence. Therefore, I referred to papers on (a) invertebrates, where clumping behavior has not been studied very much in any context (e.g., it is mentioned only briefly by Holling, 1959a, 1959b, 1961, 1963, 1964, 1965, 1966), (b) fish, where it has been studied extensively (reviewed by Shaw, 1967), (c) birds and (d) mammals, where it has received moderate attention. I then attempted some simulated predation experiments to clarify certain aspects of the problem which were left unclear by the literature review.

Before reporting on my review, it is necessary to consider some of the concepts involved. At first glance the question seems straightforward, but Lent (pers. comm.) has pointed out that the phrase 'predation rates' may be taken in at least three different ways — (1) changes in numbers of prey per unit of time removed from an entire population, (2) changes in vulnerability to predation of individuals in clumps compared with individuals not in clumps and (3) changes in consumption rate per individual predator.

Bergerud (1971) proposed his generalization in connection with a discussion of natural selection; therefore when he stated that dispersed distributions are "more effective against predators" presumably he was referring to a decrease in the vulnerability of individuals. I agree that this is the ultimate question, but the relative vulnerability of prey in clumped or unclumped distributions is usually a matter of judgement on the part of the person conducting the study. Frequently the only good evidence is the number of prey taken from differently dispersed populations. Since one would expect decreased vulnerability of individuals to bring about a decrease in the number of animals taken from the population if all other factors remained constant, it seemed worthwhile looking at the changes in predation rates on populations as further evidence of the relative vulnerability of individuals. Negative evidence might only mean that this variable had little importance compared with such well-known factors in the predation equation as changes in density (Holling, 1961), and that the latter had changed enough to mask any effects of clumping. But positive evidence might tentatively be taken as support for the generalization. Changes in predation rates by individual predators, on the other hand, were considered only as they affected these other questions. Thus, the precise question for each study reviewed was either (1) does the author consider that individual prey in clumps are more or less vulnerable than individuals outside clumps, or (2) given populations of prey and predators of fixed densities in a stable environment, did clumping by prey tend to increase, decrease or leave unchanged the number of prey taken during a given time interval?

'Dispersed' and 'clumped' distributions I take to be statistical designations related to spatial relationships among the animals. Clark and Evans (1954) provided an example involving actual measurements. Using the distance to nearest neighbor as a measure of spatial relationships in a population, they calculated that the ratio between the expected mean distance and that obtained by measurement would be 0 for a clumped distribution, 1 for a random distribution and 2.1491 for an evenly-spaced distribution. Although such precise measurement is seldom accomplished, this is the sense in which I will use the term 'clump'; thus clumping behavior will refer to any behavior which produces such a distribution and will include both groups and aggregations.

Bergerud's (1971) meaning concerning cooperation among members of clumps is less clear. Presumably active defense would be one kind of cooperation. Animals running off together might be another kind. I shall take cooperation to mean any activity by some or all members of the clump which reduces the chances of individuals in that clump being taken by predators.

The most obvious way of testing Bergerud's (1971) generalization would be to look for instances in the literature where the authors believed the vulnerability of individual prey in

dispersed populations had been reduced and additional instances where dispersed populations had resulted in fewer prey being taken than in comparable clumped populations. However, such a search would be difficult because (1) dispersed populations are common and therefore seldomly remarked upon, and (2) suitable clumped populations are infrequently at hand for comparison. A corollary to Bergerud's (1971) generalization might be that clumping by prey leads to increased vulnerability and therefore clumped animals are preyed upon more heavily than dispersed animals if other conditions remain constant; all exceptions should be explainable as being the result of cooperation among members of a clump. Since many studies of clumped prey have been reported in the literature, this statement can be tested.

EXAMPLES OF INCREASED PREDATION DUE TO CLUMPING BY PREY

A number of studies have shown increased predation on clumped prey as would be expected from the corollary to Bergerud's (1971) generalization. They can be classified as instances of indiscriminate predation, individual predation and increased prey densities.

Indiscriminate Predation

Some predators capture prey in large numbers rather than individually. When this happens, clumping by prey seems a distinct disadvantage to the prey. Most of these instances occur among fish and marine mammals. Examples are anchovetes (*Cetengraulis mysticetus*) which passively filter small organisms from the water (Hobson, 1968:78) and mackerel (*Scomber scombrus*) which prey on plankton in a similar manner (Sette, 1950). Bullis (1961:195) described a whitetip shark (*Pterolamiops longimanus*) feeding on a dense ball of threadfins (*Polydactylus* sp.) about 6 feet in diameter, "biting off mouthfuls of fish, much in the manner of a person eating an apple." Other well-known examples occur among the whales which strain out small invertebrates (chiefly krill, *Euphasia* spp.) by taking vast numbers into their mouths along with water, then forcing the water out through horny plates which act as sieves (Storer, 1943:716).

Although the evidence is not conclusive it seems likely that clumping in each of these instances increases the vulnerability of individuals in the clumps and also results in more animals being taken from the population than if they were not clumped. But this kind of indiscriminate predation is relatively rare when considering the entire animal kingdom. It may be, as Bergerud (1971:51) argued in a parallel situation, that the prey have evolved ways of reducing the more usual kind of predation and these indiscriminate predators have merely exploited the resulting situations. To find out if this is the case, it is necessary to look at the more common particulate feeders. The rest of the paper will be concerned mainly with them.

Individual Predation

A number of studies have shown that clumping by prey made predation easier for individual predators. Banks (1957) reported that coccinellid larvae (Coccinellidae) searching for aphids (Aphididae) would wander, apparently aimlessly, over the leaves of plants until they touched an aphid; then they would immediately attack. After finding the first aphid, the search pattern would change and the larvae would move in small circles rather than wandering. The result was that aphids in clumps were found by the individual larvae time after time. Banks (1957:23) concluded: "Aphids which are widely scattered on leaves are not likely to be found so readily."

Hobson (1968:78) mentions the possibility that fish in schools might retard the efforts to escape of the first individuals to sense danger and thus increase their vulnerability. Kelsall (1968:253) reported a similar effect among caribou preyed upon by wolves (*Canis lupus*). "It has frequently been observed that the animals farthest away from an approaching predator will block the rapid escape of those in greatest proximity." Crisler (1956) reported wolves preying on calves in large herds of caribou (30,000) where the calves could not see the wolves approaching and were blocked from running by more distant animals that were not alarmed.

The evidence here seems to indicate that clumping by prey makes predation easier for individual predators once they have found the clumps. But it leaves unclear the effect of clumping on predation by the whole population of predators, and hence the actual vulnerability of individuals in clumps. Perhaps finding the clump is more difficult than finding dispersed individuals. In this case, the opposing tendencies could cancel out or could balance either way. One wonders, for example, how the clumping of aphids affected their chances of being found by coccinellid larvae. Banks (1957:23) reported that many coccinellid larvae starved if they failed to find aphids within 24 hours after emerging. Thus, although the clumping by aphids increased their vulnerability to individual larvae, it might have decreased their overall vulnerability to the larva population. Similarly, although caribou aggregations apparently made predation easier for the wolves through whose hunting grounds they happened to pass (Crisler, 1956), one wonders how this behavior affected predation by all the wolves on all the caribou in Alaska. Would predation have been greater or less if the caribou had been spread out? To find the effect of clumping on prey populations and thus obtain some suggestions concerning the vulnerability of individuals in clumps, it will be necessary to look at whole populations of prey and predators, not only at single individuals.

Increased Prey Densities

A number of studies have revealed increased predation on large aggregations of prey. Gibb (1958) found that tits (Paridae) preyed on concentrations of larval cone insects to such an extent that they changed the population of larvae from one of highly variable density to a remarkably uniform one. Holling (1961:179), referring to this study, commented that the predators increased the number of prey eaten per predator by responding to the higher densities of prey in concentrations rather than to average densities. Holling (1959a) also found in his own study that *Sorex* and *Peromyscus* preyed more heavily on sawfly larvae (*Neodiprion sertifer*) when the numbers of prey increased locally. Similarly Pearson (1966) found that mammalian predators responded to a local increase in the number of voles (*Microtus californicus*) by increasing consumption, immigrating to the area and increasing reproduction. Salt (1967:120), referring to the latter study, generalized, "In nearly all forms of mobile predators, unusually high concentrations of easily obtained prey will serve to attract predators even if the prey are in areas or habitats which the predator normally does not frequent."

Experimental support for these views was provided by Ivlev (1961) who fed denatured roe and tethered larvae of Chironomidae to carp (*Cyprinus carpio*) in tanks. He found that predation increased with greater clumping of the prey as long as the separate clumps of food corresponded with the area covered by a single feeding of the predator. But Ivlev (1961:29, 30) had to introduce an important exception for instances when the clumps were much smaller. In those cases, predation was appreciably less. This exception has important implications which will be explored more fully later.

From these studies, it appears that clumping behavior increases the vulnerability of

prey in instances when aggregations are large enough, relative to the size and behavior of the predators, to constitute local increases in prey density that can be exploited at a single feeding. These situations become similar to increases in the general density of prey and numerous studies have shown that more individuals are taken from dense populations of prey than from sparse ones (e.g., Chant, 1961; Pearson, 1966). But these studies leave unanswered the question, "What happens when the clumps are too small to constitute such a local increase in density?" Thus there is some support from the literature for the idea that clumping increases the vulnerability of the prey, as Bergerud's (1971) generalization implies, but only under the conditions specified above. It remains to be seen whether all instances of decreased predation can be explained by group cooperation.

EXAMPLES OF DECREASED PREDATION DUE TO CLUMPING

According to my suggested corollary from Bergerud's (1971) generalization, any decrease in predation resulting from clumping should be explainable on the basis of cooperation among members of the clumps. Some studies showing such decreases are now reviewed.

Active Defense

The most obvious example of cooperation by members of a clump is active defense made more effective by animals being together. Holling (1959a) reported that *Neodiprion* sawflies at the active feeding stage were seldom attacked by birds or mammals because of their defense mechanisms. These defense mechanisms were described and measured in more detail by Tostowaryk (1972) who reported that live sawfly larvae reduced predation by *Podisus modestus* at high prey densities by forming compact colonies and exuding resinous material that inhibited the predators. Control larvae immobilized by dipping in hot water did not show this effect. Similarly, Kruuk (1964) found that black-headed gulls had effective defenses against some of the predators which preyed on their eggs and chicks. For example, he documented a significant difference between predation by carrion crows (*Corvus corone*) on eggs inside the gull colony and eggs elsewhere. The musk ox (*Ovibos moschatus*) has long been known to form defensive circles when attacked by wolves (Tener, 1965). No examples of group defense by caribou have been reported. D. Miller described defense by individual caribou in this symposium and Bergerud (1971:52) implied that individual dams defend calves against lynx (*Lynx canadensis*). But these observations do not seem especially associated with clumping.

Mimicry

Another way in which animals may cooperate to reduce predation is by together imitating some larger animal. Breder (1959) suggested that some small fish species may deter predators by presenting their school as a single dark object which resembles a large organism. Similarly, Rowley (1965:85) describes the defense of the white-winged chough (*Corcorax melanorhampus*) against magpies (*Gymnorhina tibicen*) in Australia. The former "clump together, face the attacker with wings partly open to display the white flash and utter a loud 'hiss' . . . From the magpies' point of view the trespassing strangers of its own dimensions are suddenly transformed into a mass, ten times as big, piebald and hissing." Yet such instances of mimicry are relatively rare and this behavior has no known relation to caribou.

Improved Detection of Predators

Another way in which clumped prey cooperate to reduce predation is by detecting predators more efficiently. Hobson (1968) quoted the conclusions of Bowen (1931) and Eibl-Eibesfeldt (1962) that schooling among fish improves their ability to detect predators through the increased number of sensory receptors in the group. Schenkel (1966) maintained that the gregarious tendency of impala (*Aepyceros melampus*) with their vigilant behavior increased the probability of detecting predators. Among herbivores preyed upon by cheetahs (*Acinonyx jubatus*) Eaton (1970) found that individuals in large herds spent less time watching alertly for predators than did those in smaller herds. Presumably the larger numbers permitted adequate detection of predators with reduced contributions of time by each individual. This behavior might provide survival value by allowing the individuals more time to carry on other activities such as searching for and consuming food.

Similar improved detection of predators has been reported for aggregated caribou. Bergerud (1961) found that caribou cows with calves in aggregations exhibited greater flight distances than single cows with calves. Skoog (1968) stated that individual caribou in herds over 1,000 were less alert than those in smaller herds. Although decreased alertness has generally been considered disadvantageous to the caribou, it seems similar to the decreased alertness of African mammals in large herds and might have similar benefits. In view of D. Miller's (in press) suggestion that feeding patterns of caribou on taiga ranges during mid- and late winter are largely determined by the need to detect and escape wolves, such a reduction in alert-time might have important survival significance during this critical time of year.

Confusion Due to Swarming

Probably more important than any of the foregoing effects is the confusion created when several prey are clumped together. Any predator which is a particulate feeder must spend some time concentrating its attention on a single prey animal to the exclusion of all other individuals. In some species (e.g., Coccinellid larvae described by Banks, 1957), this may encompass little more than the time required to kill and devour the prey, but in many other species additional concentration upon an individual appears to be necessary for its capture. For example, large predatory fish like jacks (*Caranx bartholomaei*) will sometimes follow an individual prey fish through an entire school (Emery, pers. comm.). Similarly, Walther (1969) reported that cheetahs (*Acinonyx jubatus*) sometimes pass right through a herd of prey animals following one particular individual. Both agreed that when attention to an individual is necessary for capture, any distracting influence will tend to reduce success. This is true even if the distraction is the presence of additional prey animals. As Starck (1966:724) put it, "if the predator dives into the school without selecting one member of it in advance, the fish have a better chance to escape by darting in different directions."

Evidence that confusion actually reduces predation was first presented by Welty (1934) who introduced *Daphnia* in varying numbers into tanks containing four goldfish (*Carassius auratus*). He found that introducing more *Daphnia* at each feeding increased the numbers eaten to a certain critical point beyond which the numbers eaten decreased again. Welty (1934:113) explained the subsequent decrease by suggesting that "a dozen or so (*Daphnia*) in its immediate field of vision seemed to offer conflicting stimuli that blocked the feeding response." This idea is supported by modern psychology theory, e.g., by Berlyne (1960) (see also p. 481). Further evidence was supplied by Nikolsky (1963) who quoted Radakov's (1958) finding that single young coal fish (*Pollachius virens*) were eaten by cod (*Gadus morhua*) in approximately 26 seconds, but in schools the average time was 2 minutes, 15 seconds. Hobson (1968) reported difficulty in spearing fish when they were in

dense schools. He found it was necessary to identify and aim at an individual for any hope of success. Eaton (1970) showed that the hunting success of cheetahs was related to group size of the prey, being higher for groups of 30 or less. He concluded that flight of the prey as a tightly-knit herd reduced predation. Sweeney, Marchington and Sweeney (1971) found that radio-monitored white-tailed deer (*Odocoileus virginianus*) confused following dogs by joining other deer. Frequently the dogs lost the trail and continued on the track of a different deer. Walther (1969) reported that wild dogs (*Lycaon pictus*) attacking Thomson's gazelles (*Gazella thomsoni*) became diverted by other gazelles; each dog pursued first one animal and then another until the dogs became exhausted. Lent (1969) made similar observations of wild dogs and lechwe (*Kobus lechwe*). Confusion through swarming would, of course, be most effective against such predators which chase their prey rather than those which lie in ambush.

Hobson (1968) strengthened the case for a confusion effect by pointing out from his study of fish under natural conditions that this effect can be heightened by prey fish in a number of ways: (1) schooling with other fish of about the same size and appearance, (2) tightening up the school when the predator approaches so that more targets are placed in the predator's visual field, (3) radiating out in all directions as the predator rushes into the school, (4) increasing swimming speed while weaving in and out and (5) evolving colors such as flashing silvery bodies or dark and light alternating stripes which add to the difficulty in identifying an individual.

Examples of most of these characteristics have been provided by Hobson and others. (1) The effect of schooling with fish of the same size is to make individuals difficult to distinguish. It follows that any individuals which are different in any way should be more susceptible to predation. A number of studies have shown this increased predation on differing individuals. Starck (1966:730) found that fishes artificially marked for a study were quickly eaten by predators. Eaton (1970) found that cheetahs attacked the first member of a herd of prey animals to run. Possibly this was because its movement made identification of the individual possible. Eaton (1970:66) concluded, "The failure of an individual to respond in the same way as the others increased its chances of being singled out and killed."

Both Crisler (1956) and Kelsall (1960) reported that most of the caribou killed by wolves were crippled or sick. Mech (1970:228) reviewed accounts of wolves killing caribou and it was notable that nearly all victims were animals which had tripped or separated from the herd and so made themselves distinctive. D. Miller (this volume) reported that wolves caught caribou which fell behind or failed to synchronize their movements with other members of the band. Hence, the necessity for predators which are particulate feeders to identify individual prey animals and the resulting protection gained from similar appearance of the prey are widely recognized.

(2) Examples of groups tightening together at the approach of predators are also numerous. Starck and Davis (1966) found that grunts (*Pomadasyidae*) formed tight groups when approached by large predatory jacks. Verheijen (1953) found that herring (*Clupea harengus*) broke schools to feed but closed rank again when frightened. Tinbergen (1951) described the tightening of starling flocks (*Sturnus vulgaris*) when attacked by falcons (*Falco peregrinus*). Walther (1969) observed that fleeing herds of gazelles (*Gazella* spp.) drew closer together when chased by wild dogs (*Lycaon pictus*).

Caribou tightening their clumps at the approach of predators were described by Kelsall (1960:67) in his quotation from "Mr. Welk's field notes", which stated, "when the wolf was fifty yards or more away the herds joined in a tight mass of stampeding animals." Miller (in press) reported that a higher proportion of caribou travelled in bands when they were being harassed by wolves than when they were not threatened by predators.

(3) Radiating outward when attacked by predators is well known behavior among fish. For example, it was described by Breder (1959) but ascribed to a different cause. It has not been as widely reported for other animals. (4) Increased speed accompanied by weaving in and out is found not only in fish but also in impala whose "high jump in every direction" (Schenkel, 1966:104) seems to fill the same function as the weaving does in fish. (5) Confusing coloration has been exemplified by a number of species. Hobson (1968:79) himself described the "bewildering shower of brilliant flashes" produced by weaving silvery *Harengula thrissina* when predators approached. Starck (1966:724) pointed out that the dark and light striping of many tropical fish creates a "shifting maze of lines" which makes individuals difficult for predatory fish to distinguish. Perhaps it is significant that many African mammals are similarly striped.

Bright flashes may produce an additional anti-predator effect by presenting several targets to predators suddenly and simultaneously. This idea is supported by the work of Berlyne (1960) who suggested that increased reaction time was the best measure of the degree of psychological conflict. He generalized (p. 32) that such conflict would increase with (1) the nearness to equality in strength of the competing response tendencies, (2) the absolute strength of these tendencies and (3) the number of competing response tendencies. A school of fish suddenly flashing many silvery sides at a predator would probably satisfy all these conditions and hence might delay the predator's response significantly.

Among mammals, white tails may produce similar effects. Smythe (1970) has argued that white tails are not warning signals but invitations to attack. Humphries and Driver (1967) considered that the main function of erratic displays was to arouse mutually incompatible tendencies in the reactor and hence delay its response. It seems likely that a number of white tails flashed at the same time would have a similar effect. This might explain Estes' (1967:208) observation that stotting by Grant's and Thompson's gazelles becomes more striking and more effective against predators when the white rump patch is flashed also.

Caribou are not striped like some fishes and African mammals and are not known to exhibit 'stotting behavior' but they are very similar to each other in appearance and when milling in large herds may easily produce confusion effects. Evidence can be found from some forms of behavior which are common to animals known to exhibit such effects. Caribou tightening together at the approach of predators may constitute such evidence, though it may also be merely a matter of trying to obtain a central position where predation would be less likely (Williams, 1966). Perhaps of more import is the reported synchronization of movements when they are chased which suggests that any animal differing becomes easy prey.

Summary and Discussion of Decreased Predation Due to Clumping

Decreased predation on clumped prey may result from active defense, mimicry, improved detection of predators and confusion due to swarming. The first three causes fall clearly within Bergerud's (1971) category of cooperation between members, but the case for swarming is not so clear. Sudden tightening of groups in the face of danger and synchronized movements of group members might be viewed as cooperation. But to call the presence of more than one stimulus in the predator's visual field 'cooperation' would be to designate the mere act of coming together into clumps a kind of cooperation among the members, and this would make Bergerud's generalization self-contradictory. More likely this is an accidental effect due to animals coming together for other reasons (see Williams, 1966). Even if clumping itself could be considered cooperation among members, it would only be one more instance where cooperation had reduced predation. In fact cooperation

reducing predation appears to be the rule rather than the exception. Perhaps a better generalization would result from reversing the statement and generalizing that a clumped distribution reduces predation except in those cases where group cooperation is ineffective. It is impossible to be certain which way this should be stated because associated behavioral effects are so universally present that they effectively mask the contribution, one way or the other, of clumping itself.

Furthermore, another factor affecting predation has not yet been fully considered. It has become evident that predators are not merely inert entries in an equation. They too behave in ways which increase or decrease predation. The following section examines their reactions in more detail.

REACTIONS OF PREDATORS

In several of the examples examined thus far, we have run into the problem that the behavior of predators affected the result of clumping by prey. A fuller understanding of the importance of predator reactions seems warranted. Solomon (1949) classified the reactions of predators as (1) functional responses — in which the consumption of prey per predator changes, and (2) numerical responses — in which the local number of predators changes. Since this view has become widely accepted (e.g., by Salt, 1967), I have used the same classification but added additional categories for (3) behavioral responses of predators to changes in behavior of prey and (4) other behavior of predators.

Functional Response

Tinbergen (1960) found that great tits (*Parus major*) developed 'searching images' for species of insects which were abundant. The birds concentrated their predation on these species to the neglect of others. This kind of specialization on abundant prey seems to be the primary mechanism producing functional response. Ware (1971), for example, found that rainbow trout (*Salmo gairdneri*) soon developed search images for new food and he believed that this explained why the trout fed predominantly on one or two main food organisms. Functional responses are very common. For example Buckner and Turnock (1965) found that 22 out of the 28 species of birds present in the area increased their intake of the larch sawfly (*Pristiphora erichsonii*) during a period of local sawfly abundance; furthermore functional responses were involved in all the examples reviewed earlier where predation increased on clumps of prey that constituted local increases in prey density.

Numerical Response

Most numerical responses involve immigration from surrounding areas to places where food is exceptionally abundant. For example, Koplin (1972) found that woodpeckers could control small outbreaks of spruce beetles by concentrating both their numbers and their attention on these local sites of prey abundance. This association of numerical and functional response is typical. Another example is provided by the study by Buckner and Turnock (1965) who found that birds not only ate more larch sawflies per individual during local outbreaks in Manitoba, but they also immigrated to the tamarack (*Larix laricina*) bogs where the outbreaks occurred. Again this response by predators was involved in all the examples of increased predation on locally high prey densities described earlier, with the possible exception of the carp studies by Ivlev (1961) where the experimental conditions may have been too artificial (e.g., one carp per tank).

In some cases, numerical responses involve not only immigration to an area but

increased breeding also. Holling (1959a) found increased breeding among *Sorex* and *Peromyscus* preying on the European pine sawfly (*Neodiprion sertifer*) and this accounted for some of the increased predation described earlier. Increased breeding, of course, would produce a change in the population density of predators, not merely in their spatial distribution, and therefore could not be considered clumping.

Behavioral Responses of Predators to Prey Behavior

In some cases, behavior by predators modifies or counteracts the effect of behavior by prey. A most striking example involves predation on kongoni (*Alcelaphus buselaphus cokii*) by cheetahs in Africa described by Eaton (1970). He found that kongoni males often snorted when a cheetah was sighted, alerting all others and leading to 'mobbing' attacks on the cheetah especially by young kongoni males. As a result cheetahs were generally more successful when the kongoni were unaware of their presence. But one group of cheetahs learned to capitalize on the kongoni behavior and became more successful when kongoni were aware of them. The two males "simply loped toward kongoni and when, at about 60 yards a kongoni attacked and came about 25 yards closer, the two cheetahs attacked and killed it." (Eaton, 1970:62).

Many predators initiate behavior to overcome the confusion resulting from swarming prey. Hobson (1965) and Starck and Davis (1966) reported that large predatory fish concentrated their attacks on smaller fish at dusk when daytime schools of the latter were breaking up and individuals were particularly vulnerable during the disorganization. Starck and Davis (1966) also described jacks driving into schools of grunts apparently to scatter the fish and expose individuals to attack. Starck (1966:724) stated, "To circumvent this defense, large jacks first flash into the schools of grunts and scatter them so they can be chased individually." Similarly, Tinbergen (1951) described falcons carrying out sham attacks on flocks of starlings until a few would lose contact with the rest of the flock at which time the real attack would be made on a separated individual. Again, Walther (1969) mentioned that predators sometimes forced herds of Tommies to split and this would probably have a similar effect.

Even the protection of flashing colors may be turned from an advantage for the prey into an advantage for the predator by the behavior of the latter. Hobson (1963:596) reported that gafftopsail pompanos (*Trachinotus rhodopus*) apparently used the flashes of juvenile anchovetas (*Getengraulis mysticetus*) as targets, taking a disproportionately high number of them from among mixed schools of the anchovetas and herring (*Harengula thrissina*).

Additional Behavioral Characteristics of Predators

Predator behavior also affects predation rates quite independently of any clumping behavior by prey. These effects could produce false interpretations of the effects of clumping. For example, Welty (1934) found that goldfish in groups ate more *Daphnia* than they did singly. Sette (1950) believed that *Scombus scombrus* by swimming in a school acted like a group of miniature tow nets catching many plankton that darted aside to avoid other synchronized predators. He also thought that bluefish (*Pomatomum saltatrix*) cooperated in catching menhaden (*Brevoortia tyrannus*); the latter would elude one predator only to put themselves in the path of another. Similarly, Bullis and Juhl (1967) suggested that little tuna (*Euthynnus alletteratus*) fed in close formation maintaining bodily contact to prevent prey darting aside. Fink (1959) reported groups of porpoises (*Phocaena vomerina*) spaced about 30 cm apart in concentric formations feeding effectively on schools

of Pacific sardines (*Sardinops caerulea*). Similar cooperation among terrestrial predators is well known. Eaton (1970) found that single cheetahs required more hunts to make a kill than did cheetahs in groups. Estes and Goddard (1967) described the cooperation between members of African wild dog packs (*Lycaon pictus*) when hunting. Mech (1970), Kolenosky (1972) and others have described similar cooperation among wolves.

But not all predator behavior results in increased predation. Holling (1961) listed interference among predators as one of the factors likely to reduce predation. Although later computer simulation (Griffiths and Holling, 1969) suggested that this would only become important at densities higher than those occurring in nature, it still remains a possibility. One case of interference has been described among parasites. De Back and Smith (1947) showed that parasitism by *Normoniella vitripennis* on housefly puparia (*Musca domestica*) did not continue to increase at high host densities and this appeared to be at least partly due to competition among parasites. Also, competition at higher densities of 'predators' appears to be a factor limiting the numbers of moose taken from certain accessible areas of Ontario by human hunters (Cumming, in press). Therefore, it does not seem certain that this factor can be ruled out.

It is sometimes overlooked that search images can result in decreased, as well as increased, predation. Tinbergen (1960) found less predation than he expected at high prey densities and speculated that this was due to preference for variety and turning to other prey. Looking at it another way, search images must have decreased predation on alternate prey in each of the instances where they increased predation on an abundant species. As Salt (1967) observed, a functional response actually represents a shift in preference from one food species to another.

Spacing behavior may limit the ability of predators to exploit local prey densities. Koplin (1972) for example, speculated that the upper limit of numerical response by territorial woodpeckers (Picidae) to local outbreaks of spruce beetles (*Dendroctonus ponderosae*) was set by the amount of crowding the birds would tolerate during the breeding season. Similarly, Sargeant (1972) thought that predation on waterfowl was reduced when they were concentrated on good nesting areas because each of these areas was subject to the attacks of only one family of territorial red foxes (*Vulpes fulva*). Errington (1967:224) thought that, although mink (*Mustela vison*) were not strictly territorial, social intolerance still prevented them from concentrating on marshes where muskrats (*Ondatra zibethica*) were abundant. Wynne-Edwards (1962) has argued that territorial behavior is only one of many social mechanisms which tend to limit the exploitation of food sources by animals and so prevent their over-utilization. None of these mechanisms among predators can be ignored when assessing the effects of clumping by prey.

These variations in predation resulting from the behavior of predators suggest that it may be impossible to specify the effects of prey behavior without also considering the responses of predators. Perhaps it depends on predator reactions whether a dispersed distribution of prey is more effective in reducing predation than a clumped distribution. Certainly the reactions of predators obscure the effects of clumping by prey and leave conclusions as to the validity of the generalization still in doubt.

SIMULATED PREDATION EXPERIMENTS

The main problems in attempting to interpret these results have been (1) the mechanical effects of clumping are almost inevitably confounded with additional anti-predator behavior by the prey, and (2) the results are affected by the reactions of the predators. Another problem involves the idea that clumping behavior may not be related functionally to predation at all. There are many reasons for animals to come together, e.g.,

mutually improved feeding, increased efficiency in finding mates, and finding the way during migration (Davis, 1970). Williams (1966) has suggested that clumping may originate as a response to local food abundance and may affect predation only accidentally. For these reasons, no amount of literature review seemed likely to be able to clarify the basic effect on predation of prey animals coming together in clumps. Only a simulated predation experiment would provide an opportunity to isolate clumping as an individual factor in the predation equation and find its effects.

The simplest predator-prey situation involving clumping would be one predator attacking a fixed number of prey arranged in different distributions. To simulate this situation I attempted to adapt Holling's (1959b) experimental method to my purposes by asking a blindfolded person to act as a 'predator' and search for 64 sandpaper discs 4 cm in diameter thumbtacked to a board one meter square. In each trial 'the predator' removed as many discs as possible in one minute, placing each on a nearby table. A random distribution of 64 'prey' was first located on the board using a 5 cm grid with 20 X 20 units and a table of random numbers. The distribution was changed while keeping the overall density constant by locating 16 random clusters of 4 with 10 cm spacing within clusters. In a further change the spacing was reduced to 5 cm. Each experiment was replicated eight times but sometimes with the involvement of a second 'predator'.

The results show that clumping increased the rate of predation (Table 1). This appeared to be because the 'predators' discovered that the prey were clustered and therefore concentrated their searching in areas where they had already found one or more 'prey'. Tighter clumping initially reduced predation but one 'predator' learned to capitalize on the clumps and so increased predation again. Learning was evident in each case, and there were distinct differences between 'predators'. It was apparent from these results that the experiment was not answering my question because (1) behavior of the predators had not been eliminated, and (2) only lone predators had been simulated. I had merely demonstrated the response of individual predators to clumped prey which I had found in the literature review.

Beginning again, I attempted to simulate the 'basic components' of predation (Holling, 1961:163) which in this case were (1) a population of predators, (2) a population of prey, and (3) a distribution of each. Following a suggestion by Boulton (pers. comm.) I tried adapting a method proposed by Pielou (1959) for studying pattern in plant communities. On a 20 mm grid, marked on graph paper and numbered from 1 to 20, I established with overlays the location of 64 random 'prey'. Four sets of 32 random 'predators' were then picked and the distance from each 'predator' to the nearest 'prey' measured. I repeated the procedure with the 64 'prey' clumped in groups of 2, 4, 8 and 16, then finished with one experiment in which there were only 32 random prey.

The results indicated that (1) the average distance from each predator to the nearest prey increased as clump size increased (Table 2); and (2) when the number of prey was reduced from 64 to 32, the distance from each predator to the nearest prey increased from (a mean of) 804 to 1,298mm. These findings have important implications for understanding clumping and predation.

The experiment illuminates a number of points: (1) Nicholson and Bailey (1935) drew attention to the fact that the problem of finding things is of outstanding importance to animals whether the 'things' be mates, suitable places to live, or food. It is possible that the widely reported phenomenon of decreased predation accompanying lower prey densities (e.g., by Holling, 1959a; Chant, 1961) occurs because predators have more difficulty finding, or take longer contacting, prey at the greater average distances which occur when densities of prey are lower.

(2) Randomly distributed predators will be situated at greater average distances from

clumped prey than they would be from randomly distributed prey. This situation could be expected to increase their difficulty in finding or contacting prey. This increased distance between predator and prey due to clumping by the latter will be called 'the increased distance effect'. If the predators were not random but themselves formed clumps, the average distance to prey might increase even more, unless the clumps of predators more or less coincided with the clumps of prey. Then the predators might encounter prey at much closer distances than if both were random. On the other hand, evenly spaced predators, such as territorial animals, would always find clumped prey to be at greater distances than would randomly distributed predators.

TABLE 1.--Simulated predation by blindfolded 'predators' tapping for 64 sandpaper discs 4 cm in diameter thumbtacked to a 1 m² board. Each 'prey' was removed when located. Time per trial 1 min.

Experimental series, 'Predator' and replication	Distributions of 'prey'		
	Random	Clumps of 4 10 cm spacing	Clumps of 4 5 cm spacing
Series 1			
'Predator' A 1	12	13	11
2	9	13	8
3	13	13	11
4	11	16	15
Total	45	55	45
'Predator' B 1	15	16	9
2	14	20	8
3	13	13	13
4	16	18	9
Total	55	67	39
Grand Total	100	122	84
Series 2			
'Predator' A 1	12	17	16
2	12	12	15
3	13	14	14
4	14	15	15
5	15	16	18
6	13	15	14
7	14	12	11
8	17	13	17
Total	110	114	120

Note: 1) Clumping increased the numbers of prey taken.

2) Each predator improved efficiency throughout each series, apparently as a result of learning.

3) Predator B was consistently more efficient than predator A until tighter clumping was tried.

4) Tighter clumping of prey initially reduced predation probably by reducing effective density (see text) but learning by the 'predators' turned this initial advantage for the prey to disadvantage.

TABLE 2.--Results of simulated predation experiment showing accumulated distances (mm) from each 'predator' to the nearest 'prey'. 'Predators' were represented by dots on overlay grids in 4 populations of 32 and 'prey' by 64 dots clumped to various degrees and the clumps located randomly on similar grids (standard errors are shown in brackets).

Predator population	Number of 'prey' per clump*				
	1	2	4	8	16
1	777 (120.42)	1117 (590.54)	1665 (59.64)	2138 (2533.83)	2909 (4299.94)
2	849	991	1651	2031	2435
3	775	970	1310	2328	3145
4	816	1221	1583	2696	2889
Total	3217	4299	6209	9193	11378

Note: 1) The total distance and therefore necessarily the mean distance between 'predators' and nearest 'prey' increased as clump size increased.

2) Standard errors included for the first 'predator' show that variability in distance also increased with clump size.

*Clumping was tight in all cases but actual distances between members of a clump varied according to the most convenient way of locating them on the grid.

(3) The increased distance effect can also occur within time rather than space. A predator with a relatively constant rate of predation (e.g., *Amblyseus largoensis*, Sandness and McMurty, 1972) would be equivalent to an evenly arranged distribution of predators in space. If the prey for such a predator were to become abundant very suddenly, rather than randomly or systematically, their 'distance' in time from a given sample of the predator's feeding occasions would be greatly increased. This result will be called 'the time-distance effect'. Prey may become available suddenly by (1) living in aggregations so that many prey are found by a predator at one time, (2) moving in groups to encounter any predator together or (3) all being born at one time. The effect would be maximized by clumping at times when predators for one reason or another could not clump. The very widespread occurrence of synchronized spring breeding may exemplify the last two points, though abundance of summer food and maturing to self-sufficiency before winter probably constitute other important advantages of such synchronized breeding. In this connection it is interesting that Estes (1967:199) working in a tropical climate found only a minor concentration of Gazelle births (*Gazella granti* and *G. Thomsonii*) during January and February. Lent (1969:156) thought synchronized breeding by Okavango lechwe (*Kobus leche leche*) was correlated with the rainy season when food was abundant and that this advantage outweighed the disadvantage of possible increased predation. My experiment suggests that vulnerability to predation might have been decreased also by the synchronized breeding.

(4) There remains the question of what happens when clumps of prey are of differing sizes. As long as predators remain randomly distributed or evenly spaced, the number of predators likely to attack prey at any one place will be about the same. Thus, when prey are clumped, the predators will take proportionately fewer prey from large clumps than from small ones and the vulnerability of individual prey will be reduced more as clump size increases. This occurrence will be called 'the differential size effect'.

The mechanism by which clumping increases distance between predator and prey became apparent when I was choosing the points for the various 'prey' distributions. I had first to choose 64 points, then 32, 16, 8 and 4. Obviously, the clumping was reducing the effective density of prey. If any clump were to occupy no more space and be no more detectable than an individual, the effective density of prey, No^1 , would vary as the actual density No , divided by the group size, g .

$$\text{i.e., } No^1 = \frac{No}{g} \quad (1)$$

In practice this condition would never be reached because a clump of prey would always occupy more space and be more detectable than an individual. But, apart from effects such as increased scent emanating from a herd, actual clumping would come closer to this relationship as the average distance between animals in a clump, d , approached zero.

These findings can be incorporated into Holling's (9th) equation (Holling, 1961:171), derived from Nicholson and Bailey (1935) which states $NA = No (1 - e^{-aP})$ where NA is the total number of prey attacked, No the original density of prey, a the area of discovery (a constant), and P the density of predators.

The clumping factor can be introduced by using the effective density from equation (1).

$$NA = \frac{No}{g} (1 - e^{-aP}) \text{ as } d \rightarrow 0$$

It would be desirable to include some measure of clumping rather than merely the number of prey per group to describe how closely $d \rightarrow 0$, but Payandeh (1970) tested seven suggested measures of non-randomness and though he concluded that one was superior, there is currently no consensus on this point.

Thus, assuming that increased distance makes predation more difficult, clumping behavior probably tends to reduce the predation rates of randomly or evenly distributed predators without any assistance from other forms of behavior. It should also tend to reduce predation by clumped predators unless their clumps are associated with those of the prey. In other words, clumping by prey tends to reduce predation unless predators clump in response. Similar conclusions were reached by Brock and Riffenburgh (1960) after modeling the behavior of schooling fish.

It would be encouraging to be able to support these findings from actual studies but, as the review has shown, additional complicating factors are nearly always involved. The only instance that I could find where the effects of clumping appeared to be isolated satisfactorily from other factors was described as parts of the previously mentioned studies of blackheaded gulls by Kruuk (1964) and Patterson (1965). Kruuk (1964) found that although the defensive actions of the gulls were very effective in reducing predation by aerial predators, they were completely ineffective in reducing predation by foxes (*Vulpes vulpes*). He concluded that the gulls could provide little or no protection for their broods against these predators. Patterson (1965) studied the gulls' nesting losses and found that over half those for which causes of mortality could be determined were due to predation by the foxes. Yet despite the fact that these foxes were undeterred by the actions of the gulls, Patterson (1965) found that predation was proportionately less on the eggs and chicks of a sample of nests in the major colony than on those of a sample of nests scattered around it. Furthermore eggs and chicks which were part of the main hatch suffered lower predation losses than those which were earlier or later. Apparently the clumping of nests both in space

and time reduced the vulnerability of eggs and chicks to their major predators without any assistance from other behavior. This is particularly striking in view of the much greater densities inside the colony which would lead one to expect more predation there. Kruuk (1964) recognized the time-distance effect of synchronized breeding but he did not discuss the increased distance effect resulting from colonial nesting. Patterson (1965) considered both effects, referring to Cullen (1960) who had suggested that clumping in birds might reduce the chances of predators finding the clumps since the areas occupied would be reduced.

It is noteworthy that despite this reduced predation on nests in the colonies, losses were still so great that the population of gulls was decreasing. Presumably all the efforts of the gulls to avoid predation, including clumping, were not enough. Thus, the mere fact of heavy predation does not necessarily indicate that the behavior of prey is tending to increase it. Another interesting point is that although the numbers of nests inside the colony and outside were not known, it appeared likely that the total numbers of eggs and chicks taken from the colony greatly exceeded those taken from outside it even though the proportion taken from the colony was less simply because so many more birds nested in the colony. In this case densities were not constant and hence proportions were the best indicators of the effects of clumping on vulnerability.

Examples of additional principles derived from my simulated predation experiment can also be found in the literature. For example, Kolenosky (1972) found that a pack of wolves preyed disproportionately heavily on small pockets of wintering white-tailed deer (*Odocoileus virginianus*) compared with the main wintering concentration apparently as a result of a differential size effect. Other examples were included in the literature review.

DISCUSSION

The evidence indicates that a clumped distribution of prey tends to increase the average distance between predator and prey, and presumably in many cases this would make predation more difficult. The effect seems similar to that of decreasing the density of prey. However, the actual predation rate on the population varies with other factors in the predation equation and with the reactions of predators. If predators continue to live in dispersed populations, clumping by prey can be expected to reduce the vulnerability of individuals in the clumps and, other things remaining constant, result in actual decreases in the numbers of prey taken from the population.

Why then would any population of predators remain dispersed? Probably there are other benefits from spacing behavior of overwhelming importance. Perhaps, as Wynne-Edwards (1962) has suggested, one benefit is to limit population numbers below a level where the animals would over-utilize their food supplies and suffer catastrophies. Or as Williams (1966) has suggested, it may be because breeding success is greater at lower densities and the animals by dispersing are able to raise greater numbers of young. The benefits of spacing behavior are not clear (Watson, 1970:218) but they must be great judging from the wide spread occurrence of the phenomenon.

When predators do react to clumped prey, it may be by treating clumps as individuals, in the case of indiscriminate predation, or by some other change in behavior such as that of the cheetahs capturing kongoni. But frequently the reaction is one of concentrating in an area and increasing individual intake through specialization on clumps of prey that have become so large as to constitute local increases in prey density. Under these conditions, the originally advantageous actions of the prey in clumping are turned against themselves and the individual prey in clumps may actually become more vulnerable than they would have been if dispersed. In many cases, the numbers of prey taken from the population are greater

as a result. Such a reversal is not unique, for Chance and Russell (1959:67) thought that any systematic display would be exposed to counter-measures by the predator. Clumping could almost be considered such a systematic display.

If these views are correct, Bergerud's (1971) generalization suffers from three defects: (1) it does not state the effect of clumping alone correctly, (2) it fails to establish the importance of predator reactions in determining the effects of clumping and (3) its exception concerning cooperation among the members of clumps cannot be supported fully unless the term 'cooperation' is interpreted so broadly as to make the whole generalization self-contradictory. A more satisfactory generalization might be that clumping by prey tends to reduce predation unless predators take counter-measures (a) by changing their catching behavior or (b) by clumping in response. The former includes the special case of predators which catch several prey at once as well as specialization via search images and other behavioral changes. The latter reaction most frequently occurs when clumps of prey are large enough to become local increases in density. One would expect from these considerations that clump size in many species would be a compromise which increases the distance between predator and prey but stops short of attracting more predation. As Williams (1966) points out, this would not necessarily require an assumption of a group function, but would be the point at which vulnerability of individuals was minimized.

APPLICATION TO CARIBOU

One objection to my review of literature concerning the question of clumping might be that observations on invertebrates, fishes and birds have no relevance for intelligent animals like wolves preying on caribou. Haber (pers. comm.), for example, believes that wolves do not need to search for large prey but know the location of each herd within the pack's hunting ground. In such a case, clumping would probably have few benefits and might even make predation easier. Any advantage to the caribou would come from associated effects such as better observation of predators and confusion from swarming, rather than from the clumping itself. However, in this case, the wolf pack acts as a single predator. Even if predation were facilitated by the clumping this would only be one more instance when clumping made predation easier for a single predator. The situation would not provide any evidence of how the dispersion of prey relative to that of their predators affected the vulnerability of the former. In that respect wolves would have little advantage over less intelligent predators.

Actually, the idea that clumping behavior tends to reduce predation runs counter to much that has been written about caribou. Both Crisler (1956) and Kelsall (1968) thought that clumping increased predation on caribou. But again they were really concerned with the attacks of single wolf packs rather than with predation by the entire wolf population. Kelsall (1968:253) stated, "Most caribou are probably taken by wolves from bands sufficiently large that they hinder each other in running." This could be true without its increasing the overall vulnerability of caribou in clumps. In view of my simulated predation experiment and the literature review, the critical question would appear to be: "To what extent do wolves maintain their customary separate hunting grounds despite clumping by caribou and to what extent do they clump in response?" Currently available literature does not make this clear. Several authors (e.g., Kelsall, 1968) have reported wolves following caribou herds on the barren grounds, but little tagging has been done (Kuyt, 1962); thus it has never been possible to be certain whether the wolves continually observed in the vicinity of the caribou were the same ones. There may be at least some instances when they are not, for Crisler (1956) observed wolves remaining resident in an area and preying upon caribou herds which passed by and, similarly, Skoog (1968) reported that wolves in Alaska tended

to be relatively static and did not necessarily follow the movements of the caribou. In these cases, one would expect a time-distance effect to operate since too many caribou would descend upon a family of wolves at one time for the wolves to make a great reduction in their numbers. This may have occurred, for example, in the case of the caribou described by Crisler (1956:342) where local wolves managed to take only four caribou from a herd of 30,000. Similarly, Kelsall (1960:67) reported only one caribou killed from three herds numbering 80, 28 and 28. One would expect also a differential size effect in that the proportion taken from larger herds would be less than that from smaller ones, since presumably the wolves' rate of killing would remain within certain limits regardless of the herd size.

As this paper was going to press, a new study came to notice which provides additional evidence concerning this problem. Parker (1973) counted wolves and caribou from the air during winter in northwestern Manitoba and northeastern Saskatchewan. He found that nearly all wolves were located in the same general area as a large caribou concentration. However, as winter progressed, the area occupied by caribou decreased by about one fifth, though the numbers of caribou remained the same. The area occupied by wolves did not decrease correspondingly and an increasing proportion of the wolves were left outside the area of high caribou concentration. The total number of wolves in the area also decreased from an estimated 258 in January to 60 in April. Parker (1973) speculated that this decrease may have been due to the onset of breeding and a search for denning sites. Parker's (1973) study appears to illustrate several of the concepts studied in this paper. The location of so many wolves in the same general area as caribou suggests a numerical response by wolves to a locally high density of prey. The decreasing size of the caribou concentration, leaving more and more wolves outside, appears to be a case of increasing effectiveness against predators as clump size decreases, as predicted from my simulated predation experiment. The decreasing number of wolves seemed to be a case of predator behavior reducing predation; in this case presumably because the wolves' spacing behavior became more demanding with the approach of the breeding season. One would expect the shrinking caribou concentration area and increased spacing behavior by wolves to significantly reduce the vulnerability of caribou and perhaps also the actual number taken during the critical late winter period.

The differential size effect was demonstrated in one instance of 'predation' on caribou by humans. Simkin (1965:43) reported that native hunters in northern Ontario killed caribou at rates which increased only slightly for larger caribou herds. The result was a lower proportion of caribou taken from large herds than from small ones. This relatively stable predation rate would exert a selective pressure against individuals in small herds, since presumably herds below a certain size would be completely decimated. The effect on the total number of caribou taken could not be specified without considering the behavior of the 'predators'. Presumably, any advantage to the caribou would be lessened as the ease of predation increased (for example, through the use of rapid-fire rifles). If the hunters were to 'clump in response' as they do in northern Manitoba and Saskatchewan (D. Miller, pers. comm.) the behavior of the caribou would be turned from an advantage to a disadvantage. But in northern Ontario small parties traveling (at that time) by dog team would have no opportunity to report caribou herds to other hunters and thus clumping by the hunters in response to the presence of caribou would be a rare occurrence. In most other instances improved communication and transportation would facilitate a numerical response and this may explain the difference between Simkin's (1965) findings and the generally held opinion that clumping behavior by caribou makes them more vulnerable to human hunters.

Finally, my experiments and literature review illuminate a paradox which seems to be presented by two of Bergerud's papers. When studying predation by wolves on post partum

aggregations of caribou cows with calves Bergerud (1961) thought that the aggregations decreased predation and he suggested (in press) that those aggregations constituted a defense against wolves. Yet when he turned to a study of predation by lynx (1971) he found that the aggregations of cows and calves brought about greatly increased predation. He presented no evidence of cooperation against the wolves such as would be expected from the generalization arising from his later study.

The paradox is resolved if we accept as fact that clumping tends to reduce predation, but that this reduction may be offset by similar clumping behavior on the part of the predators. Wolves are known to have spacing mechanisms (Mech, 1970; Pimlott, Shannon and Kolenosky, 1969); this explains why the clumping of caribou both in time (synchronized calving) and space (aggregations) was highly effective in reducing predation by wolves. But as Bergerud (1971:49) pointed out, no such spacing mechanisms are known for lynx. Therefore, they were able to congregate around the calving grounds (numerical response) and by concentrating their predation on calves (functional response) turn what would otherwise have been an advantage for the caribou into a disadvantage.

Bergerud (1971) observed that wolves are the traditional enemies of caribou. This fact may partly account for caribou being normally found in much larger aggregations than those of woodland cervids such as white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*). In these latter species, animals can escape to protective cover and thus do not need to gather into large aggregations. This suggestion parallels Hobson's (1968) observation that fish feeding on plankton in midwater dive under cover for protection from predators rather than forming large schools for protection as pelagic species do.

Probably the individual caribou on an open plain running to the herd at the approach of danger is analogous to the individual white-tailed deer in an open field running to a woodlot at the approach of danger. For the caribou the herd, for the deer the wood, represents escape cover. In either case the individual which seeks escape cover will be less vulnerable to predation than one which does not. The clump is certainly functional for the individual in this respect. Whether one sees an additional function in terms of the group with Wynne-Edward's (1962), or denies any such group functions with Williams (1966) seems to depend on one's ideas of how evolution operates since critical evidence is lacking (Watson and Moss, 1970:200). Undoubtedly Williams (1966) is right in declaring that many functions ascribed to groups have been without adequate support. On the other hand, I found his efforts to explain away all group functions unconvincing. Especially difficult to explain in other terms are some examples of group defense, mimicry and improved detection of predators. Some ways of increasing confusion effects might also be included. Yet, whether clumping can be viewed as a group function or merely an accidental occurrence which happens to benefit the individuals, the conclusion remains the same; its primary tendency is to decrease the vulnerability of members of the group.

SUMMARY

I tried to find from the literature whether Bergerud (1971) was right in generalizing that a dispersed population of prey is more effective against predators than a clumped population unless cooperation among members of clumps is sufficiently effective to overcome the disadvantages of concentration.

A number of studies have shown increased predation resulting from clumping as would be expected from this generalization. These include (1) instances when the predators caught several prey at once rather than one at a time, (2) instances when the predation rate being investigated was the number of prey per individual predator and (3) instances when the clump of prey was so large as to constitute a local increase in prey density.

Examples of decreased predation were due to (1) active defense, (2) mimicry, (3) improved detection of predators and (4) confusion due to swarming. Though the first three categories might be construed as 'cooperation' the last cannot be without making Bergerud's (1971) generalization self-contradictory.

The effect of clumping was further obscured by the reactions of predators which may (1) consume more prey per predator from clumps, (2) increase their numbers locally by immigration to areas of locally high densities of prey, (3) adopt behavioral counter-measures to clumping by prey and (4) vary their behavior in ways unrelated to clumping by prey but still affecting the amount of predation on the population of prey.

Simulated predation experiments revealed that clumping by prey tends to increase the average distance between predator and prey in both space and time. This effect is similar to decreasing the density of prey. Through extension of this idea it appeared likely that vulnerability of individual prey would decrease with greater clump size as long as clumps remained small, relative to the size and feeding habits of predators.

I concluded that Bergerud's generalization cannot be fully supported and suggested that clumping by prey tends to reduce predation unless predators take counter-measures such as changing their method of catching or clumping in response.

This conclusion runs counter to much that has been written about caribou where clumping has generally been seen to be a factor increasing predation. The extent to which this occurs is not clear because too few studies have concerned whole populations of prey and predator and because not enough attention has been paid to the reactions of predators.

The suggested generalization helps enlighten a new observation of caribou and wolves, and two apparent paradoxes: (1) tightening of caribou aggregations in late winter combined with the onset of wolves' spacing behavior related to breeding should reduce predation during that critical period, (2) some humans took smaller proportions of caribou from larger herds while others found hunting for caribou in herds easier because the former could not clump in response while the latter did and (3) spring aggregations of caribou cows with calves appeared to discourage predation by wolves which have strong spacing mechanisms but facilitated predation by lynx which could clump to take advantage of the aggregated prey.

The clump appears to serve as escape habitat and thereby reduces the vulnerability of the individuals in clumps.

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Q FEVER AND ALASKAN CARIBOU

Cluff E. Hopla
Department of Zoology
The University of Oklahoma
Norman, Oklahoma 73069

ABSTRACT—The caribou located on the north slope of the Alaskan Range commonly referred to as the Delta herd were used in this study. A total of 355 animals were sampled between 1967-1970. Twenty cc. of blood were removed from the jugular vein, and visceral tissues were removed for microbiological assay from those animals that succumbed to the tranquilizing agent. Q fever antibody titers ranged from 1:32 to 1:512. Thirty-seven animals had significant antibody titers, and Q fever organisms were isolated from one animal.

Theories as to the origin of Q fever in Alaska are: (1) imported domestic cattle, (2) imported American bison, (3) caribou bringing the organisms from the Palearctic at the time they crossed over to North America via the Bering Landbridge and (4) migrating birds disseminate the organisms during their northward migration.

The causative organism of Q fever, *Coxiella burnetii*, was discovered almost simultaneously by Derrick (1937) in Australia and by Davis and Cox (1938) in the western United States. Since these initial discoveries, most of the literature has dealt with Q fever as a disease of man and his domestic animals.

Little is known about the occurrence of *C. burnetii* in nature, particularly its distribution among wild animals. In North America the first isolations of Q fever organisms from wild animals other than arthropods occurred when Stoenner *et al.* (1959) reported finding three species of rodents, *Peromyscus maniculatus*, *Dipodomys ordii*, and *Dipodomys microps* naturally infected. These isolates were only weakly pathogenic for guinea pigs, rarely produced fever and could not be passed reliably in this animal. Burgdorfer *et al.* (1963) isolated organisms from *Citellus lateralis*, *Neotoma cinerea cinerea* and *Eutamias amoenus*. Parker (1971) summarized the findings of the studies started in 1960 in western Utah. He and his colleagues found *Eutamias minimus*, *Ammospermophilus leucurus*, *Perognathus formosus*, *Dipodomys microps*, *Dipodomys ordii*, *Peromyscus maniculatus*, *Onychomys leucogaster* and *Lepus californicus* naturally infected. Studies by investigators in other parts of the world [Babudieri and Moscovici (1952) in Italy; Blanc *et al.* (1947) in North Africa; Derrick and Smith (1940) in Australia; Basova *et al.* (1960) and Pavlovsky (1966) in the Soviet Union] strongly indicate that a variety of small mammals, especially rodents, and birds play a significant role in maintaining Q fever in nature. Burgdorfer *et al.* (1963) tabulated known hosts from which Q fever had been isolated.

Jellison (1965) reviewed unpublished data in the files of Drs. Luoto, Philip and Lackman at the Rocky Mountain Laboratory, Hamilton, Montana. These data, serological tests on man, dairy cattle and milk, and from skin tests on humans strongly supported the presence of Q fever in the Anchorage-Matanuska Valley areas of Alaska. Hopla (1965) tested 178 dairy cattle in the Fairbanks-Delta environs and found that 19 animals, approximately 10 per cent, had significant antibody titers for Q fever. These data compared favorably with those reported by Luoto (1960).

Of particular interest is the dearth of information pertaining to the wild Artiodactyla. The only reference I know is the antibody titers reported by Gilmour (1968) from *Odocoileus hemionus* in western Utah. The purpose of this paper is to report my observations concerning Q fever in relation to the caribou (*Rangifer tarandus*) in Alaska. The data reported here are only a part of a study of zoonoses in Alaska initiated in 1964 and terminated in 1971.

MATERIALS AND METHODS

The caribou located on the North Slope of the Alaskan Range commonly referred to as the Delta herd were the principal source of samples for microbiological assay. Supplemental specimens were secured from caribou adjacent to Anaktuvuk Pass.

Specimens were secured from caribou in the Delta herd by 'shooting' them from a helicopter with succinylcholine chloride (Succostrin) 20 mg per cc. The dosage ranged from 0.6 cc to 1.0 cc depending upon the condition of the animal. Twenty cc of blood was removed from the jugular vein, centrifuged on return to the field laboratory, and shipped in liquid nitrogen to the Zoonoses Laboratory, University of Oklahoma. The specimens were then transferred from liquid nitrogen to Revco low temperature freezers until microbiological procedures were initiated. Specimens from Anaktuvuk Pass were taken by the hunters shooting the caribou. Spleen and kidney samples were taken only from those caribou that succumbed to 'Succostrin' or were shot by hunters. Therefore, the principal source of data was derived from antibody titers rather than the isolation of organisms.

At the time the caribou were immobilized, numbered ear tags secured from the Alaska Department of Fish and Game were applied. Nylon ear ribbons were also used to aid in obtaining data concerning the wanderings of these animals. Three hundred and twenty-five animals were tagged between 1966 and 1970.

Antibody titers were established by the use of the complement fixation test (CFT). Other methods such as the capillary agglutination test (CAT) (Luoto, 1956), and the radio-isotope precipitation test (RIPT) (Tabert and Lackman, 1965) were considered. The RIP test was the most sensitive of the methods used when testing sera from ungulates, however, because it is not a commonly used test, a large backlog of data are needed to establish its value when working with wild animals. Data from this test will be published elsewhere. As used here the CFT was similar to the method of Welsh *et al.* (1959). A titer below 1:32 was not considered significant. Q fever (American strain, 9 mile) diagnostic antigen from Lederle Laboratories was used.

To attempt isolation of Q fever organisms, spleen and other tissues were homogenized in a 5 ml of sterile skim milk to which 1000 units of penicillin was added. Five tenths of a ml (0.5 ml) of this suspension was injected intraperitoneally into each of two male guinea pigs weighing from 250-500 grams. A 1:10 dilution of the homogenate was then made and 0.5 ml injected into each of 10 fertile chicken eggs which had previously incubated for five days at 37.5° C. The remainder of the homogenate was sealed in ampules and stored at -60° C for future use.

Rectal temperatures of the guinea pigs were measured daily for three weeks. If a temperature of 40° C or above was maintained for three consecutive days the animals were bled, and transfers of the blood injected into embryonated chicken eggs. Figure 1 further summarizes the technique followed.

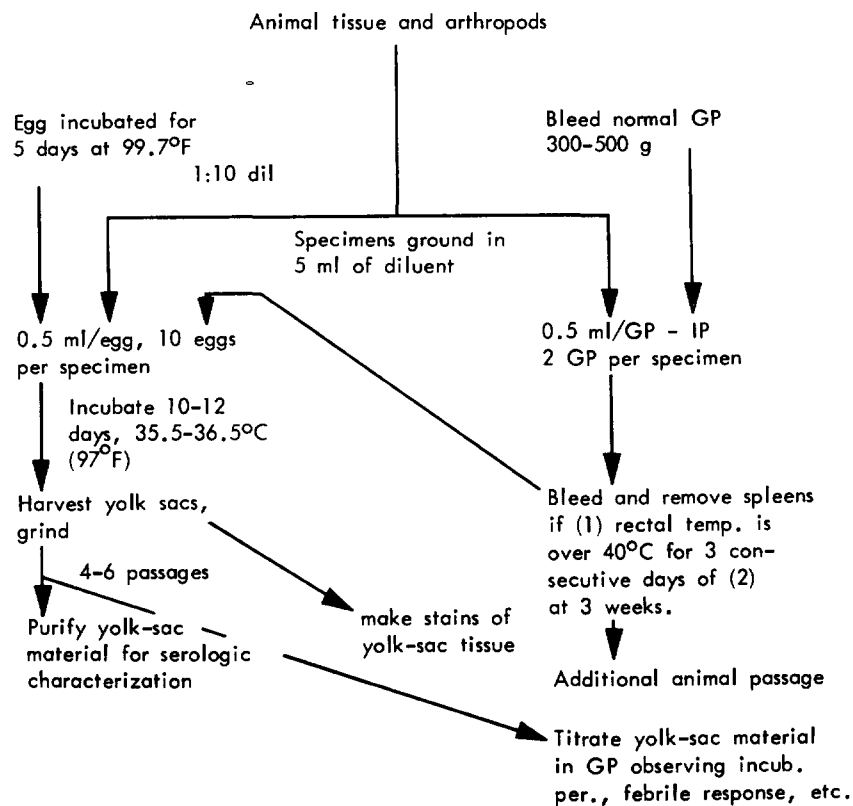


Fig. 1.—Schematic representation of the procedure used to isolate *Coxiella burnetii*.

RESULTS

The results of the antibody survey of 355 caribou from the Delta herd are summarized in Table 1. Thirty-seven had titers ranging from 1:32 to 1:512 indicating 10 per cent of these caribou had significant antibody titer. No sera from the Anatuuvuk Pass caribou were positive.

TABLE 1.—Positive serological data, Delta caribou herd, Alaska.

Locality	Nos. Pos.	Complement fixation titer				
		32	64	128	256	512
Buchanan Creek	10	4	4	2	0	0
Delta Creek	8	5	2	0	1	0
Donnelly Summit	6	1	4	1	0	1
Little Delta River	7	5	1	0	0	0
Portage Creek	6	2	0	3	1	0

In Table 2, I have presented data on the seven positive sera out of 28 bison tested in

TABLE 2.--Positive serological data, Delta bison herd, Alaska.

Lab. No.	Complement fixation titer			
	32	64	128	256
385		+		
387	+			
388				+
396	+			
418				
422			+	
*2915				+

*First sampled 1966. Second sample 1967 = 1:128, third sample 1968 = 1:1:64.

the Delta area. These data are included here because the range of the bison overlaps with domestic cattle and the caribou in this particular locality. Most of these data were obtained in 1965 and aroused my interest to investigate the caribou. These bison were shipped into Big Delta area from the National Bison Range, Montana during 1928. The sample is too small to be taken as representative of the bison herd, but the results are interesting.

The size of the bison herd varies from time to time. Early in 1965 about 250 animals were stated to be present and in 1967 the number was reduced to approximately 150.

The number of caribou in the Delta herd are not known for a certainty and probably varies from one year to the next. Scott *et al.* (1950) reported 300 animals. Until 1970 hunting pressure had been slight but at that time a sharp up-swing was noted. Estimates from various individuals within the Alaska Department of Fish and Game in 1965 ranged from a "few hundred up to as high as 1,000 animals." In March of 1967 a herd was sighted by Sam Stoker and Richard McIntyre which they estimated as 3,000 and 5,000 animals respectively. The following day the herd had broken up into small bands which were widely dispersed. One would not have gained an impression then that they were nearly so numerous.

Figure 2 indicates the known range of the caribou and bison herds. Undoubtedly, the caribou may extend further east into the Gerstle River and the Johnson River area, but I have gathered no information one way or the other during the course of this study. I have not yet uncovered recent data by other investigators that would furnish valid information. Endicott (1928) reported caribou in the vicinity of Berry Creek and the Macomb Plateau; however, at that time caribou were common throughout central Alaska.

The initial attempts to isolate *C. burnetii* from caribou spleens utilizing guinea pigs proved unsuccessful. Having tissue samples for only 30 caribou from the Delta herd, it was decided to inoculate hamsters with a 1:25 dilution of the original homogenated suspensions. The decision to use hamsters was based upon the observations of Stoenner and Lackman (1960) who found strains of *C. burnetii* in Utah so weakly pathogenic for guinea pigs that they rarely produced fever, and could not be readily passed in them.

Tissue homogenate numbers 2607, 2616 and 2924 taken originally from caribou at Buchanan Creek, Little Delta River and Donnelly Summit respectively were of interest. During the initial attempts at isolation the guinea pigs had shown a slight elevation of temperature — 39° C for one or two days. Sera from blood samples of guinea pigs

innoculated with tissue homogenate number 2924 had shown low CF titers at levels I deemed nonspecific, 1:8-1:16.

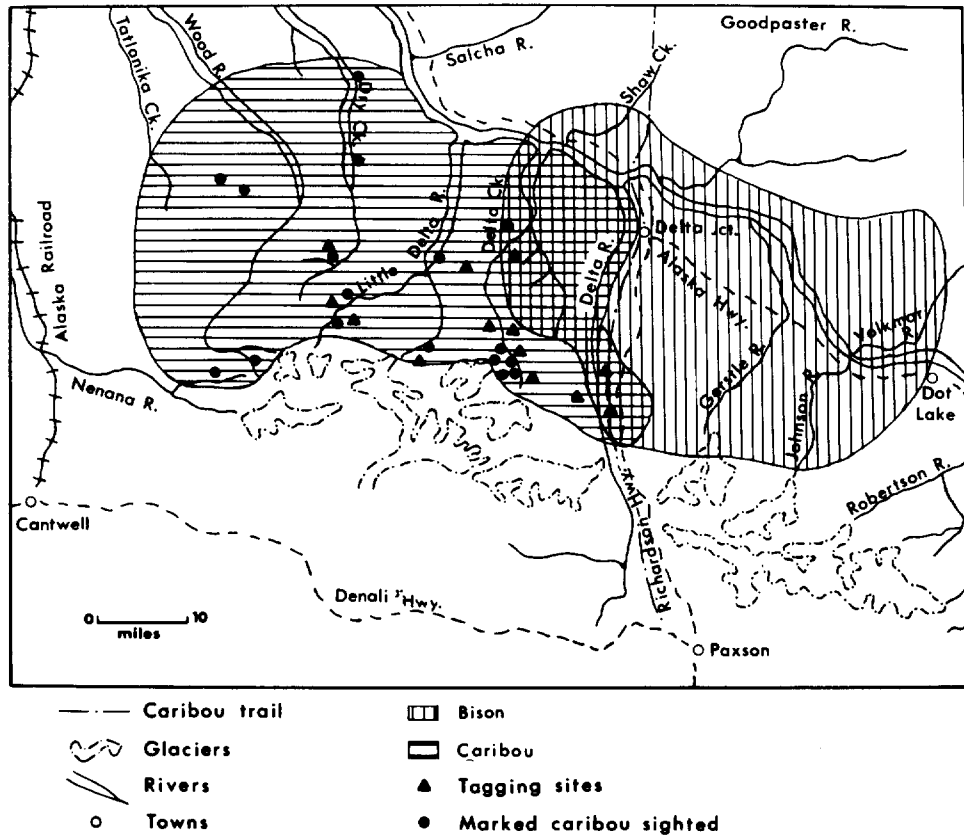


Fig. 2.—Known range of the Delta caribou and bison herds.

The hamsters were bled 40 days after inoculation (Stoenner and Lackman, 1960) and sera tested for complement fixing antibodies against *C. burnetii*. All sera were negative with the exception of 2924. All four sera for 2924 had titers ranging from 1:128-1:256. When repeated a fourth time the results were essentially the same — with some higher titers noted (Table 3).

TABLE 3.—Antibody response in hamsters induced by caribou strain 2924.

Passage	Mean CF titers		
	1:64	1:128	1:256
First		+	
Second			+
Third	+		
Fourth			+

Some hamsters were overwhelmed by the injection. A 1:25 dilution of homogenated spleen was injected into yolk sacs of fertile chicken eggs. By the third passage, a moderate growth of rickettsial organisms was observed when stained smears of yolk sac preparations were examined.

At the time of preparing this manuscript ID₅₀ determinations against a standard known strain of *C. burnetii* had not been undertaken. However, sufficient evidence is presented to warrant the conclusion that at least one caribou was infected with *C. burnetii* at the time of necropsy.

DISCUSSION

A small scale investigation of the Delta herd of caribou was undertaken with the anticipation of obtaining data regarding herd size, range, and their relationship to zoonoses, especially Q fever.

The herd size varied, but this might have been more apparent than real. Methods for counting caribou populations differ considerably. Habits of the caribou, such as aggregating into a herd and suddenly disbanding into small groups which disperse rapidly and for a considerable distance, mitigates against obtaining accurate information. However, the Delta herd is larger than previously estimated. The highest count was taken in 1967 when approximately 5,000 animals were reported.

Much yet remains to be learned about the range of this particular herd of caribou. The meager data indicate that the caribou move more widely than originally anticipated. One tagged animal was shot by a hunter near a tributary of the Nenana River in the Healy-Suntrana area. The 1969 tagging operation took place six miles south and west of Donnelly Summit on a high plateau. These animals possibly could migrate south into the Paxson region, or in the case of the animals found adjacent to Healy-Suntrana area, into McKinley Park.

When the tagging study was first started in 1966 the bulk of the herd was located in the Wood River-Dry Creek area. In 1967 they were encountered more commonly near Buchanan Creek with some numbers present near Delta Creek. During the tagging operations in 1968, the major concentration of the herd was the Delta Creek area. The caribou were most abundant six miles west and south of Donnelly Summit. Richard McIntyre and I found 2,000 to 3,000 caribou adjacent to the Tanana River across from Pile Driver Slough during 1970.

The observations just reported were taken each year during February and March prior to and during the tagging operation. Occasional scouting expeditions were made at other times of the year. The caribou tended to be in widely dispersed bands varying from 10-125 animals in the upland tundra during the summer. During the winter months they tended to aggregate into large bands from 75 to 500 animals and were at lower elevations not far from the taiga. Frequently during the winter months caribou were observed in the climax black spruce stands along Delta Creek. Similar sightings were made at Little Delta River and Portage Creek.

The caribou trail in Figure 2 while theoretical was based upon separate conversations with Dr. John F. Buckley, the late Mr. John Hajdukovich and Mr. Sam O. White. Messrs. Hajdukovich and White stated that during the period from 1920-1940 they had seen caribou from the area now generally occupied by the Delta herd moving toward the Tanana Hills. Messrs. Hajdukovich and White assumed these caribou eventually joined the larger Steese herd.

Whether part of the Delta herd migrates to join with the Nelchina herd or those of McKinley Park is not known. Buckley (pers. comm.) remembered seeing winter caribou

trails "heading in the right direction" to make contact with the Nelchina herd.

From the foregoing account it appears logical to assume that the Delta herd is not static with regards to population and range. I am reasonably well convinced that a part of the herd does emigrate and join with major herds in those localities. Movement of these caribou is of interest in relation to zoonotic studies.

The association with Q fever is an interesting one. Four hypotheses are advanced to explain the association: (1) direct contact with the bison imported from Montana in 1928, with the assumption that some of the bison were infected at the time of importation; (2) bison obtained their infection after arriving in Alaska from domestic cattle and thence transmitted it to the caribou; (3) caribou brought the organisms with them when they migrated across the Bering Landbridge; and (4) birds disseminate *C. burnetii* in the process of their northward migration each year.

Admittedly, sufficient information is not available to support any of the concepts completely. However, direct contact with the bison appears most logical to me. From what is known of the strains of *C. burnetii* isolated from wild animals in Montana, it would seem likely for the bison to have transported organisms similar in virulence to that of the Nine Mile strain or those isolated from rodents by Burgdorfer *et al.* (1963). No one knows what kind of Q fever organisms the bison might have had. The bison has not been investigated from this standpoint.

The second theory relating to dairy cattle may have validity. However, a conflict in viewpoints exists among investigators. For example, one concept holds that there are two cycles of Q fever: a domestic animal-human cycle and the one existing in nature among wild animals (Luoto, 1960). To the contrary, Pavlovsky (1966) in referring to the importation of Q fever by transportation of domestic animals from endemic foci stated that a focus of Q fever springs up in a pasture, i.e., in nature, by way of a reverse migration of the pathogenic agent from farm animals to wild (exoanthropic) animals and tick vectors. If Pavlovsky's concept is followed, domestic cattle would be a reasonable suspect.

The possibility of caribou bringing Q fever across the Bering Landbridge is not tenable at the present time because the 200 samples from the Arctic herd proved negative for *C. burnetii*. A subsequent larger sampling could prove me wrong.

Birds have been reported as carriers of Q fever organism by various authors (Basova *et al.*, 1960). Again conflict exists in the published data (Tarasevich and Kulagin, 1961). Be that as it may, were birds efficient carriers, *C. burnetii* ought to be a common widely dispersed infection in nature.

The isolation of *C. burnetii* from one caribou does little to explain the ecology of the disease in relation to this animal or its possible significance to man. This statement is placed in better perspective when I state it was the only isolation out of several thousands of attempts from other animals. The calving grounds for the Delta herd are not known. The survival of the organisms in soil, etc. in the subarctic has not been investigated. Indeed the "door has only been cracked." An enormous investment in time and financial resources must be invested before this study is brought to full fruition.

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THE HELMINTH FAUNA OF THE WILD REINDEER OF WESTERN TAIMYR

N. M. Shalaeva
Department of Invertebrate Zoology
Moscow State University
Moscow V-234, USSR

ABSTRACT—68.4 per cent of the animals examined were found to be infected. Helminths of two classes were recovered: cestodes and nematodes. 61.5 per cent of the animals examined were infected with *Cysticercus*. Three species of cysticercus were found: *Cysticercus tenuicollis*, *C. parenchimatosa* and *C. tarandi*. Cestodes *Moniezia expansa* and *Avitellina arctica* were found in the intestines. 61.5 per cent of the examined animals were affected with monieziosis. In our investigations of soil fauna we discovered representatives of the families Oppiidae and Cerconidae which may serve as intermediate hosts. Two species of lung nematodes were encountered: *Dictyocaulus eckerti* and *Dictyocaulus hadweni*. 53.8 per cent of the animals investigated were infected. The percentage of animals infected by intestinal nematodes was 23 per cent. Two species were found: *Nematodirella longissimespiculata* and *Nematodirus tarandi*. A characteristic feature of the helminth fauna of the reindeer of Western Taimyr is the absence of trematodes.

The investigations described were carried out in July-August 1968 in the basin of the river Pyasina and its tributaries, the rivers Chernaya, Agapa, Pura, Yangoda. Nineteen wild reindeer were killed and examined using the method of complete helminthological necropsy. 68.4 per cent of the animals examined were found to be infected, of them 46.1 per cent were females, 30.7 per cent males and 23.2 per cent calves. Helminths of two classes were recovered: cestodes and nematodes. Many organs of wild reindeer may be invaded by helminths: lungs, kidneys, heart, musculature, mesentery, liver, large and small intestines.

CESTODES

The cestodes were located in the lungs and the small intestine. Larval stages (bladder worms) were discovered in the liver, on the mesentery and in the muscle tissue. Larvae of the thin-necked cysticerc (*Cysticercus tenuicollis*) were found on the mesentery of only one reindeer (a female). The invasion was not intensive as it consisted of only three bladder worms. Bladder worms of *Cysticercus parenchimatosa*, the larvae of *Taenia parenchimatosa*, were recovered from the liver. These larvae may also invade the heart and the lungs. The intensity of invasion ranged from three to 30 specimens and more. Larval stages of *Taenia krabbei* — *Cysticercus tarandi* — were found in the intermuscular connective tissue. 61.5 per cent of the animals examined were infected with *Cysticercus*. Thus cysticercosis ranks first among the helminthoses of wild reindeer. Cestodes of the suborder Anoplocephalata were found in the intestine and were represented by long thick strobiles of *Moniezia expansa*. Four species of *Moniezia* occur in the reindeer: *Moniezia expansa*, *Moniezia benedeni*, *Moniezia baeri* and *Moniezia rangiferina*. The two latter species occur most frequently in the wild animals and were not recorded in the domesticated reindeer. 61.5 per cent of the examined animals were affected with monieziosis. *Moniezia* utilizes oribatid

mites as intermediate hosts. In our investigations of soil fauna we discovered representatives of the families Oppiidae and Cerconidae which may serve as intermediate hosts. Beside *Moniezia expansa*, the cestode, *Avitellina arctica*, of the suborder Anoplocephala, was discovered in the intestine. This cestode occurs only in the wild reindeer. It has been described from a wild reindeer from the Jamal-Nenets Autonomous Region.

NEMATODES

Nematodes occurred in the lungs and in the small and large intestines. Two species of lung nematodes were encountered: *Dictyocaulus eckerti* and *Dictyocaulus hadweni* (family Dictyocaulidae). 53.8 per cent of the animals investigated were infected. The intensity of invasion ranged from three to 40-50 specimens.

Representatives of the family Trichostrongylidae were recovered from the intestine. The percentage of animals infected by intestinal nematodes was 23 per cent. Two species were encountered: *Nematodirus tarandi* and *Nematodirella longissimespiculata*; the first species in the small intestine, the second in both small and large intestines. The intensity of invasion is very high, reaching several hundred specimens in one host.

TREMATODES

A characteristic feature of the helminth fauna of the reindeer of Western Taimyr is the absence of trematodes. According to data from the literature (Mitskevich, 1957, 1963; Poljanskaja, 1963) the following trematodes are known to infect the wild reindeer: *Fasciola hepatica*, *Dicrocoelium lanceatum*, *Paramphistomum cervi* and several species of the genus *Cotylophoron*. All trematodes, as known, utilize mollusks as intermediate hosts. The intermediate hosts of *Dicrocoelium lanceatum* are shelled, land mollusks. We found only one land mollusk, the slug, *Deroceras levi*, in the forest tundra. No shelled land mollusks were discovered in the tundra subzone. The intermediate host of the liver-fluke, *Fasciola hepatica*, the water snail, *Galba truncatula* L., was absent from the Western Taimyr lands we examined. The intermediate hosts of *Paramphistomum cervi* and *Cotylophoron*, freshwater Planorbidae and Limnaeidae, did occur, but we failed to discover these trematodes. This possibly may be explained by the fact that the reindeer were examined during the summer period while the outbreaks of diseases caused by trematodes take place in autumn and early winter.

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WARBLE FLY DISTRIBUTION AMONG SOME CANADIAN CARIBOU

John P. Kelsall
Canadian Wildlife Service
10025 Jasper Ave.
Edmonton, Alberta
Canada

ABSTRACT—Observations suggest that warble fly larvae infestation on caribou can be judged from counts of breathing holes and scars on tanned hides. Using these criteria, assessment was made by sex of symmetrical, geographical and numerical distribution of warble larvae among nine Canadian caribou populations. Larvae tend to be equally distributed bilaterally and to be approximately twice as abundant on the posterior, as compared to anterior, half of the animals. Warble infestations and the number of warbles per animal tend to be greater on males within populations and to increase from north to south between populations. Morphology and behavior of caribou may govern larvae distribution on individuals. Behavior of herds and climate — particularly temperature — generally seems to account for differences in infestation observed between herds.

Warble flies (*Oedemagena tarandi* L.) are a common parasite of caribou and reindeer (*Rangifer* sp.) throughout the holarctic region. There are numerous statements in the literature referring to the abundance of larvae under the skin of Canadian caribou, and of the way in which they damage the hides for domestic purposes (e.g., Stefansson, 1913). However, systematic studies of the parasites seem to be lacking in North America. Hadwen (1927) and Skoog (1968) provide information from Alaska. Banfield (1954) and Kelsall (1968) have summarized what is available regarding warble flies among barren ground caribou (*R. tarandus groenlandicus*) in Canada.

This study was prompted by my observation that estimates could be made of warble infestation of individual caribou from the examination of museum hides. Skins taken from caribou through winter to July, and tanned, show the characteristic round holes, like buckshot holes, cut by the larvae in order to breathe. Skins taken after the larvae emerge to pupate on the ground in late May and June show rapidly diminishing numbers of holes which are replaced by characteristic round spots of scar tissue. By September the holes are gone but diminishingly visible scars remain until holes from the next crop of larvae develop.

With the above information at hand, it was decided to try an assessment of warble fly infestation among Canadian caribou through an examination of hides wherever they might be found.

MATERIALS AND METHODS

Of several hundred hides examined, 173 from males and 139 from females were judged to be useful to this study. Hides were examined personally, or by paid or volunteer cooperators, at the American Museum of Natural History, the British Museum, the National Museum of Canada, the Royal Ontario Museum and the Saskatchewan Museum of Natural History. Data were also secured from several dozen hides from a variety of miscellaneous

sources — sportsmen, taxidermists, university museums, fellow biologists and from 26 animals taken personally in the western Canadian Arctic. A few of the latter were raw mid-winter hides and dead and living larvae, rather than holes and scars, were counted.

A standard form (Fig. 1) was used for the collection of data from tanned hides. The

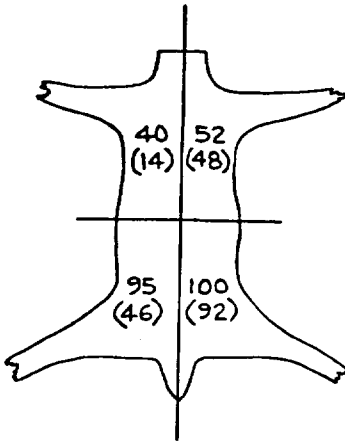
CANADIAN WILDLIFE SERVICE
EXAMINATION OF CARIBOU HIDES FOR WARBLE SCARS

Instructions

1. Complete general data queries as fully as possible — sex, date and place of collection are particularly important.
2. Show the number of warble scars in each hide quadrat on the diagram below as well as the total number of scars. Scars should be recorded as they appear when the hide is spread fur side down.
3. Both negative and positive reports are required.

<u>Museum:</u> Am. Museum of Nat. History	<u>Age if Given:</u>
<u>Museum No.:</u> 29031	<u>Total Length:</u> 76"
<u>Collector:</u> E. T. Seton	<u>Hind Foot:</u> 19"
<u>Date of Collection:</u> Aug. 2, 1907	<u>Height at Shoulder:</u>
<u>Place Collected:</u> East Shore Artillery L. Mackenzie	<u>Ear Length:</u>
<u>Species or Subspecies:</u> Rangifer tarandus arcticus	<u>Tail Length:</u> 6"
<u>Sex of Animal:</u> ♂	<u>Weight:</u>

Remarks (by collector or observer):

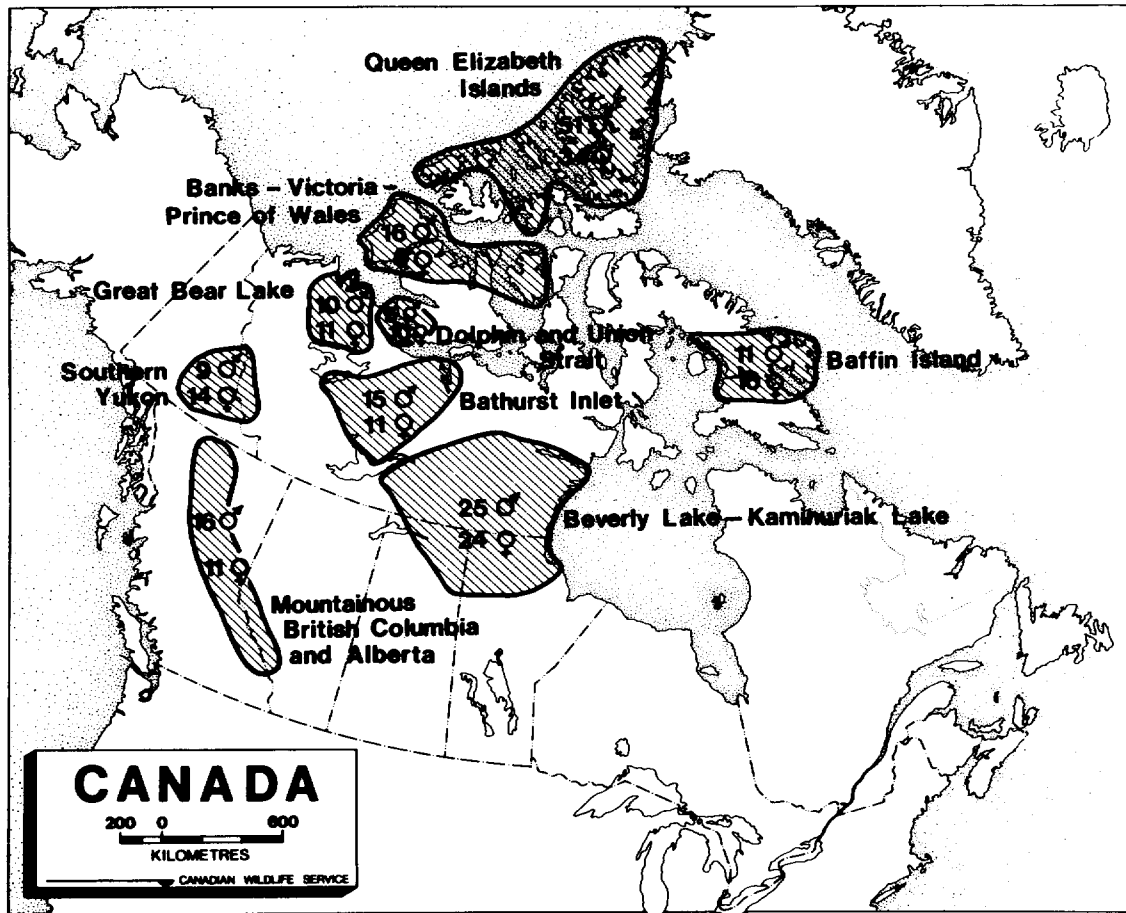


Scars - 287
Holes - 200
Total Scars: 487

Fig. 1.—Completed warble fly larvae questionnaire.

division of the diagram into quarters permitted the assessment of bilateral and anterior-posterior symmetry in warble larvae infestations. Data from all but about 36 animals were collected on such forms. Unfortunately, the forms did not call for a mandatory distinction between holes and scars. The distinction was not always made with the result that scar to hole ratios are based on data from only 96 hides.

Map 1 shows the geographic and numerical distribution of the specimens. The



Map 1.—Geographical, numerical and sexual distribution of study hides.

boundaries shown, with one exception to be mentioned later, are within those for existing populations of Canadian caribou. They show approximately the limits within which specimens were taken rather than the outer limits of the populations concerned. In many cases, data with the museum hides gave only approximate points of collection. Several caribou populations are not represented, particularly in eastern Canada, since an arbitrary decision was made to deal only with cases where there were 10 or more total samples. Some island populations, and two herds west of Hudson Bay (commonly called the Beverly Lake and Kaminuriak Lake herds) have been lumped to provide reasonable sample sizes and thus broaden the total area from which some representation could be derived.

Dennis Benson, statistician with the Canadian Wildlife Service, consulted extensively on analysis of the data. It was concluded that small and varied sample sizes (Map 1) and

TABLE 1.--Infection by warble fly larvae of caribou populations shown on Map 1, and the approximate latitudes at which the larvae pupate in each case.

Population	Sample size and sex	% caribou infected	Mean larvae per infected caribou	Range	North latitude
Queen Elizabeth Islands	51♂ 34♀	37 21	11 4	0-57 0-14	78°
Banks-Victoria- Prince of Wales	16♂ 6♀	63 50	74 13	0-205 0-21	73°
Baffin Island	11♂ 10♀	55 80	58 43	0-120 0-101	69°
Dolphin and Union Strait	5♂ 10♀	80 50	73 54	0-248 0-78	69°
Great Bear Lake	10♂ 11♀	100 100	230 87	4-576 8-355	69°
Bathurst Inlet	15♂ 11♀	87 82	197 78	0-507 0-315	67°
Beverly-Kaminuriak Lakes	25♂ 24♀	88 92	113 46	0-487 0-309	63°30'
Southern Yukon	9♂ 14♀	100 86	321 187	14-913 0-598	62°
Mountainous B. C. and Alberta	16♂ 11♀	100 82	489 164	8-2,190 0-510	56°

great variability in warble infestation within populations (Table 1) made sophisticated statistical analysis of questionable value. As the extreme example, a series of 16 male hides from the mountains of British Columbia and Alberta showed a range of eight to 2,190 larvae per hide with a mean of 489. It was also concluded that, despite the above, mean differences between populations were consistent, real and could stand by themselves for purposes of population assessment. Probabilities based on Student's 't' test were calculated in some cases where they would be useful.

RESULTS

Seasonal Changes in Scar and Hole Counts

The numbers of breathing holes of warble fly larvae in museum hides, per month, are shown in Figure 2 as a percentage of the total count of holes and scars. There are no data

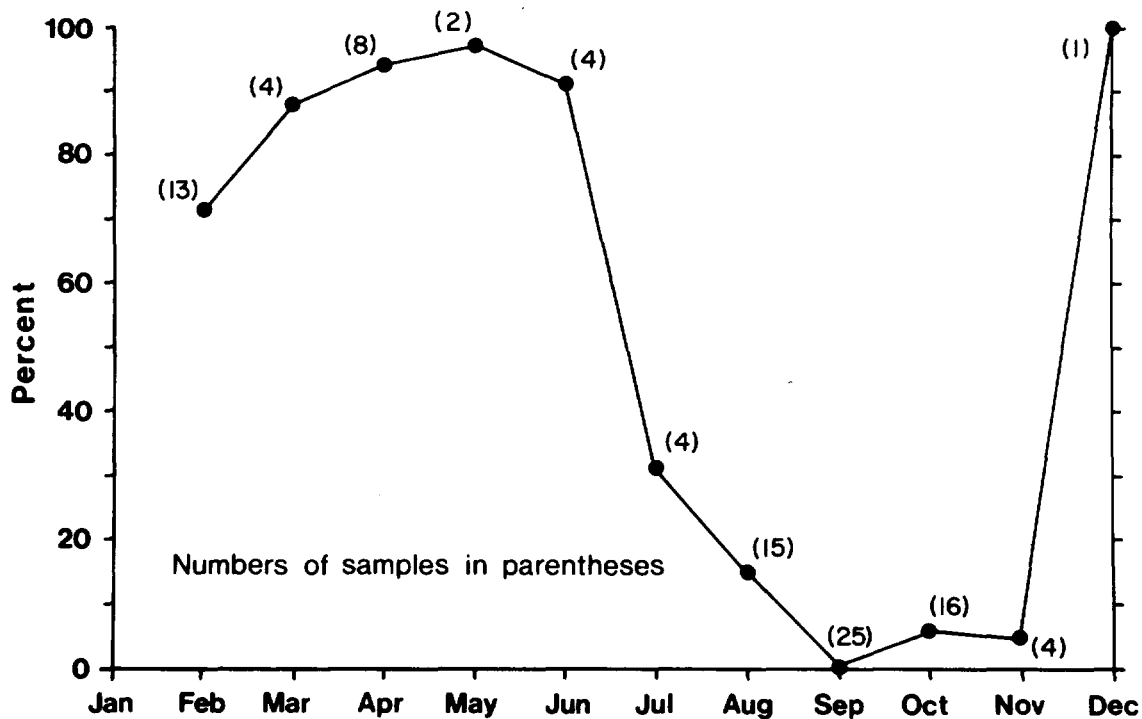


Fig. 2.—Warble larvae holes, as a per cent of holes plus scars on caribou hides, by month of collection.

for January, and December is represented by a single hide, but the pattern seems clear. In September there are virtually no holes on the caribou hides. Those that are present then, and some of those in October and other months, seem to be artifacts due to breaking up of scar tissue by rough handling during tanning. There are 5 per cent holes in November, when larvae are in various stages of subcutaneous migration from points of oviposition, and some are already established at positions favored for larval development. (Skoog, 1968, reported the first new breathing holes of the season in Alaska on September 26.)

The number of holes must rise rapidly through December and January (and the

number of visible scars diminish concurrently) since, from February through June, there are from 71 to 97 per cent holes (Fig. 2). I attribute most scars during the late winter months to mortality among the larvae and the subsequent formation of scar tissue over their breathing holes. Dead larvae are often found on fresh caribou hides in winter, completely encapsulated and partially absorbed. Dead, or living, larvae seldom seem to cause serious pathological conditions in Canada (Banfield, 1968), although Hearle (1938) reported some in Alaskan reindeer.

The larvae emerge through their breathing holes in late May and through June, dropping to the ground where they pupate. The rapid rise in relative numbers of scars through July indicates great rapidity in the healing process. Where there are 91 per cent holes in June, there are only 31 in July, 16 in August and 0.3 per cent in September (Fig. 2).

The data, and personal observation, both suggest that the sum of holes plus scars taken from tanned caribou hides gives a reasonable approximation of total warble fly larvae infestation in a single year. That assumption provides the basis for this paper. There are obvious biases which would warrant compensation given a larger body of data. For example, larvae which die early in a winter may not be represented on hides taken in spring or summer since the scar tissue may already have disappeared. Also, unusually large scars, perhaps caused by infection, may persist for long periods of time. However, the numbers of persistent scars seem to be small. Because of paucity of data, no general compensation is possible here for annual variability in warble infestation which doubtless occurs among all caribou populations.

Symmetry in Infection by Warble Larvae

There were no statistical differences between numbers of warble fly larvae on the right and left sides of either infected male caribou ($n=97$: $p=0.8$) or infected females ($n=62$: $p=0.6$). However, infections on some individuals (e.g., Fig. 1) were markedly asymmetrical.

Despite great individual variation, ranging from 1 to 2,190 warble larvae per infected animal, the average number on caribou forequarters were consistently about half those in the hindquarters. Among infected animals, males had an average of 77 larvae on the forequarters to 131 on the hindquarters while females had a ratio of 28 to 65. The differences were statistically significant for both males ($n=99$: $p=0.05-0.02$) and females ($n=70$: $p=0.01-0.001$). Within populations these differences were not always statistically significant probably because of great variability and small sample sizes.

Infection Rates by Population, Sex and Age

Table 1 shows, by sex, the per cent of animals infected, the mean number of warble larvae per infected animal and the range of infection for each of the populations shown on Map 1. It also shows the approximate mean latitude at which the larvae emerge and pupate. The per cent infection among females is equal to (once), or more often (6 times) less than that among males, although the Beverly-Kaminuriak Lakes and Baffin Island populations are exceptions. The number of larvae per infected male is always greater than that for females and the upper range of infection is always greater in males.

The exception of the Baffin Island population in having greater incidence of infection among females seems explicable in terms of annual variability in the severity of warbles, and an unfortunate mix of specimens from one year. Six of seven Baffin Island specimens taken in 1925 were males and there was only a single warble among them all. That year was obviously very poor for the flies and it is unfortunate that nearly half the male sample came

from it. The greater incidence of infection among females in the Beverly-Kaminuriak Lakes population is not statistically significant.

It is noticeable (Table 1) that per cent infection and the number of larvae per infected animal both tend to increase from north to south among the various populations. The tendency is particularly marked if the Great Bear Lake population is recognized as having characteristics that make it unusually vulnerable to parasitism by warble flies. Of all the tundra populations only it, and to a much lesser extent the Bathurst Inlet population, tend to summer in the very areas where their warble larvae emerge and pupate.

Perhaps the most interesting population shown on Table 1 is that from Dolphin and Union Strait. Those animals, now extinct or nearly so, used to winter on the mainland, cross to Victoria Island on the sea ice in late May and early June, and return to the mainland when the sea froze again in October. That habit presumably gave them the advantage of having fewer biting insect pests to cope with than other mainland populations (Kelsall, 1968). The data seem to confirm this speculation in regard to warble flies as well. While those caribou had a higher rate of infection among males, and more larvae per animal among females than caribou resident on Victoria and immediately adjacent islands, they had far fewer than their near mainland neighbors, the Great Bear Lake population. Many of the larvae from the Dolphin and Union Strait animals doubtless emerged on the mainland or were lost by emerging onto the sea ice. I have seen the latter occurrence among migrating caribou at Bathurst Inlet on several occasions.

Accurate ages were designated for few of the museum specimens. However, it appeared probable that, except in the case of young of the year, any variability by age would be masked by the enormous individual variability among all animals. Judging from a handful of samples, young of the year of both sexes appear to have lower mean numbers of warble larvae, but not lower rates of infection (see Kelsall, 1968), than older age classes. This may simply be because the smaller body size of juveniles provides less warble habitat than older and larger animals. Even so, a female calf from the Alberta foothills had 300 warble larvae holes in its hide.

DISCUSSION

There are many morphological, behavioral and ecological factors which cause variability in warble fly infection. Most can be dealt with in only a speculative fashion for Canadian caribou.

Differences in the symmetry of infection and between sexes would seem dependent on morphology and behavior. Forequarters are probably less highly infected than hindquarters simply because caribou are apt to see and evade a frontal approach by a fly. Some of the difference between sexes, in regard to number of larvae per animal, may be due to the larger body size of the males literally providing more habitat in cases of heavy infection.

Especially among the tundra populations where sexual differences in individual infection are greatest, males may be more open to infection because of their rapid, wide ranging behavior. Females and young tend to move away from areas of larval emergence and pupation, crossing them perhaps only once during southward movement in August. Males, on the other hand, may repeatedly cover the same ground, often traveling in small, loose aggregations that may make them especially vulnerable to attack by warble flies.

Other factors are apparent when one considers the behavior of some of the particular caribou populations. Caribou that remain on the same general ranges from the time the warble larvae drop to the ground through pupation and until the flies emerge are much more apt to be infected than others. I believe, for example, that the high rates of infection

and numbers of larvae per animal among populations in the western mountains are because those caribou are relatively sedentary on alpine meadows in spring and summer. The Great Bear Lake caribou, which feed in summer on the same coastal ranges where many warble larvae emerge, are similarly highly infected. So are those in Newfoundland (372 larvae/animal among 3 males), where sample numbers were too small to warrant detailed presentation here, but where the summer ranges are restricted.

On some of the high arctic islands, on the other hand, where vegetation is sparse, the animals range widely. There it is entirely possible that by the time warble flies emerge from their pupae caribou may move on beyond the effective range of the flies.

The most important ecological factors regulating the degree of success of warble parasitism, annually and between populations, doubtless relate to climate. Brejew (1956) has defined and discussed a number of parameters of importance to warble flies including temperature, direct sunshine, windspeed, humidity and light intensity. The warbles are limited in activity by only high winds (in excess of 8-9 m/sec or about 32 km/hr) if other conditions are favorable. Humidities above 89 per cent and light intensities under 5,000 lux inhibit flight.

Temperature is doubtless the most important factor, as a general principle, and particularly toward the north. According to Brejew, the minimum temperatures for warble activity are in the range 13-15° C. Optimum temperature range is 15-27° C. Direct solar radiation can raise the body temperature of the flies by 7-9° and thus lower, by a similar amount, the range of air temperatures which are favorable for flight.

The limits for Canadian warbles are probably not significantly different from those of the Eurasian tundra studied by Brejew. Judging from data from weather stations near areas of warble emergence (Canada Dept. of Transport, 1968), the warble populations would be increasingly inhibited by less favorable temperatures in the ascending order shown on Table 1. In British Columbia, Alberta and the Yukon, the mean daily maximum temperature would permit warble flight from June through September. At the other extreme, on the Queen Elizabeth Islands, the mean daily maximum temperature exceeds the minimum required for warble flight even with the help of direct solar radiation, only in July.

Very likely flight temperature, its frequency and duration, alone and in combination with other climatic limiting factors, is of generally greatest importance in governing warble fly success, in both the long term and short term, on the Canadian tundra. Behavioral factors can be of major importance particularly, as suggested, in caribou populations that either tend to summer on the same areas where warbles emerge and pupate or move away from such areas before the adult flies emerge.

ACKNOWLEDGMENTS

In addition to Dr. Benson, previously acknowledged, I am indebted to the Canadian Wildlife Service for logistic arrangements in the examination of caribou hides and to the many persons who examined hides for me. Mr. Richard Harington of the National Museum of Canada was of particular help. Mr. S. C. Zoltai of the Canadian Forestry Service helped translate a key reference, and Dr. John Holmes of the University of Alberta made a number of helpful suggestions on the manuscript. Mr. Bryan Chubb of the Canadian Wildlife Service made the map and figures.

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**LARGE SCALE FIELD TRIALS AGAINST LARVAE OF
OEDEMAGENA TARANDI AND *CEPHENOMYIA TROMPE*
IN SWEDISH REINDEER**

**Magnus Nordkvist
National Veterinary Institute
Stockholm, Sweden**

ABSTRACT—Large scale field trials involving about 25,000 reindeer were undertaken after prior testing of several larvicidal drugs. Since reindeer are likely to panic if pressed through chutes for treatment, traditional reindeer handling methods were adapted for mass treatment. Experienced reindeer herders were trained in injection techniques. About 120 reindeer per hour could be treated by each person provided he was relieved every second hour. The number of people giving injections was limited only by the number of people available for roping the animals. With six persons giving injections and replacing each other at regular intervals, 2,500 reindeer could be treated during an eight-hour day. This represents about the average number involved in roundups in most Swedish reindeer corrals. The smallest field unit in a campaign against these parasites can advantageously be a team built up around six persons trained to give injections.

Estimated annual losses to the Swedish reindeer industry reaching 10-15 per cent of the total production income have caused demands for an irradiation program against the warble and nostril flies of reindeer (*Oedemagena tarandi* and *Cephenomyia trompe* respectively).

The purpose of these field trials was to develop a system allowing rapid, safe and in so far as possible, inexpensive mass treatment of reindeer.

EXPERIMENTAL

To date about 25,000 reindeer have been involved in the project which has extended over five years. Details of the project are listed as follows:

Year	Period	No. of treated reindeer
1967	Oct-Nov	600
1968	Oct-Dec	4,200
1969	Oct-Dec	3,500
1970	Jan-Mar	4,500
1970/71	Nov-Feb	11,300
1971	Nov-Dec	<u>1,500</u>
		25,600

The results of preliminary tests of different preparations and application methods have been published (Nordkvist, 1967). For the subsequent field trials, Warbex (35 per cent American Cyanamid Corp.) was selected, the active ingredient of which, Famphur, is described as 0,0 dimethyl, 0,p- (dimethylsulfamoyl) phenyl phosphorothioate. It was injected intramuscularly at a dosage of 30 mg/kg body weight by means of an automatic

hypodermic syringe (Ultra-Matic, Henkel). The effect of Warbex on both species has been a 90-95 per cent reduction of larvae. In case of overdosing (usually double-dosing), atropine sulphate was used as an antidote. Erne and Nordkvist (1970) showed that the disappearance rate of Famphur was high except at the injection site where traces of the compound under certain circumstances could be found 21 days after treatment. To prevent any chance of food contamination, an interval of at least six weeks was specified between treatment and slaughter. Every treated animal was marked with a spray of yellow dye (2 per cent picric acid in 99 per cent ethyl alcohol) in order to prevent double treatment and to avoid slaughtering within the prohibited period.

The injections were made by reindeer herdsman specially trained for weight estimation, injection techniques, etc. In this paper they will be referred to as 'injectors.' The men responsible for this branding of the reindeer are called 'painters.' The men who caught the reindeer and lead them to the injectors are called 'catchers.' Finally one man was employed to supply the injectors with the larvicidal preparation, to change the hypodermic needles, and to see that the injectors were relieved at regular intervals. This man is called the 'supplier.'

The efficiency of the injection system was tested by drawing blood samples for ChE-tests from three injectors and one supplier immediately before and after a three-hour treatment day. In every case, the ChE test showed that the injection system was leak proof.

Influenced by the obviously successful use of chutes for reindeer handling by Hadwen and Palmer (1922), we started with chute tests. Very soon it became obvious that our reindeer were disposed for panic reactions to a degree that appeared definitely hazardous to both man and animal. Consequently, we returned to traditional Scandinavian reindeer handling methods and experienced no further difficulties along this line.

Corral Arrangements

The common Swedish reindeer corral is circular shaped and has a diameter that corresponds to the number of reindeer usually rounded up in it. A funnel shaped fencing arrangement makes the entrance of reindeer easier. Commonly there are several separating pens attached to the outside perimeter of corral (Fig. 1A).

Using this corral as the basic design, several modifications were tested for treating purposes (Fig. 1B through F). Testing criteria included: rate of treatment by ordinary crew, number of injectors and catchers needed to maintain a minimum treatment rate, and stress to man and reindeer.

In arrangement B, treatment was made in the milling crowd of reindeer in the main corral without separating treated from untreated reindeer.

In arrangement C, treatment and separation of the animal were performed simultaneously. One crew was placed in each separating pen around the corral.

In arrangement D₁, the main corral was divided into two parts by cloth sacking stretched across the corral. The reindeer at the beginning were herded in one part and after treatment, were pushed under the sacking into the other part. As the number of untreated animals decreased, the sacking was moved so that the reindeer were kept close together.

In arrangement D₂, the reindeer after treatment were released into a resting pen outside the corral but the sacking was managed in the same way as in arrangement D₁.

Finally arrangements E, F₁ and F₂ were variations of the same scheme. One hundred to 400 reindeer were driven from the main corral into a smaller catch pen from which 1-3 gates led into a larger resting pen. A treating team consisting of one injector and one painter at each gate. In the small catch pen, the catchers roped the reindeer or caught them by the antler or a hind leg. The animal was drawn towards one of the gates where it was treated and

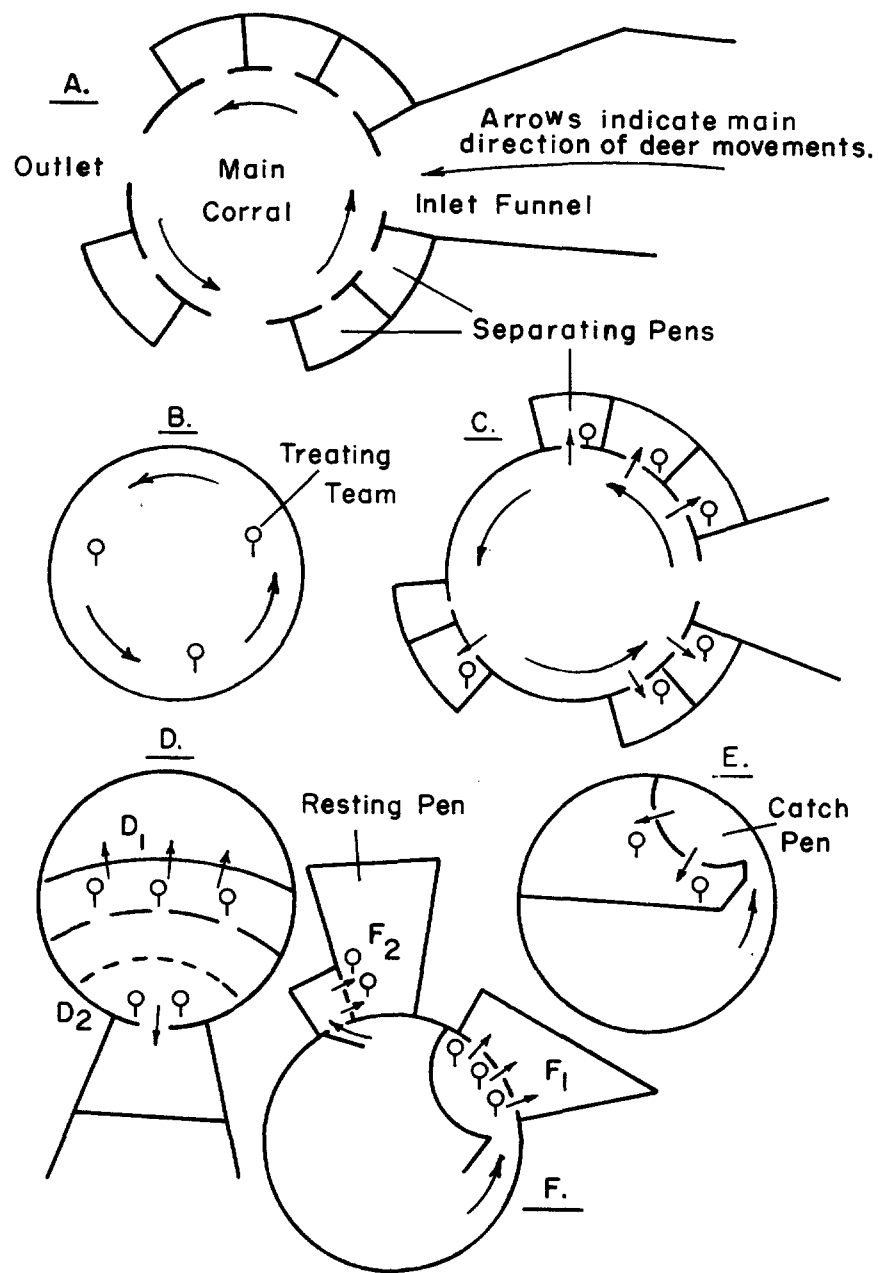


Fig. 1.—Corral arrangements.

then released in the resting pen.

RESULTS AND DISCUSSION

Corral arrangements. Arrangement B could only be used in bright daylight as the yellow brand was difficult to see when daylight faded or when in artificial light. Another disadvantage was the prolonged disturbance of the entire herd. Newly dyed reindeer often transferred some dye color to undyed ones when milling in the corral. This resulted in confusion in selected untreated reindeer. However, this arrangement was used successfully for smaller herds that could be treated during daylight hours.

Arrangement C was fully practicable except that it required a relatively large number of men. In practice, the several separating pens around the corral were often not fully occupied and the injectors had difficulty in keeping their equipment and solutions from freezing when not in use.

Arrangements D₁ and D₂ were only tested once but it was obvious that the reindeer, if startled, could easily stampede through the fence of cloth sacking and escape or mix with the other reindeer.

Arrangement E, F₁ and F₂ were the most satisfactory and therefore were the most thoroughly tested. Only a small part of the herd was disturbed by the treating measures at any one time; the main herd rested in the corral or, after treatment, in the resting pen. The number of teams could easily be changed according to the number of available catchers and thus the injectors occupied continuously.

The treatment. Using corral arrangements E, F₁ and F₂ (Fig. 1) the average treating rate was approximately 110 reindeer per injector hour. Early in the treating season, the animals were heavier and thus more difficult to handle than later in the winter. Thus the treating rate usually increased during the season. The treatment rate at different occasions throughout this study ranged from 90 to 200 reindeer per hour.

The injection work proved laborous and for that reason the injectors usually were relieved every second hour. Catching and dragging reindeer is a difficult job too, especially in deep early winter snow. In order to maintain a sufficiently high treating rate, four to five catchers were needed to supply each injector. In a small treating pen, two or three crews, each consisting of one injector and four to five catchers, were about maximum capacity. During the treating period, daylight hours were short and therefore it was important to illuminate the treating pens especially when larger herds were rounded up.

Finally, the vital importance of having access to warmed premises, e.g. tents, trailers, or houses, placed not far from treating pens has proved essential for the efficient operation of the treatment crews. Under above mentioned conditions the number of treatments, with three treating teams working side by side, averaged about 300 an hour, or, theoretically, about 2,500 a day.

CONCLUSIONS

Conclusions based on these large scale experiments may be summarized as follows:

1. Treating season: October-January
2. Corral arrangements: Types E and F are preferred since only a small part of the herd is disturbed for a relatively short time
3. Field crew: Four to six well-equipped injectors and four to six painters divided into two shifts, one supplier, one patrol leader and four to five catchers per injector
4. Climatic obstacles: Treatment during adverse weather conditions and especially during severe cold (below -25° C) should be avoided. At temperatures between -10° C and

-20° C special precautions must be taken to protect the solutions, syringes, etc. from cold damage. Measures that have proved effective include: open fires in or near the treating pens, insulation of bottles, tubing, etc., and frequent rotation of the treatment crew, especially the injectors.

ACKNOWLEDGMENTS

I wish to express my great gratitude to all those hundreds of people who have been involved in these field experiments, to those herdsmen particularly who labored as catchers and to those who developed great skill as injectors. A special thanks to Johannes Blind who has participated as a skilled supplier and man-of-all-work in most of these round ups. Finally I thank the Royal Agricultural Board for supporting my work. The work has been granted by The Swedish Council for Forestry and Agricultural Research, Labour Market Board and Department of Agriculture.

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ESOPHAGEAL AND RUMINAL FISTULIZATION OF REINDEER

R. A. Dieterich
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

ABSTRACT—A successful esophageal fistulization technique was employed in reindeer with long term survival. A fistula was produced by surgical incision in the mid cervical region over the esophagus with the esophagus being sutured to the muscle and skin lying above. Mechanical closure of the fistula when not in use was accomplished by using a plastic trough plug which was halved to facilitate insertion and removal. Diligent aftercare was required to prevent secondary infections or esophageal plugging with coarse foods. Rumen fistulization was carried out using a two step method. First the rumen was exteriorized through a 4 cm incision made in the upper left flank in the angle between the last rib and the transverse processes of the lumbar vertebrae. An external clamp held the rumen in position until the serosal surface of the rumen had healed to the peritonium, muscles and skin. After 10-14 days the exposed rumen above the clamp became necrotic and could be easily removed. A soft Jarrett type rubber cannula was placed into the fistula completing the preparation.

Esophageal and ruminal fistulization techniques have been employed for a number of years in nutritional and physiologic studies in domestic animals. These same techniques are now being adapted for use in wildlife. The successful application of fistulization techniques to wild ruminants is dependent on the use of well trained tractable animals and easily maintained mechanical devices for closure of fistulas when not in use. Several techniques have been developed and described for use on domestic animals (Bishop, 1970; Markowitz, 1959; Torell, 1954; Van Dyne and Torell, 1964). The purpose of this report is to describe the successful adaptation of these techniques to reindeer.

Esophageal Fistulization

Reindeer in good health and capable of being led by hand were used. A complete blood count (CBC) was determined preoperatively to be used as baseline data in the event of postoperative complications. The animals were denied access to feed for 24 hours and water for 12 hours before surgery. Reindeer were anesthetized with xylazine hydrochloride (Rompun, Chemagro Corp., Shawnee Mission, Kansas 66201) at a dosage rate of 0.75 mg/kg body weight and placed on their right side in lateral recumbency. The left side of the neck was clipped, cleaned, and painted with surgical antiseptic. Standard surgical sterile techniques were adhered to throughout the procedure. A 0.7 cm stainless steel rod equipped with a 2.5 cm plastic ball on its tip was introduced into the esophagus and positioned at the junction of the upper and middle third of the neck. Gentle pressure was applied to the rod so that the ball on the end of the rod in the esophagus protruded at the surgical site between the brachiocephalicus and sternocephalicus muscles. A 2 cm longitudinal incision was made over the ball through the skin and esophagus with a scalpel. One simple interrupted suture (Vetafil, Dr. Jackson, Washington, D. C. 20014) was placed through the skin and esophagus

on each side of the incision. The tails of the sutures were left long and used as retractors. Simple interrupted chromic cat gut sutures were then placed at approximately 0.5 cm intervals around the incision. Suturing was completed as soon as possible to prevent wound contamination with saliva or rumen contents. The finished fistula should be slightly smaller than the plug to insure a tight seal with minimal leakage. Nitrofurazone (Furacin powder, Eaton Laboratories, Norwich, N. Y. 13815) powder was applied to the surgical site and an esophageal plug inserted and secured. Esophageal fistula plugs were synthesized from acrylic plastic tubular and solid stock (Plexiglas, Rohmand Haas, Philadelphia, Pa. 19105). Adults should have a stem and trough diameter of 2.5 cm (Fig. 1); smaller reindeer require plugs with stem and trough diameters of 2 cm.

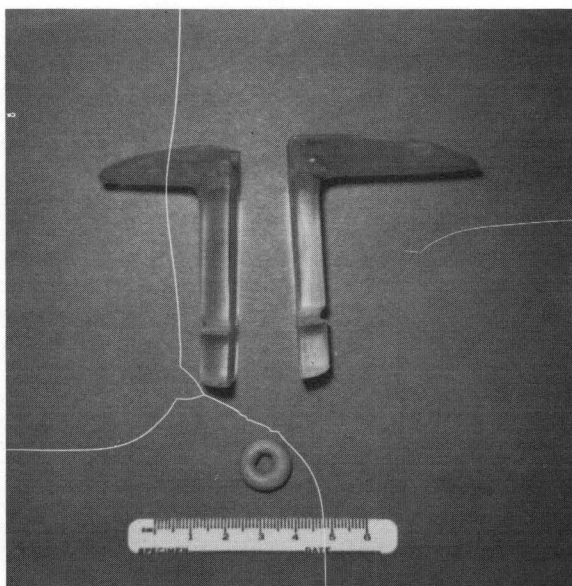


Fig. 1.—Esophageal fistula plug with retainer and elastrator ring.

Postoperative care included the administration of procaine penicillin G (1,000,000 I.U.) and dihydrostreptomycin sulfate (1.250 gm) daily for three days and the daily cleaning of the surgical site plus the application of nitrofurazone powder. Bacterial infections at the fistula sites were the most common postoperative complication encountered. *Corynebacterium pyogenes* was isolated from several of the local infections. The majority of these infections responded rapidly to cleaning and the administration of antibiotics. In the case of severe infections, good response was observed after parental administration of kanamycin sulfate (Kantrim, Bristol Laboratories, Syracuse, N. Y. 13201; 250 mg) twice daily. Approximately 15 to 20 days were required for the surgical site to heal and the animal to adapt to the presence of the esophageal fistula. After that time, collections can be initiated.

Routine maintenance was minimal after complete healing had occurred. When coarse feeds were given, blockage of the esophagus occurred unless a retainer was fitted over the stem of the esophageal plug to hold the trough of the plug against the wall of the esophagus. The retainer was held in place with an elastrator ring. Reindeer were given free access to mineral salt blocks to assure replacement of any minerals lost during sampling or from leakage around the fistula plug. Several months after the installation of the fistulas, an enlargement of the opening was observed in two reindeer allowing leakage of saliva and

food. The proper size of the fistula was regained by placing a purse string suture around the opening and drawing it closed to the correct dimensions.

Ruminal Fistulization

The same preoperative procedures were followed before ruminal fistulization as were used before esophageal fistulization. Reindeer were sedated with a tranquilizer (Acepromazine, Ayerst Laboratories, New York, N. Y. 10017; 0.4 mg/kg) and the area of the left flank clipped, cleaned, and painted with a surgical antiseptic. Lidocaine hydrochloride (Trico Pharmacentrical, San Carlos, Ca. 94070) was injected locally as an analgesic. The reindeer were allowed to stand during the procedure. A 50 cm barrier was placed between the front and rear legs of the animals to support them if they attempted to lie down. Standard surgical sterile techniques were used throughout the operation.

Rumen fistulization was carried out using a two step method (Hecker, 1967). First a 4 cm incision was made through the skin and subcutaneous tissues in the upper left flank in the angle between the last rib and the transverse processes of the lumbar vertebrae. Blunt dissection was used to enter the abdominal cavity. The rumen was exteriorized through this opening and held in place against the skin by an acrylic plastic clamp. One suture was placed through the skin, under the clamp, then through the skin on the opposite side and tied over the top of the clamp (Fig. 2). This suture held the skin against the serosal surface of the

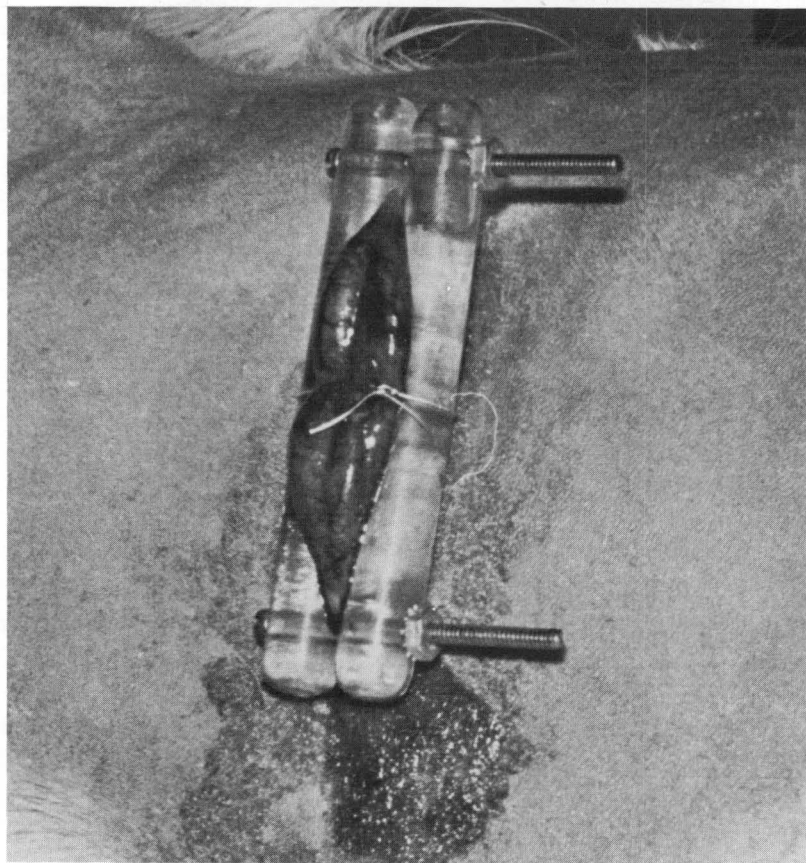


Fig. 2.—Rumen clamp secured in place with suture.

rumen. The clamp and suture were allowed to remain in place for 10-14 days. During this period the surface of the rumen healed to the peritonium, muscles and skin. The exposed rumen above the clamp became necrotic and was easily removed after healing was complete. A soft Jarrett type rubber cannula (South Australian Rubber Mills, Edwardstown, S. A. 5039 Australia) was then placed into the fistula sealing the opening and completing the preparation (Fig. 3). Sampling was accomplished by removing the plug in the rubber cannula and inserting or withdrawing material as needed.

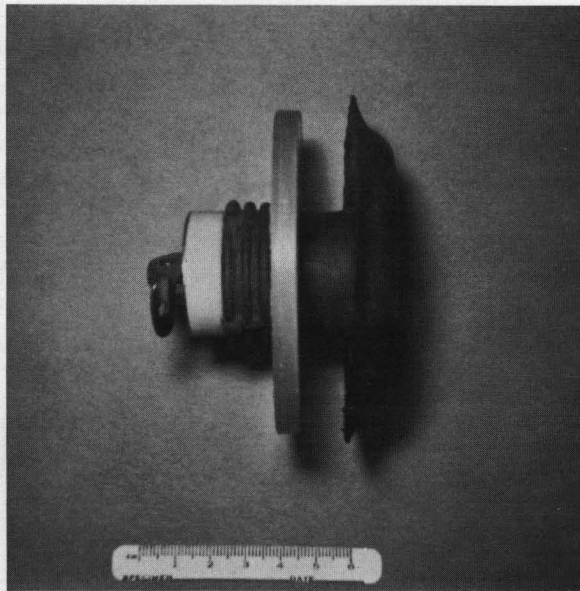


Fig. 3.—Rumen fistula cannula with outer retaining ring and plug.

Postoperative care was minimal with this preparation. Antibiotics were administered and the surgical wound cleaned daily as described for the esophageal fistulization. Once healing was complete, little or no after care was required and no adverse effects were seen in animals allowed to live outside at temperatures as low as -45° C. The plug for the rubber cannula was secured in place with wire to prevent accidental loss of rumen contents.

DISCUSSION

Esophageal fistulization was performed in six reindeer. One of the six died three days postsurgically due to tearing of the sutures and massive wound contamination with food and rumen contents. Functional fistulas were produced in the remaining five animals. The use of the technique described in this report was developed and improved with each reindeer esophageal fistulization. At the present time esophageal fistulas can be produced rapidly and with confidence of subject survival.

Ruminal fistulization was performed in nine reindeer. All animals survived and had functional rumen fistulas. Postoperative care was minimal on all animals. Ruminal fistulization was judged a much easier procedure than esophageal fistulization and required little after care.

ACKNOWLEDGMENTS

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**REINDEER WITH ESOPHAGEAL FISTULA IN RANGE STUDIES:
A STUDY OF METHODS**

S. Skjenneberg
Norwegian State Tame Reindeer Research Institute
Harstad, Norway

P. Fjellheim
Veterinarian College
Oslo, Norway

E. Gaare
Norwegian State Game Research Institute
Trondheim, Norway

D. Lenvik
Consultant of Reindeer Husbandry
Røros, Norway

ABSTRACT—Three reindeer (males, 1½ year) with esophageal fistulas were kept on four types of fall and winter pastures located from coastal to alpine regions. The plant cover of the ranges was described and the amount of each species expressed by the percentage cover. Collections from fistulas were taken on three successive days, giving nine samples from each locality. Saliva was removed by filtering. The samples were analyzed botanically and chemically.

No significant differences were found between animals when the samples were estimated chemically on localities with relatively homogeneous vegetation. These similarities were not found in the botanical estimation. A fourth locality with a heterogenous plant cover had a wider variation of the chemical composition, suggesting that the methods were valid on homogenous plant societies. The influence of saliva on chemical composition was determined in a separate study.

When saliva is removed, the fistula sample overestimates protein 17 per cent and ash by four times that in the pure reindeer lichen diet. For grass, the sample underestimates protein 16 per cent and overestimates ash by 120 per cent. The techniques of preparing and operating an esophageal fistula are described.

Approximately half of Norway is mountain pasture which is utilized by sheep and reindeer. Until recently, evaluation of these pastures, including measurements of productivity, has been based upon experience with range use by sheep only. Efforts directed towards estimating the value of the ranges for reindeer production have been limited by a lack of information on the grazing habits of reindeer.

The present paper outlines some of our efforts directed towards obtaining a description of range vegetation which would allow future calculations of the likely nutrients and energy available to reindeer. The paper describes priorities in the selection by reindeer of plant species on a given pasture and within a given season, late September to mid-November.

To overcome some of the complicating factors such as selection patterns in evaluating a

natural pasture from a botanical description (Hardison *et al.*, 1954; Meyer *et al.*, 1957), a method was used which allowed reindeer to select desired plant species and thus, to tell us how they perceive the pasture. Reindeer used in the range studies were fitted with esophageal fistulae as described for sheep and cattle (Torell, 1954; Van Dyne and Torell, 1964). Limitations in the interpretations of analysis of esophagus egesta were that saliva contamination affected the chemical analysis and analysis for species composition gives an instantaneous estimate of selection patterns on certain pasture types.

METHODS

Sampling localities. The Reindeer Research Station is situated at Hinnøya, Northern Norway and four grazing sites (A - D) were selected in the area. Geographical latitude is between 68°20' and 68°30' N.

Sites A, B and D lie 10-15 km apart in a granite area of the island Hinnøya, while C is 50 km east, on the mainland in a cambrosilurean area.

Animals were taken to the sites by motor transport.

Esophageal fistulation. Three male reindeer aged 1½ years were chosen for esophageal fistulation. After anesthesia (ataraxicum and local infiltration) a rubber hose was conducted down the esophagus to allow localization of the operation site on the left-hand side of the neck. A cutaneous incision was made slightly cranial to a line between the first and second one-third of the neck. Blunt dissection was used to locate the fistulae in a space between the sternocephalic muscle and the jugular vein, parallel and as close as possible to the vein. The esophagus was opened by a cut, 5 cm long, and the edges of the wound were sutured to the edges of the cutaneous wound. Special care was taken to suture both the muscle layers and the mucosal membrane of the esophagus to the skin. The fistula was closed by means of two, curved plastic plates, one inner and one outer tied together with a string. This arrangement could easily be adjusted to give the proper pressure. The inner plate was about 6 by 2½ cm, the outer one being a little larger. This method is similar to the one illustrated by Van Dyne and Torell (1964).

During this form of the operation, saliva and eructated fluids may cause contamination of the wound. This can be overcome by suturing the esophagus to the skin before it is opened. Some few days later it is opened. This simplifies the operation and gives a better healing of the wound.

This type of fistula closure demands daily care. Granulation, especially in the caudal angle of the fistula, decreased the size of the opening. There was also a necrosis of the tissue in the lower rim of the fistula, causing leakage. The conclusion of our experiences is that this type of fistula closure has to be improved.

Description of vegetation. Vegetation stands were described in 5-10 (or occasionally more) plots in each site. Percentage cover of each species was determined; unimportant mosses and crustaceous lichens were treated collectively. The stands were classified according to the phytosociological system of sociations, associations, alliances, etc., and their relative amounts determined by line transects.

Sampling protocol. Esophageal fistula egesta, plant material plus saliva, was collected in plastic-coated canvas bags attached to the neck of animals (Fig. 1). Towards the end of a collection period mixed contents sometimes spilled over the anterior rim of the bags when the animals were grazing downhill. The use of non-waterproof material in the construction of the bags could assist in separating saliva and forage and would minimize such losses.

During experiments the three esophageal fistulated animals were grazed with a very tame 2½ year old castrate and a female calf. The tame castrate acted as a group leader and was tied in the middle of the sampling site. Fistulated members of the group were allowed to

graze freely within the borders of the site. Each animal was equipped with a long nylon line which made them easy to catch whenever necessary.



Fig. 1.—Esophageal fistulated reindeer grazing with bag for collecting esophageal ingesta.

All three esophageal fistulated animals were sampled on three successive days on each site. Hence, the nine samples collected on each site gave some opportunity to study the variation between animals and between days. The sampling time was adjusted to the normal grazing rhythm of the reindeer. The morning period proved best as the animals grazed more eagerly at this time. Each period lasted about one hour. Toward the end of a grazing period, care had to be taken as contamination by eructated rumen contents had to be avoided. Contaminated samples were rejected.

After collection, all samples were screened through a 100 mesh screen without squeezing. The 'dry' sample was divided into two subsamples; one small sample was used for botanical analysis; the other sample was kept for chemical analysis. Pollution of the sample

by reindeer hair was frequently a problem during early winter; hairs were removed before sieving the sample.

Between sampling periods, animals were kept at the Reindeer Research Field Station at Harstad and were fed a mixed ration consisting of ground hay, straw, flour and minerals. The chemical composition (per cent of dry matter) of this ration was: crude protein, 9.6; crude fat, 2.6; nitrogen-free extract (NFE), 52.4; crude fiber, 18.8; and ash, 5.9. In addition, the animals were allowed to graze for about two hours daily. No digestive disturbances were noted when the animals were taken from the artificial feed to the natural pasture. During the trial period animals declined slightly in body weight. For future experiments we recommend a feed be used which is of higher digestible carbohydrate and lower crude fiber content.

Chemical analysis. All samples were treated as a standard feedstuff; analyses were made for crude protein (as Kjeldall N x 6.25) fat (ether extract) crude fiber, NFE, ash, calcium and phosphorus.

Botanical analysis of the fistula samples. The relative amounts of plant species present in a sample were determined by a 200 point analysis using a stereomicroscope with paracratic optics (10-40). In most cases determination of species was possible, but at times a point reading had to be referred to one of the following groups, woody plants, graminoids, herbs, mosses or lichens. The readings were converted to per cent without any adjustment for variances between densities of different plant species. According to Gaare (1968) the relative dry weight of woody plants in rumen content are underestimated and grasses overestimated this way. We suggest that other errors inherent in the technique are sufficiently large as to justify no sophisticated correction for this bias.

RESULTS AND DISCUSSION

A strong synchrony in grazing behavior was noted, all animals started and stopped grazing nearly simultaneously. Since no differences were noted between the fistulated and non-fistulated animals in the duration of the grazing period, it is suggested that filling of the rumen apparently had no influence upon the feeling of satiation.

The chemical composition of fistula samples is shown in Table 1. Further discussion is confined to the discussion of each study site.

The forage samples were contaminated with saliva as the samples were collected in water-tight bags.

To gain some insight into the effects of this contamination on the chemical composition of the egesta, reindeer were given the following feeds, of known chemical composition, for comparison with the composition of the esophageal fistula egesta:

(a) mixture of *Cladonia arbuscula* and *Cl. rangiferina*.

(b) handclipped aftermath of *Phleum pratense*. Three esophagus fistulated animals were given 500 g of forage (a) on two successive days. Forage (b) was given once to each animal. All samples of the same fodder type were analyzed together and the results are shown in Table 2.

The consistence of the (b)-type egesta allowed squeezing through a screen and the dried sample was analyzed separately from the out-squeezed fluid.

In both cases we see that the ash content of the egesta was increased compared with the original fodder.

In the second (b) treatment, the fluid shows the largest difference. The ash content of the squeezed sample was similar to the fodder.

The protein content was increased in the first (a) treatment from 2.3 in fodder to 2.7 (g/100 g DM) in the egesta. Screening fluid from the grass egesta (b) lowered the protein

content from 7.6 g/100 g in fodder, to 6.4 g/100 g in the egesta. Much protein was apparently removed with the saliva and mixed fluid.

TABLE 1.--Chemical composition of esophageal fistula samples
(expressed as g/100 g dry matter).

	Animal No.	Crude Protein	Fat	Crude Fiber	NFE	Ash	Ca	P
SITE A:								
	3/67	11.4	2.5	24.4	51.2	8.2	0.33	0.39
	48/67	6.3	1.3	29.1	55.5	5.4	.20	.22
	101/67	13.2	2.8	24.2	50.7	7.0	.37	.38
Mean		10.3	2.2	25.9	52.5	6.9	.30	.33
S.D.		3.9	0.7	3.7	4.6	1.6	.11	.11
SITE B:								
	3/67	3.3	1.3	32.5	59.2	3.6	.13	.10
	48/67	3.5	1.5	31.3	60.1	3.5	.13	.13
	101/67	3.9	1.6	32.8	58.5	3.3	.12	.12
Mean		3.6	1.5	32.2	59.3	3.4	.13	.12
S.D.		0.6	0.2	1.8	1.9	0.6	.01	.03
SITE C:								
	3/67	3.8	0.9	35.0	57.0	3.3	.13	.12
	48/67	3.3	1.0	35.5	56.5	3.7	.14	.15
	101/67	3.4	1.1	34.6	57.1	3.7	.13	.12
Mean		3.5	1.0	35.0	56.9	3.6	.13	.13
S.D.		0.5	0.3	1.2	1.2	0.4	.01	.03
SITE D:								
	3/67	5.4	1.0	23.1	62.9	7.6	.22	.28
	48/67	4.1	0.9	22.3	65.6	7.3	.19	.21
	101/67	5.5	0.6	20.5	66.5	6.9	.20	.24
Mean		5.1	0.8	22.0	64.9	7.2	.20	.24
S.D.		0.9	0.2	2.0	2.4	0.6	.01	.05

S.D., Standard deviation; NFE, Nitrogen-free extract.

We conclude that for accurate analyses, both saliva and fodder should be collected and analyzed together. However, separate analysis of saliva for chemical composition is needed to correct these values. For less accurate studies we suggest that fistula samples could be collected in nylon bags which allow the fluid to drip off. The length of the collection period should be standardized to secure comparable results.

TABLE 2.--Effect of saliva on the chemical composition (g/100 g DM) of forage. Mean of 3 experiments with (a) *Cladonia* mixture and (b) *Phleum* aftermath.

	Lichen (a)	Grass (b)
Dry matter intake (g)	281	72
Saliva contamination (g/g DM)	3.4	9.1
Ash content of forage	0.8	9.4
" " of fistula sample	3.4	
" " of squeezed fistula sample		11.0
" " of outsqueezed fluid		31.8
Protein content of forage	2.3	7.6
" " of fistula sample	2.7	
" " of squeezed fistula sample		6.4
" " of outsqueezed fluid		22.1

SITE A:

Description. This site, of 50 x 25 m, was a low-alpine reindeer pasture typical for the summer and fall seasons. The granite ground and the high precipitation, 1500 mm a year, had a marked influence upon the vegetation which was a conglomerate of snowbeds, grass and dwarf bush heaths. Twelve sociations were present and could be classified into six different alliances (Table 3). Grasses and sedges played a prominent role in most of the stands, *Deschampsia flexuosa* and *Carex bigelowii* being most important. All stands were dominated by mosses, lichens were unimportant. The more important plant units are shown together with results from the study of fistula samples in Table 4 and Appendix 1.

Grazing (September 29–November 1). There was a tendency of the animals to selective grazing. One of the animals used the *Phyllodoce-Myrtillion* heath the first two days when it evidently selected lichens. The two other animals preferred the typical snowbed. The third day there was more variety in the grazing suggesting that the animals were becoming a little bored by the same area.

Botanical and chemical analysis of fistula samples. Table 4 shows that the reindeer consumed mainly grasses and herbs and also a selection for lichen.

The great variation in choice of plants is evident also in Appendix 1. Animal No. 48/67 which consumed most lichen had a low content of protein in the samples during the first two days. On the third day however, the protein content was similar to the other individuals. This corresponds to some extent with the intake of lichens.

SITE B:

Description. This site (100 x 25 m) was situated 200 m from the seashore, at an elevation of approximately 15 m. It is a late fall and early spring pasture. The landscape was a mixture of fens and knolls with heaths and large rock outcrops. Pine and small birches grew scattered in a heath dominated by *Calluna* and *Empetrum hermaphroditum*. A line transect of 212.7 m showed dominance by a *Calluna-Empetrum* sociation (Table 5). In the *Calluna* heath mosses, *Pleurozium* and *Hylocomium* sp. were abundant, lichens *Cladonia*

sp. were sparse (Table 6, Appendix 2). Lichen were also sparingly present in the *Rhacomitrium* mounds.

TABLE 3.--Site A; Relative amount of plant communities determined by line transect (396.2 m).

Ref.	Plant Community	%
	PHYLLODOCO-MYRTILLION	20
250	<i>Vaccinium uliginosum</i> - <i>Dicranum</i> soc.	(7)
251	<i>Vaccinium myrtillus</i> - <i>Rhacomitrium lanuginosum</i> soc.	(13)
	NARDO-CARICION BIGELOWII	47
252	<i>Deschampsia flexuosa</i> - <i>Rhacomitrium lanuginosum</i> soc.	(23)
254	<i>Deschampsia flexuosa nudum</i> soc.	(11)
	<i>Nardus stricta</i> soc.	(4)
255	<i>Carex bigelowii</i> - <i>Lophozia alpestris</i> soc.	(8)
	<i>Sibaldia procumbens</i> - <i>Carex bigelowii</i> soc.	(1)
	LACTUCION ALPINI	8
	<i>Salix phylicifolia</i> - <i>Deschampsia flexuosa</i> soc.	(7)
	CASSIOPO-SALICION HERBACEAE	14
256	<i>Salix herbacea</i> - <i>Orthocaulis floerki</i> soc.	(14)
	CRYPTOGRAMMO-ATHYRION ALPESTRIS	9
	<i>Athyrium alpestre</i> soc.	(9)
	POLYTRICHION NORVEGICI	1
	BOULDER	3

TABLE 4.--Site A: Comparison of plant group composition of range with esophageal fistula samples.
(See Appendix 1 for individual species analysis.)

Plant group	Vegetation (% cover)	Esophageal sample (% of 200 points)*
Woody plants	21	8 (3.8)
Graminoids	31	47 (15)
Herbs	7	16 (9)
Mosses	45	2 (0.6)
Lichens	0.9	27 (20)

*Value in parenthesis is the standard deviation.

The site included also a small part of a fen area, mostly occupied by a *Scirpus caespitosus* sociation with a dense cover of peat mosses, *Sphagnum*.

Grazing (October 10-12). During the first day, animals chose the ridge with some short visits to the *Calluna* heaths between the rocks. The second day they grazed mostly on the northern slope with the *Calluna* heath. The third day they seemed to be more restless.

Partly they used the *Calluna* heath, but made some short visits to the fen where they evidently searched for water in the small puddles.

TABLE 5.--Site B: Amount of plant communities determined by line transect (212.7 m).

Plant community	% abundance
<i>Calluna</i> - <i>Empetrum</i> sociation	59.8
<i>Racomitrium lanuginosum</i> mounds	22.1
Rock covered with crustaceous lichens	18.1

Botanical and chemical analysis of fistula samples. As shown in Table 6 there was a strong preference for reindeer lichens. We also noted a high percentage of mosses in the egesta samples. As mentioned, *Cladonia* spp. occur only in dense moss carpets or tufts on this site. We believe that most of the eaten mosses, *Racomitrium* and *Pleurozium*, followed involuntarily with the intake of the highly preferred lichens. Mosses are, however, evergreen plants and may have a higher nutritive value than the available dried grasses and herbs at this time. The botanical picture of the fistula samples from this site showed much less variation than from site A and this observation corresponded with the more homogeneous plant cover on the site.

TABLE 6.--Site B: Comparison of plant group composition of range with esophageal fistula samples.
(See Appendix 2 for individual species analysis.)

	Vegetation cover (%)	Esophageal sample (% of 200 points)
Woody plants	85 (27)	8 (3.5)
Graminoids	0.4 (1.3)	0.3 (0.6)
Mosses	25 (13)	12 (6.7)
Lichens	6 (7)	79 (10)
Litter	13 (14)	0

Value in parenthesis is the standard deviation.

Chemical analysis of fistula samples. A striking homogeneity was also noted in the chemical composition of the egesta from this site (Table 1). It is very difficult to find a correspondency between the amount of plant groups and the content of crude protein in the fistula samples. However, it must be emphasized that the point-score method of estimating the amount of dry matter from different plants in fistula samples is not free of bias (Gaare, 1968).

SITE C:

Description. This locality (50 x 20 m) was situated on the mainland in the low-alpine belt at an altitude of 360 m. It is usually pastured with reindeer during the late fall and winter. The site was lying in a south exposed mountain slope, and was a low east-west directed, rocky ridge, with a slight slope towards north-east. To the south the site ended

with a steep slope where an outcrop of bedrock was covered with crustaceous lichen communities. Northwards, soil depth increased gradually and the vegetation growth was in zones oriented vertically with the increasing soil-water content. A progression in plant types was also noted; at lower elevations rocks were covered with *Racomitrium lanuginosum* moulds with some few reindeer lichens, followed by a heath dominated by *Empetrum hermaphroditum* (Table 7, Appendix 2). The northern rim was a *Scirpus caespitosus* fen with

TABLE 7.--Site C: Comparison of plant group composition of range with esophageal fistula samples.
(See Appendix 2 for individual species analysis.)

	Vegetation cover (%)	Esophageal sample (% of 200 points)
Woody plants	20 (14)	16 (5)
Graminoids	3 (6)	1 (1.4)
Mosses	60 (18)	8 (2.4)
Lichens	17 (21)	4 (4)
Litter	12 (9)	0

Value in parenthesis is standard deviation.

some *Eriophorum angustifolium* in the wettest parts. The tops of hummock fields, caused by frost action, were covered with *Empetrum* heath. Because of the gradually changing water conditions the dwarf-bush heath, *Empetrum hermaphroditum* — *Pleurocium schreberi* sociation, was heterogenous.

Grazing (October 23–25). During the trial, there was a very fluffy snow cover of 1/3 – 1 m thickness. The animals grazed nearly the entire period within a small part of the site dominated by *Empetrum* heath. Occasionally they grazed the tops of the small hummocks in the fen.

Botanical and chemical analysis of fistula samples. Table 7 shows a pattern of intake with a high concentration of lichens which is common for this season. Green plants or plant parts were also slightly preferred. Among the dwarf bushes, crowberry was the main one eaten. There was remarkably little variation between animals or days in plant species intake. This was probably due to the snow cover which limited the possibilities for selecting food.

Similar to the botanical analysis the chemical composition of egesta sample was also homogeneous with respect to between animals and between days (Table 1). Taking into consideration the influence of saliva contamination, as discussed above, the content of crude protein for reindeer lichen with a 30 per cent content of other plants was similar to that from Site B. The lower content of lichens in samples from Site C has thus not increased the content of crude protein and ash compared to Site B.

SITE D:

Description. This was a special site located only a few meters from the sea on the south end of Hinnøya Island and at an altitude of 15-35 m. It consisted of a knoll with many projecting rocks, the space in between being covered with heath communities. The rocks were mostly steep (inclinations of 60-70°) but they were seldom more than 2 meters high. On the rocks the vegetation was dominated by a *Parmelia omphalodes* sociation (Table 8, Appendix 3). The heath vegetation was mostly an *Empetrum* - *Pleurozium schreberi* sociation. Small ponds with mire-vegetation were common. Reindeer lichens, *Cl. mitis* and

Cl. uncialis, were few being confined to patches of *Rhacomitrium lanuginosum*. The lichen carpet was collected from 20, 500 cm² plots (totally covered with lichen) and a lichen biomass of 736 g dry matter/m² was noted. Determination of the ash content gave 7.9 per cent even after removal of visible mineral particles.

TABLE 8.--Site D: Comparison of plant group composition of range with esophageal fistula samples.
(See Appendix 3 for individual species analysis.)

	Vegetation cover (%)		Esophageal sample
	rock	ground	(% of 200 points)
Woody plants		90	2 (0.8)
Graminoids		3	2 (0.6)
Herbs		1	0.0 (0.0)
Mosses		42	6 (1.9)
Reindeer lichens		0.0	7.5 (2.6)
Fruticose lichens	2 (1.7)		22 (6)
Folious lichens	61 (17)		60 (9)
Bare rock	34 (12)		

Value in parenthesis is the standard deviation.

Line transects showed that 57 per cent of the rock surface was covered by the *Parmelia omphalodes* sociation, another 19 per cent of various communities of crustaceous lichens, the rest, 24 per cent, was bare rocks. The latter was probably due to grazing. Thus, more than 80 per cent of the rock surface was useful lichen grazing.

Grazing (November 19-21). Reindeer showed little interest in the ground vegetation grazing almost exclusively on lichens on the rocks (Table 8). The animals seemed thirsty and visited the small ponds frequently.

Botanical and chemical analysis of fistula samples. The samples reflect observed grazing patterns. Table 8 shows that nearly 90 per cent of the intake was lichen sociation from the rock. The 7.5 per cent content of reindeer lichen was accompanied by a moss content of 6 per cent. Again it seems obvious that the intake of mosses like *Rhacomitrium lanuginosum* and *Pleurozium* followed the intake of reindeer lichen in places where lichens grow only in a moss carpet. Among the lichens growing on the rock, a preference was noted for the fruticose *Alectoria pubescens*. Together with *A. chalybeiformis*, *A. pubescens* has a branched thallus which protrudes from the mat; they are probably easy to nibble and thus, dominate the egesta sample.

There was little variation in the chemical content of the samples (Table 1). The mean crude protein of 5.1 per cent was higher than expected from the botanical analysis, as the *Parmelia omphalodes* sociation was characterized as having a 2.3 per cent crude protein. This higher protein content could be due to saliva contamination or the moss content. Also, impregnation of plants with sea water and intake of guano from bird resting places and of green grasses characteristic of this climate, may result in increased protein intake.

The records of the chemical and botanical composition of the esophageal fistula samples show a variation caused by either differences in the individual grazing habits or by differences in plant composition from site to site. With this limited amount of data based on three animals only, a sophisticated statistical analysis was not justified. Thus, calculations of significance levels have been carried out based on Students t-test.

No significant differences were noted in the chemical composition of egesta between animals on the same site. Except for Sites B and C, which were homogeneous with respect to chemical composition, between site differences were significant on the 0.1 per cent or 0.5 per cent level for all nutrients. On the other hand, botanical composition of the samples showed variation between both individuals and sites; this was removed when groups of plants (e.g. lichens, mosses, etc.) were used for comparisons of differences between animals on the same site. Our experiments indicate that all three animals exhibit similar intake of nutrients with a different intake of plant species.

When a reindeer selects food the choice can be divided into three different levels: (a) area, (b) plant community and (c) plant species or parts of plants (Gaare *et al.*, 1970). In our trials the choice is nearly restricted to (c) except on Site A which was a conglomerate of plant communities. Our conclusion is that the present protocol is suitable for describing the choice of plants made by reindeer within one community.

The choice of community may be studied in other ways particularly by visual observation of unrestrained domestic or wild animals, recording the time they graze on each community. Such a study of community selection (Gaare and Skogland, unpub. observations) will be published in the future.

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Authors: S. Skjenneberg, P. Fjellheim, E. Gaare and D. Lenvik.

APPENDIX I

Site A: comparison plant composition of vegetation with fistula samples

Ref. no. Line transect (%) No. plots/sample	Vegetation % cover							Fistula samples % of 200 points			
	250	251	252	254	255	256	MEAN ¹	3/67	48/67	101/67	MEAN
	7	13	23	11	8	14		3	3	3	
	5	5	10	7	10	5					
WOODY PLANTS	50	38	7	0.1	14	34	21.0	2.8	11.3	10.2	8.1
Betula pubescens									0.3	1.0	(0.4)
Empetrum hermaphr.	10	13				0.0	(3.2)		0.3		(0.1)
Juniperus communis			0.0								
Salix glauca leaf										0.5	(0.2)
Salix herbacea	0.1	1	7	0.1	11	34	(9.7)	1.7	4.2	2.2	(2.7)
Salix phylicifolia					3				0.2	5.8	(2.0)
Vaccinium myrtillus	6	24	0.0				(4.7)	0.2	4.5	0.2	(1.6)
Vaccinium uliginos	34						(3.1)				
Undetermined								1.0	1.8	0.5	(1.1)
GRAMINOID	7	2.6	43	88	30	4.4	30.8	55.8	26.5	59.2	47.2
Agrostis borealis			0.2	6.0	4.1						
Anthoxan. odoratum		0.2	12	0.6	0.2	1.6	(4.1)	0.2		0.3	(0.2)
Calamagrostis purp.				22				3.7	3.0	1.0	(2.6)
Carex bigelowii			0.0	0.2	20		(2.2)	3.2		0.2	(1.1)
Carex canescens			0.2								
Carex lasiocarpa					1.5						
Carex oederi				0.1							
Carex sp.								7.5	4.7	10.0	(7.4)
Deschampsia flexu.	7	2.4	31	59		2.5	(23.6)	26.0	16.2	34.7	(25.6)
Festuca sp.								9.0	1.3	7.8	(6.1)
Juncus filiformis					0.0						
Juncus trifidus								0.5			(0.2)
Nardus stricta					3.4						
Phleum commutatum			0.0	0.1	0.2	0.0		2.2	0.7	1.3	(1.4)
Poa cf. glauca								0.7	0.3	0.7	(0.6)
Scirpus caespitosus					0.0						
Undetermined								3.0	0.3	3.2	(2.2)

Appendix I (continued)

Ref. no. Line transect (%) No. plots/sample	Vegetation % cover						MEAN ¹	Fistula samples % of 200 points			MEAN
	250	251	252	254	255	256		3/67	48/67	101/67	
	7	13	23	11	8	14		3	3	3	
	5	5	10	7	10	5					
HERBS	10	3.5	6.7	7	2.4	13	7.2	26.5	5.5	17.2	16.4
<i>Alchemilla alpina</i>		2	1.9		1.4			1.3	0.2		(0.5)
<i>Cerast. cerastoides</i>			0.0								
<i>Chamaenerion angus.</i>			0.0								
<i>Cornus suecica</i>	10										
<i>Cystopteris fragil.</i>								1.0		0.2	(0.4)
<i>Epilobium horneman.</i>			0.0		0.0	0.0		0.5	0.3		(0.3)
<i>Epilobium sp.</i>								0.3			(0.1)
<i>Gnaphalium norvegic.</i>			0.2	0.1		0.1		6.2	1.2	4.7	(4.0)
<i>Gnaphalium supinum</i>			0.6			2.4		1.0			(0.3)
<i>Hieracium alpinum</i>			0.2								
<i>Leontodon autumnal</i>			0.0	0.1	1.2	0.4					
<i>Lycopodium alpinum</i>	0.0										
<i>Melampyrum silvatic</i>	0.1	0.2	0.1								
<i>Polygonum viviparum</i>	0.1	0.4	0.3	0.3	0.4	0.7			0.8	1.7	(0.8)
<i>Pyrola minor</i>		0.2	0.1								
<i>Ranunculus acris</i>			0.0	0.1				0.5		0.2	(0.2)
<i>Rumex acetosa</i>			1.5	1.6	0.3					0.2	(0.1)
<i>Sibbaldia procumbens</i>			0.0			5		0.7			(0.2)
<i>Solidago virgaurea</i>	0.1	1.2	2.3	1.7		0.0		2.3	0.5	1.8	(1.6)
<i>Taraxacum sp.</i>						0.0					
<i>Trientalis europaea</i>	0.02	0.5	0.2	0.3				2.3		0.5	(0.9)
<i>Veronica alpina</i>						0.0		0.2			(0.1)
<i>Viola biflora</i>			0.2	0.7	0.4	0.5					
Undetermined								8.5	2.5	7.7	(6.2)
MOSSES ²	44	42	44	2	47	82	44.9	1.7	3.0	1.7	2.1
<i>Calliergon sarment.</i>									0.2		(0.1)
<i>Campyllum stellatum</i>			2			30					
<i>Dicranum sp.</i>								0.2	1.0	0.2	(0.5)
<i>Dicranum fuscescens</i>	40	6	2	0.1							
<i>Drepanocladus uncin.</i>			0.0	0.4	5			0.3	0.2	0.7	(0.4)
<i>Orthocaulis floerkii</i>	0.2		30	0.2		45		0.5	0.2		(0.2)
<i>Racomitri. canesc.</i>			5								
<i>Racomitri. lanugin.</i>		35									
<i>Racomitri. sp.</i>								0.6	1.0	0.4	(0.6)
<i>Sphagnum rubellum</i>					3						

Appendix I (continued)

Ref. no.	Vegetation % cover						MEAN ¹	Fistula samples % of 200 points			
	250	251	252	254	255	256		3/67	48/67	101/67	MEAN
Line transect (%)	7	13	23	11	8	14					
No. plots/sample	5	5	10	7	10	5		3	3	3	
LICHENS ³	6	0.4	0.6		0.5		0.9	13.5	55.6	11.7	26.9
Cladonia sect. Clad.	3.3	0.9	0.1		0.2		(0.5)	7.9	43.3	7.7	(15.4)
Stereocaulon pasch.	0.5	0.2					(0.1)	2.5	5.7	2.7	(3.6)
Humus	0.6		0.2								
Stone			3.0	0.8	6						

¹This mean is weighted by the line transect scores.

²About 25 mosses were determined, only the most important ones are noted here.

³About 15 lichen species were found, mostly Cladonia sp.

APPENDIX II

Site B and C: composition of vegetation and fistula samples.

Animal number Numb. pl/samp.	SITE B							SITE C						
	Vegetat.		Fistula samples					Vegetat.		Fistula samples				
			3	48	101					3	48	101		
	14		67	67	67	MEAN		20		67	67	67	MEAN	
	MEAN	S.D.	3	3	3			MEAN	S.D.	3	3	3		
WOODY PLANTS	85	27	9.2	9.5	6.0	8.2		20.0	14	12.3	17.2	17.3	16.2	
Betula pubes.	0.1									1.0	2.8	2.7		
Populus trem.	0.1													
Sorbus aucup.	0.1													
Andromed. polif.	0.3	0.5	1.8	1.0	1.2	1.3		0.6	0.4	1.0	2.8	2.7	2.2	
Arctostaph. alp.	1.2	2.4						1.1	2.9			0.2	0.0	
Arctostaph. uva-ursi												0.2	0.0	
Betula nana								2.2	3.8	2.2	5.0	4.0	4.1	
Calluna vulgar.	41	26	5.5	6.3	2.8	4.9		0.3	1.1					
Empetr. hermaph.	40	25	1.2	2.0	1.7	1.7		11.7	9.2	6.8	7.8	10.7	8.4	
Juniper. commun.	0.3	1		0.2	0.2	0.1								
Loiseleur. proc.								1.5	5.5		0.7		0.2	
Lycop. cl. selago	0.0							0.0						
Phyllod. coerul.														
Salix herbacea												0.5	0.2	
Salix sp.			0.2			0.1								
Vaccin. myrt.	0.7	1.2						0.2	0.5	1.2		0.8	0.2	
Vaccin. uligin.	1.1	3.0						1.7	2.1					
Vaccin. vitis-ida.	0.4	0.4	0.3			0.1		0.7	7.2	0.2			0.0	
GRAMINOIDS	0.4	1.3	0.2	0.8		0.3		3.2	6					
Deschamp. flexu.	0.1	0.3						0.0						
Eriophor. angus.	0.0		0.2			0.1								
Eriophor. vagin.								0.0						
Festuca ovina								0.0						
Juncus trarifid.								0.0						
Nardus stricta	0.3	1.0												
Scirpus caesp.	0.0							3.2	6.7					
Undetermined				0.8		0.3				2.0	1.2	0.7	1.3	

Appendix II (continued)

Animal number Numb. pl/samp.	SITE B						SITE C					
	Vegetat.		Fistula samples				Vegetat.		Fistula samples			
	14 MEAN	S.D.	3 67	48 67	101 67	MEAN	20 MEAN	S.D.	3 67	48 67	101 67	MEAN
			3	3	3				3	3	3	
HERBS	0.2	0.5					0.1	0.2	0.0			
<i>Cornus suecica</i>	0.1	0.3					0.0			0.2		0.1
<i>Dactylor. macul.</i>	0.1	0.3										
<i>Potentilla erect.</i>	0.0											
<i>Rubus chamaem.</i>							0.0	0.2				
MOSSES	25	13	10.5	16.5	10.0	12.3	59.6	18.1	6.0	7.2	9.3	7.5
<i>Dicranum mont.</i>	7	7					24.0	22.0				
<i>fuscescens</i>												
<i>Orthoc. floerkii</i>				0.3		0.1						
<i>Pleuroz. schreb.</i>	13	13	4.1	5.8	5.5	5.3	16.2	18.5	3.3	5.8	5.7	4.9
<i>Polytricum sp.</i>							0.0		0.2	0.3	1.2	0.3
<i>Ptilid. ciliare</i>	0.7	0.4	1.8	1.3	1.0	1.4	18.5	22.1	1.6	1.0	2.0	1.5
<i>Racomit. lanug.</i>	5	8	4.2	8.5	3.5	5.4			1.2		0.5	0.6
<i>Sphagnum nemor.</i>	0.0						0.9	3.3				
LICHENS	6	7	80.3	73.2	83.5	79.1	17.2	20.9	78.3	74.5	69.3	74.7
<i>Cetr. delisei</i>							0.3	0.4				
<i>Cetr. islandica</i>				1.0	0.7	0.3	0.0		6.0	0.8	2.5	3.2
<i>Cetr. nivalis</i>							0.0					
<i>Clad. alpestris</i>			0.8	2.0		0.9						
<i>Clad. mitis</i>	2.1	3.1	42.9	36.0	37.3	38.8	1.7	9.1	12.3	14.3	14.3	13.5
<i>Clad. rangifer.</i>	3.9	5.2	2.5	1.5	0.5	1.5	13.6	20.4	0.3		0.3	0.2
<i>Cl. sect. Cladina</i>												
Undetermined ²			33.2	33.0	45.5	36.6			56.0	53.9	51.2	53.7
<i>Cl. bellid.</i>												
<i>Cl. burcata</i>												
<i>Cl. gracil.</i>	0.1	0.2					0.2	0.9				
<i>uncial.</i>	0.2	0.5					0.2	0.4				
<i>Nephroma arctic.</i>	0.1	0.4					0.9	2.2				
<i>Stereoc. pasch.</i>							0.3	1.1	4.5	5.2	2.7	4.1
Reind. hair									0.3			0.1
Litter	19	14					12.1	9.3				

¹ mostly leaves.² most of the material is probably *Cladonia mitis*.

APPENDIX III

Site D: composition of vegetation and fistula samples.

	VEGETATION		FISTULA SAMPLES			
Animal number	Rock	Ground	3	48	101	
Number plots/samples	6	12	67	67	67	
	MEAN	S.D.	3	3	3	MEAN
<hr/>						
WOODY PLANTS		90	2.0	2.2	0.5	1.6
Betula pubescens		7				
Juniperus communis		1				
Populus tremula		0.0				
Sorbus aucuparia		0.0				
Arctostaphylos alpina		10				
Calluna vulgaris		7	0.8	0.7	0.7	0.7
Empetrum sp.		60	1.0	1.3		0.8
Vaccinium myrtillus		1	0.2			0.1
Vaccinium uliginosum		1				
Vaccinium vitis-idaea		3		0.2		0.1
Graminoids, mostly		3	2.2	2.5	1.0	1.9
Deschampsia flexuosa						
Carex nigra etc.						
HERBS, 12 species		1				
MOSSES		42	7.0	7.0	3.3	5.9
Pleurozium schreberi		40	2.2	2.8	0.8	1.9
Ptilidium ciliare			0.3			0.1
Racomitrium lanuginosum		2	4.5	4.2	2.5	3.9
LICHENS	63.2	0.0	88.7	86.5	94.2	89.8
Fruticous lichens	2.0	1.7	0.0	25.3	39.5	24.7
Alectoria chalybeiformis	0.0					
Alectoria pubescens	1.4	1.5	12.3	28.3	16.7	19.1

Appendix III (continued)

Animal number	VEGETATION		FISTULA SAMPLES				
	Rock	Ground	3	48	101		
Number plots/samples	6	12	<u>67</u>	<u>67</u>	<u>67</u>		
	MEAN	S.D.	3	3	3	MEAN	
Cladonia sect. Cladina			0.0	9.7	9.0	3.8	7.5
Ramalina subfarinacea	0.0			2.5	2.2	3.2	2.6
Sphaerophorus fragilis	0.0						
Sphaerophorus globosus	0.6	0.7					
Foliose lichens	61.2	17	0.0	63.4	47.0	69.5	60.0
Hypogymnia physodes	0.2	0.4		10.3	5.3	10.7	8.9
Nephroma arcticum			0.0				
Parmelia conspersa	0.0						
Parmelia omphalodes	56.3	17		34.9	19.8	24.4	27.3
Parmelia saxatilis	0.3	0.7					
Parmelia solediosa	0.0						
Parmelia stygia	4.2	9					
Parmelia sulcata	0.0			0.5			0.2
Parmelia sp.				11.8	19.7	33.3	21.6
Umbilicaria hyperborea	0.0						
Umbilicaria polyphylla	0.1			3.0	2.2	1.0	2.1
Umbilicaria torrefacta	0.1						
Xanthoria sp.	0.0						
Crustaceous lichens	2.8	4.2		0.8	0.5	0.8	0.5
Lecidea subfuscum	1.0	2.2					
Ochrolechia frigida	1.7	2.4		0.8	0.5	0.8	0.2
Rhizocarpon sp.	0.1	0.1					
Bare rock	34.2	12					
Plants from the rock				78.8	77.5	89.5	82.1
Plants from the ground				21.2	22.5	10.5	18.3

ARE ARCTIC ECOSYSTEMS REALLY FRAGILE?

A. W. F. Banfield

ABSTRACT—The current ecological concept that more diverse (and hence more complex) communities are more stable than simple communities because they provide more energy pathways, is questioned in the light of recent experimental data. The definition of community stability as the ability to return to ground state after an external perturbation is favored. Arctic ecosystems are considered to be as stable as many others, considering other facets of stability. The speed at which temporary oscillations are dampened after perturbation is considered to be the quality described as fragility.

The fragility of arctic biotic communities has been discussed by biologists for many years. Authors usually commence by quoting MacArthur (1955) as the originator of the concept. He considered the role of species populations in community stability and credited Odum (1953) with the concept that "the amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community." For his part, MacArthur concluded: "Where there is a small number of species (e.g., in Arctic regions) the stability condition is hard or impossible to achieve; species have to eat a wide diet and a large number of trophic levels (compared to number of species) is expected. If the number of species is too small, even this will not assure stability and, as in the Arctic, populations will vary considerably."

Later authors have enlarged upon this thesis. Slayter (1969) wrote: "The stability of an ecosystem is largely a matter of its diversity. In turn this is largely a matter of nutrient cycling or rate of energy flow. An ecosystem with little diversity is vulnerable to invasion, especially if energy flow is slow. [Such systems] . . . are unable to adapt to change without a period of marked instability. (examples: invasions of rabbits and prickly pears in Australia). Nature obtains stability by allowing energy to flow smoothly through the ecosystems, recycling and encouraging species diversity."

Murdoch and Connell (1970) added: "most ecologists would agree that complex communities are more stable than simple communities. Physical complexity providing hiding spots for prey may increase stability. Biological complexity provides more species, more interactions and therefore more stability." They postulated that the more complex communities are stable (i.e., able to resist invasion by new species) by having all the niches filled. As a consequence of this concept, tropical communities are considered more stable than temperate communities and arctic communities are even less stable.

Odum (1969) in his discussion of ecosystem strategy concluded that "an increase in the variety of species . . . can be accepted as a general probability during succession." He cited low species diversity and poor stability as indicators of a developmental stage in ecosystem maturation. Cowan (1969) elaborated with reference to the Arctic. "However, the passage from pioneer stage to climax is also a transition from an unstable state to a stable state. In the highly unstable early stages there is a rapid change in the total biomass of biological material. There is an equally rapid change in species composition. At the other end of the time scale there is relatively little change in the amount of living material from year to year (climax community) . . . the great surges in numbers of field mice, rabbits and moose take place generally in the early phase of the arctic-subarctic ecosystems."

It would be useful at this point to review briefly what we know about arctic and subarctic communities in the context of these definitions of stability.

We know that the physical factors of the environment are severe as far as the organisms are concerned. (1) The average temperatures are low, and what is more important, the annual temperature oscillation is extreme. Cold winter temperatures combined with low humidity and strong winds produce high windchill that is highly detrimental to exposed living tissue. (2) The total annual precipitation is so low that much of the area is classified as cold desert. Only the low temperatures prevent dessication as a result of low partial water vapour pressure. (3) The underlying permafrost layer holds the ground water in the frozen state, preventing root penetration and withholding ground moisture. The chilled active layer above the permafrost slows down chemical activity, decomposition and leeching of nutrients. (4) The wide annual oscillation of solar radiation from winter darkness to continuous summer daylight restricts the annual period of photosynthetic activity. Much of the spring solar radiation is unavailable to the green plants because of the low temperatures prevailing during March, April and May. As a result primary production is limited to about 100 days per year, in contrast to 365 days in tropical communities. This restriction also affects the consumers, limiting the season of green food and the season of reproduction. (5) A final factor that is often overlooked is the youthfulness of the environment. The plant and animal communities we now observe over much of arctic and subarctic Canada are less than 10,000 years old. In some places even less time has elapsed since the melting of the last Wisconsin glaciation. In a few glacial refugia (including much of Alaska and the northern Yukon Territory) the biotic associations are admittedly older. If we consider the maximum time available for the evolution of northern communities during the cold Quaternary Period, only about two million years have elapsed in the arctic region, compared to about 22 million years of refrigeration in Antarctica (Dunbar, 1968).

The short timespan since much of the northern terrain was scraped clean by the grinding glaciers is a main reason for the thinness of the mineral soil and humus layers as well as the low level of nutrients in arctic soils.

The facts we have gathered concerning the arctic plant and animal communities are more easily understood after this review of the physical environment. First of all primary production is low for terrestrial communities (Bliss, 1970). Secondary production is similarly low for succeeding trophic levels. Ungulate density is much lower on the arctic tundra than on the East African veldt. Another feature of arctic consumers is migration. Large numbers of birds that raise their young in arctic and subarctic communities migrate to temperate and tropical communities in winter. This results in a continual export of annual production and nutrients to other ecosystems upon the death of the migrants away from their birthplace. The same phenomenon occurs with anadromous fishes, some arctic whales and caribou and reindeer to a lesser extent.

The paucity of species at each trophic level is also well recognized for northern communities. One may note the decreasing number of species of mammals (Simpson, 1964), birds, insects and plants (Cailleux, 1954) as one proceeds from the Equator to the northern limits of land. This indicates that the limited energy available to arctic ecosystems flows through relatively few main food chains divided among a few dominant species, consisting for the most part of large populations of individuals.

Two main factors are involved in this low species diversity. The short timespan available for the evolution of an endemic northern flora and fauna has already been mentioned. The arctic fauna contains few autochthonous species. A great number of the endemic species belong to monotypic genera and often are representatives of primitive genera and families of the higher taxa. There are few examples of adaptive radiation, although the diversity of microtine rodents in the circumpolar region is a good example and

there are undoubtedly others.

The second factor has been the natural selection for euryecious organisms that could withstand the severe physical environmental factors. Several authors have previously compared the broad niches of arctic species with those of stenoecious species of tropical communities where natural selection was associated more with interspecific strife and the partitioning of ecological niches. As Stonehouse (1971) has recently put it, "there is an appealing biological economy about Arctic organisms . . . There is none of the ragbag clutter of the Tropics, where thousands of species jostle for space and ecology is a tangled web."

A third factor that has been frequently suggested is that there has not been enough time for the arctic ecosystems to progress to the climax community stage. If they did there would be more niches into which the flora and fauna might diversify.

We are all well aware of the disturbances to arctic communities caused by such external perturbations as forest fires, water impoundments and thermal erosion resulting from seismic lines and vehicle tracks. Somehow we tend to overlook the effects of external perturbations on tropical communities on lateritic soils. Clear cutting is far more damaging to tropical forests than to temperate or boreal forests. Such a forestry practice in tropical communities results in severe erosion, gulying and loss of fertility. Other human activities in the tropics have caused as severe damage as elsewhere. Woodwell (1970) reported: "After spraying the climax forest in Vietnam, it has been found that bamboo thickets replace the forests reflecting drastically lowered potential of these sites to support living systems. The time it takes to re-establish a forest with the original diversity depends upon the availability of nutrients and is probably very long in most lateritic soils."

DISCUSSION

At this point one can make several generalizations concerning arctic and subarctic communities relative to the various definitions of community stability. In the first place community biomass and annual productivity are relatively low compared to many tropical and temperate communities. These are the results of the combination of certain physical environmental factors such as the annual oscillations of solar radiation and temperature. However these facts do not bear on the problem of stability. Annual productivity may be quite stable in some arctic communities such as lakes and sub-nival habitats because of the stability of the physical factors.

The communities are also less diverse than temperate and tropical communities, but this is largely a result of the youthfulness of the environment. It might better be considered a biogeographic rather than an ecological fact. The premise that more complex food chains provide more choice for energy to follow through the ecosystem is an attractive one. However certain practical factors seem to have been missed in the mathematical model. Certainly the breadth of the species niches is involved in the analysis. It seems logical that the abundant, widespread, euryecious arctic species have a better chance to resist ecosystem perturbations than the less abundant, often restricted, stenoecious tropical forms.

The concept of community stability increasing with succession has come under critical study. The investigation of the effects of ionizing radiation upon vegetative communities (Woodwell, *op. cit.*) casts considerable doubt upon this relationship. It has been found that ionizing radiation (an external perturbation) exerts greatest destruction upon the climax communities (pines and oaks), less effect upon the shrub story and least effect upon the ground vegetation of herbs, grasses and mosses. The explanation postulated was that the sensitive biomass ratio between photosynthesizing green leaves and the respiring trunks and limbs of the arboreal climax species was destroyed. The same sort of result can be seen in the neighbourhood of Sudbury, Ontario, where the emission of sulfur dioxide from smelters

over a long period of time has destroyed the arboreal successional communities, but the pioneer grass, forb and shrub communities have continued. The Arctic has several vigorous native pioneer plants such as *Epilobium*, *Senecio*, *Calamagrostis* and *Eriophorum*, that are quick to reclaim disturbed terrain and provide an impressive, quick, primary production.

At this point it appears preferable to adopt the ability of a community to withstand an external perturbation as a test of stability as Hurd and his associates have done. If we include the concept of community equilibrium shifting in a periodic orbit (Levin, 1970), then we could expect the community to drift to other planes of stability when there was a slight perturbation in some environmental factor. Accepting this definition, fluctuating populations would no longer be an indication of community instability.

The attraction of this definition is that it permits an external test of community stability that is amenable to experimental and mathematical treatment. In an experimental community one would expect to find initial fluctuating or steady populations that could be measured in terms of density or biomass. After the application of a measured external perturbation, one would expect a transient state, characterized by dampening oscillations as the community sought another plane of equilibrium. Afterwards one would expect a return to a relatively steady state, although not necessarily the same as the initial state as far as species density is concerned. Instability would be characterized by an explosive population growth to infinity (an irruption) or a decrease to zero (extinction) by one of the community members after the perturbation.

A legitimate test of community stability would be the introduction or deletion of a species, measured physical environmental factor, or nutrient. It is interesting to note in this connection that the most striking cases of successful introduction of exotics have been in temperate and tropical communities. House sparrows, starlings, rats and house mice have conquered most of North America, but have made little progress in the arctic and subarctic communities — nor have many Eurasian weeds. Similarly there have been few extinctions in arctic communities.

Another advantage of this concept is that it permits separation of the idea of ecosystem fragility or vulnerability from that of ecosystem stability. Vulnerability, or fragility, would be measured as the time taken to dampen the oscillations after the perturbation. Communities could be legitimately compared by the speed with which they recovered from environmental disturbances.

An oscillation that was dampened over a short time interval could be defined as a disturbance, while an oscillation period that took a long time to be dampened could be considered as more serious damage to the community structure.

CONCLUSION

This discussion of current definitions of community stability with special reference to arctic and subarctic communities has led to the identification of weaknesses in the current ecological concept that more species diversity (and therefore complexity) leads to greater community stability. The adoption of the ability of a system to maintain or return to its ground state after an external perturbation, as a test of community stability, would greatly clarify the related problems.

Arctic and subarctic communities may be generally less diverse and have lower annual productivity and biomass than many temperate and tropical communities. However they often show considerable stability in annual production and exhibit an ability to recover from local environmental disturbances. Considering the severe physical factors of the environment, arctic communities appear ecologically well adapted from an evolutionary point of view.

We may review the major components of the ecosystem stability concept that have been enumerated by previous authors:

1. Stability increases with the number of trophic levels,
2. Stability increases with species diversity,
3. Steady population levels are considered stable, fluctuating populations indicate instability,
4. Stability increases with successional stage.

On the basis of these criteria arctic and subarctic communities are considered less stable than temperate, and tropical communities because they have fewer species, many species are characterized by population fluctuations and the food chains are less complex.

To question this piece of orthodox ecological theory is like questioning the sanctity of motherhood! However the special status of motherhood in today's society is being questioned in some quarters. So it behooves us as ecologists to reappraise our theories continually in the light of new knowledge.

The problem with this thesis is that it lacks an independent definition of stability. As Margalef (1958) pointed out: "In this sense, stability means, basically, complexity." The proliferation of definitions of ecosystem stability continues. Another part of the problem is one of semantics. Stable is a clear enough adjective. The opposite condition is unstable, however, fragility is another quality. Can the stable condition be compared? Can one situation be more stable (or less fragile) than another? I hope to clarify the situation with respect to arctic and subarctic communities.

OBSERVATIONS

A number of other definitions of stability have been proposed besides species diversity. These include:

1. The ratio of gross production/standing crop biomass (P./B. ratio) is low in stable climax communities (Odum, 1969).
2. Steady populations (MacArthur, *op. cit.*).
3. Steady annual community productivity.
4. Stable physical environment factors. (Hill, 1971, equates the frozen Arctic in winter with environmental stability.)
5. Convergent points in a n-dimensional field (Lewontin, 1969).
6. The ability of a system to maintain or return to its ground state after an external perturbation. This latter definition was developed by Hurd *et al.* (1971), in their experimental test of stability and diversity in an old field community near Syracuse, New York. Such a definition is used in the physical sciences and permits graphical and mathematical treatment. It involves the amplitude of the deflection from the ground state as a result of a quantifiable perturbation and the rate at which the deflection is dampened. Biologists have included the concept of perturbations in the physical environment in their discussions of community stability for some time. This definition also ties in well with the concept of the environment as a n-dimensional hypervolume, with community equilibrium shifting about a periodic orbit when factors alter slightly. This is the 'neighbourhood stability' of Lewontin (1969). "In the case of the periodic orbit, this does not require that the perturbed state return to the point from which it was perturbed, but merely to some arbitrarily small neighbourhood of the periodic orbit as a whole" Levin (1970).

Incidentally, Hurd (1971) found that "in contrast to current ecological theory, greater diversity at a trophic level was accompanied by lower stability at the next higher level" in their study.

This definition also aids in distinguishing between two community qualities: stability and fragility. Stability has only two possible states: stable and unstable. While fragility refers to the ability of a stable community to recover from an external perturbation (often a human disturbance). Two communities may be compared as to the time taken to recover from a disturbance and one found to be more fragile (or vulnerable) than the other. However, a community can't be more or less stable than another, any more than a person can be more or less pregnant!

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