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Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska

By

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ECOLOGY OF THE CARIBOU (*Rangifer tarandus granti*) IN ALASKA

Ronald Oliver Skoog

ABSTRACT

Alaska's caribou population consists of six regional sub-populations and eleven herds. For each region the author hypothesizes a *center of habitation*, which consists of optimal caribou habitat, supports the main herd, and acts as a focal point for population buildup and dispersal. As density increases the movements become more erratic and extensive, and the animals begin to utilize marginal areas. If other population "controls" are not evoked, eventually an emigration to other regions occurs. After the decline, remnant herds may be found in certain portions of the region, but the main sub-population remains at the *center*. A herd is defined as any group of caribou which uses one calving area repeatedly over a period of years, distinct from the calving area of any other group. An historical review of caribou distribution and numbers revealed a considerable flux of animals between all six regions. It was believed that the population shifts noted merely reflected the normal vagility of this species, which becomes accentuated at densities between 5 and 10 animals per square mile. Population highs were evident during the 1860's and 1920's, and lows during the 1890's and 1940's. The exact causes for these changes in numbers are not known, but food shortage was not an important factor. Caribou densities have remained far below the carrying capacity suggested by the forage available. The estimate for caribou numbers (calves excluded) in Alaska for June, 1964, was 600,000 animals.

This study was based upon 12 years of field-work, 1952-1964, although the main study period encompassed 1955-1962. Emphasis was placed

on the Nelchina herd in southcentral Alaska. The population data obtained from that herd constitute the central theme of this dissertation, and the results are summarized below.

1) The Nelchina range is a highly diversified region, having a variety of climatic conditions and vegetation types and thus offering a number of different habitats to caribou. Twelve major vegetation types have been identified, four of which--Dwarf Birch, Dwarf Heath, Sedge Meadow, and Willow--comprise about 51 per cent of the range vegetation and are of most importance to the caribou. Overgrazed areas are few, and abundant year-round forage remains.

2) The seasonal distribution centers about the traditional calving grounds. With increasing densities the movements have become more extensive, and the herd has split seasonally into several major groups. Excursions outside the normal range have occurred, and a shift in winter-use has occurred to the northwest and east.

3) Sex-ratios were as follows: Secondary (at birth), 51 per cent males; Tertiary (at 12-months), 55 per cent males; Quaternary (at 24-months), 50 per cent males; Quinary (at 10-years+), 23 per cent males. In 1962, males comprised 39 per cent of all animals 1-year+, 35 per cent of those 2-years+, and 30 per cent of those 3-years+.

4) The peak of rutting activity occurred about October 6. The fertility rate was found to be 72 per cent of all females 1-year+, 84 per cent of those 2-years+, and 89 per cent of those 3-years+. Natality was assumed equal to the fertility rate. The peak of calving occurred about May 25. Each October calves comprised an average of 21 per cent of the herd.

5) During the first year of life, an average of 40 per cent of the calves died; of these, 70 per cent died between June and October.

Mortality among animals older than calves averaged 14 per cent annually: hunters, 8 per cent; wolf predation, 2 per cent; and other mortality, 4 per cent.

6) Total numbers increased from 40,000 animals to 71,000, at an average annual rate of 9 per cent. Yearling production averaged 22 per cent. The maximum annual increase for the herd under "natural" conditions (i.e.,disregarding hunter losses) would have been 20 per cent.

7) Weather, predation, and emigration were considered to be the main factors controlling caribou numbers in Alaska.

ECOLOGY OF THE CARIBOU (*Rangifer tarandus granti*) IN ALASKA

PREFACE

The rigorous climate, the vastness, and the emptiness of the far north long have intrigued man and challenged his adventurous spirit. The image portrayed in the minds of most is an inhospitable land where one constantly wages fierce battle with the environment. Perhaps no other animal typifies more the ruggedness of this vast region than the caribou, whose nomadic wanderings across the arctic wastes and huge seasonal migrations have fascinated man for thousands of years. The successful exploitation of this rigorous environment required the evolution of a number of unique morphological and physiological adaptations and behavioral mechanisms. A knowledge of these is basic to an understanding of the ecology and population dynamics of this species.

The first research directed to this species was associated with the reindeer industry. In Eurasia the caribou had been domesticated for hundreds of years, but in North America the industry did not become established until the introduction of reindeer from Siberia to western Alaska in 1892. A superficial type of research was carried out during the first 15 years or so, but not systematically enough to provide significant results. Nevertheless, many of the general observations and statistics kept during this period have been of value. Taxonomic studies by Lydekker (1898) included some life-history observations, as well; other taxonomic work was carried out in Alaska by Stone (1900) and Allen (1901). Observations by a number of sportsmen and naturalists during the early 1900's have proved valuable (e.g., Selous, 1907; Millais, 1907; Dugmore, 1913;

and various others). Nevertheless, no detailed studies were initiated until the early 1920's. At that time, E. W. Nelson, head of the U. S. Biological Survey, initiated an extensive research program in Alaska which sought to obtain data on the biology, life-history, and range requirements of reindeer and caribou. Publications resulting from this early work included Hadwen and Palmer, 1922; Palmer, 1926, 1934; Hadwen, 1927; and Murie, 1935. This program continued into the 1930's, but with ever decreasing emphasis. Little research was carried out after the mid-1930's.

During the late 1920's an intensive research program on reindeer began in the U.S.S.R., which has continued to the present. Much of this research has been excellent. Unfortunately, few of the many publications relating to this work have been translated into English. During my own studies I have attempted to translate some of the more recent publications, particularly those which have summarized past years' work. In this manuscript I have included references to the Russian research wherever possible.

In Alaska, Adolph Murie's (1944) study of the wolves of Mt. McKinley National Park included valuable observations and statistics pertaining to the caribou of that region. An organized research program on caribou, however, was not initiated in Alaska until 1948, under E. F. Chatelain of the U. S. Fish & Wildlife Service. About the same time, A. W. F. Banfield (1951; 1954) initiated his study of the caribou on the mainland of northern Canada. After that, caribou research expanded rapidly in both countries. In Alaska, R. F. Scott elaborated upon Chatelain's work, aided by myself and S. T. Olson. D. R. Klein's work (1959; 1968) with the St. Mathew Island reindeer herd was of especial value. In Canada,

D. A. Munro, J. P. Kelsall, and A. G. Loughrey expanded Banfield's work, later continued by R. Ruttan. A. T. Bergerud's excellent research on the Newfoundland caribou began about 1955, and has contributed valuable data on many facets of caribou ecology. Of particular value has been P. C. Lent's (1966) exceptional study in northwestern Alaska of the social behavior of caribou during the calving period.

My own research on Alaska caribou began in the fall of 1952 at the University of Alaska with a 3-year study of the Fortymile herd (Skoog, 1956). This work expanded to the Nelchina herd in 1956 under the auspices of the U. S. Fish & Wildlife Service, and continued to the fall of 1964, when I started graduate work at the University of California, Berkeley, under Dr. A. Starker Leopold. During the last 5-years of my field-work, I was in charge of the caribou research being carried out by the Alaska State Department of Fish and Game, and my studies extended into all portions of the State (except the Southeast). The Nelchina herd continued to receive the main emphasis, however. I had the opportunity to work with all six major herds at various times--Alaska Peninsula, Arctic, Fortymile, McKinley, Nelchina, and Porcupine--and to examine all of the caribou ranges. I worked on the calving grounds of one or more caribou herds during 11 of my 12 years of research; on hunter check-stations in fall and early winter during 10 years; on the rutting grounds in late September and early October during 5 years; and spent 6 summers gathering range data in the Nelchina region. During 1962-1964 I was involved in a cooperative study between the U. S. Public Health Service, the U. S. Department of Agriculture, and the Alaska Department of Fish and Game; as member of a 5-man team, I examined the effects of disease in the Arctic herd. Needless to say, the airplane played an especially important role

throughout. Aerial counts were used to evaluate natality and to trace calf mortality through the first year of life; reconnaissance flights traced the distribution and movements of the Nelchina herd throughout each year and of other herds at various times.

The main purpose of this study has been to obtain a comprehensive set of data concerning caribou ecology in Alaska, relative to understanding the population dynamics of this species and to the proper management of this population in future years. The main effort focused on the Nelchina herd in an attempt to obtain maximum data on one population unit, which then, presumably, could be applied to other herds and other areas. The field-work concentrated on gathering data concerning the three main population "forces"--reproduction, mortality, and movements. Considerable effort was expended also in vegetation studies with the hope of eventually being able to evaluate caribou-range relationships. These data are not presented in detail here, but will be assembled later into a separate manuscript.

I have organized this presentation into three main parts: I. The Species, II. The Population, and III. The Nelchina Subpopulation. The first discusses the species in relation to Alaska, emphasizing those aspects of the caribou's biology which are pertinent to an understanding of its population dynamics. I have searched the literature to find as much pertinent information as possible regarding certain facets of the caribou's life-history and much of this is included. Data obtained from Alaskan herds has been stressed. The second presents a detailed historical account of the fluctuations in distribution and numbers among Alaska caribou during the past 100 years and more. This documentation was necessary in order to illustrate the fluid nature of this caribou population. The

third includes the more specific data which were obtained from a population study of a major population unit--the Nelchina herd. These provide a detailed picture of the factors influencing and the changes occurring within a caribou herd over a relatively short period of time. The concluding section discusses the regulation of numbers in this species, relative to the Alaska-Yukon population. In total, I have attempted to review much of what is currently known about *Rangifer tarandus* and to synthesize this and my own research data into a comprehensive picture of this species' ecology. I believe the effort has been rewarding, and the work will provide a good base for future caribou research in Alaska, as well as in other regions. The population data should prove valuable to all animal ecologists interested in ungulate species.

ACKNOWLEDGEMENTS

In the course of a long research project such as this, one necessarily obtains assistance from a great number of people. In 1952, at the start of my graduate "career", I received a much valued stimulus from talks with A. S. Leopold and F. F. Darling, who at that time were examining the wildlife resources of Alaska. The impact of such professional wildlife-ecologists upon a newly "hatched" zoologist cannot be overstated. My early development was guided along "righteous" paths by the patient "understanding" of John L. Buckley and Robert F. Scott. I benefited greatly from their constructive criticism and long discussions and also from simply being able to observe competent professionals in action. To my argumentative, narrow-minded, bullheaded field companions over the years--B. L. Burkholder, A. W. Erickson, J. G. King, D. R. Klein, W. L. Libby, K. A. Neiland, S. T. Olson, and R. A. Rausch--I extend my heartfelt thanks for many hours of warm companionship, hard work, stimulating discussion, heated debate, and pleasant memories. Those "good old days" will never be forgotten!

Various members of the U. S. Fish & Wildlife Service extended much help. I especially wish to thank "Pete" Nelson, Ray Woolford, and Theron Smith for their many "votes of confidence" in the organization and execution of "cooperative" field ventures. Of course, without those intrepid, hard-working FWS pilots--Neil Argy, Bob Burkholder (master of slow flight with full flaps), Abe Thayer, and Ray Tremblay--much of the work never could have been accomplished. The rocky ridgetops, short river-bars,

and mushy tundra landings and take-offs, in combination with bent propellers, sagging landing-gears, and aching "pushing" muscles, provide me with many a poignant memory. Those moments of "stark terror" have a way of creeping back into one's consciousness!

Of the many assistants who have worked with me, I wish to thank especially Ed Keough, Charles Lucier, Willy Miller, and Rich Winters. Their hard work, dependability, and sense of responsibility greatly facilitated the execution of this research project in the later years. I wish to acknowledge also the assistance and moral support from some of my other Alaska co-workers and friends: Dr. R.L. Rausch and B. E. Huntley of the Arctic Health Research Center; Dr. J. King of the U. S. Department of Agriculture; and Drs. B. Kessel and F. C. Dean of the University of Alaska.

My chats and correspondence with some of the Canadian biologists--A. W. F. Banfield, J. P. Kelsall, A. G. Loughrey, and W. Fuller--have proved especially rewarding and enjoyable. We have shared in a vicarious fashion some of the many disappointments and frustrations associated with caribou research. My lengthy correspondence with A. T. Bergerud, former Newfoundland biologist, and our exchange of data have been most stimulating and valuable. I have been especially grateful for his willingness to share his findings with me, and I look forward to the day when we can meet and exchange "caribou thoughts" at first hand. While Peter Lent was a graduate student at the University of Alberta, we maintained contact concerning our respective studies, and here, too, the discussions and correspondence were of great value.

Of course, a multitude of other Alaskans were involved in the caribou work at various stages and in various capacities. These are too many to mention specifically, but their efforts always were greatly

appreciated, as I am sure they realize.

At the University of California I must thank Dr. Leopold once again for his encouragement and for his guidance through "finishing School"--a rather appropriate sequel to our initial meeting in Alaska 16 years previously. I am most grateful to Drs. Heady and Pearson for critically reading this dissertation and making valuable suggestions for changes--not an easy task, considering the length of the manuscript. During my stay at the University I enjoyed and appreciated much the use of the facilities at the Museum of Vertebrate Zoology. The stimulating discussions with both staff and fellow graduate students constituted some of the most valuable experiences of graduate school. I was especially grateful for being able to attend the "eco-lunches" held by Drs. Pitelka and Paris; I particularly benefited from the pertinent, enlightening and most critical discussions of a wide variety of ecological principles and studies. Dr. Pitelka's continued support and help during my stay at Berkeley was most appreciated.

Finally, I must extend my deepest and warmest thanksto the girls: my sister Arline Moberly and my wife Patricia, who typed and worried their way through to the final page.

PART I. THE SPECIES

The caribou, or reindeer, Rangifer tarandus (Linnaeus) 1758, has ranged the tundra and taiga biomes of the Holartic region for more than a million years. According to Banfield (1961) the earliest record of the genus Rangifer is from central Germany about 440,000 years ago, during the Antepenultimate Glaciation, Mindel phase. He states (p. 29), "We only know that it migrated into Western Europe... and later became abundant there. Its origin was probably in Alaska, Beringia, or in the mountains of northeastern Asia." The earliest record of the species in North America has been found in the Fairbanks district of Alaska from sediments interpreted to be from the Penultimate (Illinois) Glaciation, over 150,000 years ago (Banfield, 1961: 35). These two datings both need revision, however, in light of recent evidence that has shown the start of the Pleistocene epoch to be approximately two million years ago instead of the previously supposed one million (Wright and Frey, 1965).

Simpson's (1945) comments on the Subfamily Odocoileinae (to which Rangifer is presently assigned) suggested a much earlier occurrence in North America than the Alaska finds have indicated. He stated (p. 268) that it seemed probable that this taxon "... represents an Old World cervine offshoot that sent some members into the New World at a relatively recent time, probably well along in the Pliocene." This group then diversified into the typical forms found in the Americas, and, as Banfield has stated (op. cit., p. 29), "Because of its many primitive characters, Rangifer may have been near the offshoot." Thus, although the progenitors for Rangifer have not yet been determined, it seems likely that the genus was well established early in the Pleistocene epoch.

In ancient times this animal was distributed much more widely than it is today. At the height of the Wisconsin Glaciation caribou were abundant south of the ice-sheet throughout Europe, Asia, and North America--in the last region, as far south as the mountainous region of New Mexico and Nevada (Hay, 1927). Today's distribution is much more restricted. Populations have declined under the northern advance of civilization, and Canada and Alaska presently contain most of the world's supply of wild caribou. As man continues to encroach upon the caribou's range, the future can foretell only a further decline.

A few caribou populations still occur in various parts of northern Eurasia, and one on the Taymyr Peninsula, north of the Central

Siberian Plateau, has been estimated in excess of 100,000 animals (Krechmar, 1966). The numbers and distribution of these wild populations remain rather restricted, however, because of the great emphasis upon reindeer husbandry in the northern countries, i. e., USSR, Finland, Sweden, and Norway. Wild populations are particularly undesirable in areas of reindeer herding, because of the close competition for food and space. Further problems are caused by the tendency of reindeer to run off to nearby caribou bands whenever the opportunity arises. In North America the reindeer industry has not expanded sufficiently as yet to exert much influence upon the caribou populations; it has occupied only a small proportion of the total available habitat.

It has been implied thus far, and intentionally so, that the vernacular name "caribou" refers to the wild Rangifer and "reindeer", to the domesticated. Banfield (1961: 3) commented as follows:

> There has been almost as much confusion in vernacular names for the species as in scientific names. All western European names are thought to be derived from "reino", the Lapp name for a young reindeer (Dutilly, 1949). Thus we have--Scandinavian, ren; German, Rentier; English, reindeer; Old English, Rain-Deer, Rein; French, renne; Old French, rangier, rangifere....the last form...apparently produced the presently accepted generic name Rangifer (Linnaeus, 1746).

Thus, "reindeer" should be the accepted name for the species. Early French explorers of eastern North America, however, generally adopted "caribou", or some closely related form. Walton (1928) believed that

the name was derived from the French "carre boeuf" (four-horned ox). Further research (Wright, 1929), however, revealed that the word actually originated from the language of the Micmac Indians in New Brunswick, who referred to the animal as the "xalibu" (the pawer or shoveler). At any rate, "caribou" came to be the vernacular name for Rangifer in North America.

The two names result in some confusion, but can provide a convenient means for differentiating between the two "forms" of Rangifer--wild and domesticated. The latter is referred to universally as "reindeer"; both names are used for the first; "caribou" is used for the wild form. In this paper, "reindeer" will refer only to the domesticated form and "caribou", only to the wild form, except for material quoted from other sources.

This part of the dissertation is intended to provide background information concerning the caribou as a species. An emphasis has been placed upon those aspects of its biology which are pertinent to an understanding of the animal's population dynamics in Alaska. The various sections included--morphology, boreal adaptations, movements, and food habits--are not intended as complete discussions and/or evaluations, but rather as pertinent summaries of current knowledge, based on my field observations and data collections, as well as on information from a variety of other sources. Observations concerning the Nelchina and other Alaskan herds are stressed.

TAXONOMY

Caribou belong to the deer family of the ruminant group of the even-toed, hoofed mammals: Order Artiodactyla, Suborder Ruminantia, Superfamily Cervoidea, Family Cervidae, Subfamily Odocoileinae, and Genus Rangifer. As an Artiodactyl this species has an even number of toes (3rd and 4th digits equal), cloven hooves, a total of 19 thoracic and lumbar vertebrae, no clavicles, a complex stomach, small caecum, bicornuate uterus, and an indeciduate placenta. Like other ruminants it has a stomach with four compartments, lacks upper incisors, has incisiform lower canines, selenodont cheek teeth, inguinal mammae, and an epithelio-chorial, cotyledonous placenta. As a member of the deer family it lacks a gall bladder and has deciduous antlers. The genus Rangifer is typified by animals of medium to large size, having functional lateral digits, large, crescentic-shaped hooves, upper canines, deciduous antlers borne by both sexes, and a number of physical adaptations to an arctic or sub-arctic environment.

The taxonomy of the caribou has been in a rather confused state for quite a number of years. Lydekker (1898) considered all members of the genus Rangifer to be of the same species. Other workers, such as Grant (1903), Seton (1927), Jacobi (1931), and Murie, O. J. (1935), chose to divide the group into various species and subspecies. At the present time,

however, it is generally considered that the genus has but one living species, Rangifer tarandus (Flerov, 1952; Hall and Kelson, 1959; and Banfield, 1961).

Two groups of caribou are recognized, as designated by Jacobi (1931): the tundra caribou, group Cylindricornis; and the woodland caribou, group Compressicornis. In general, the former inhabit the tundra regions of the arctic, frequently migrating into the taiga in winter. The latter inhabit the bogs and alpine tundra in the forested regions of the boreal zone. Banfield's (1961) classification of the caribou is as follows:

SPECIES: Rangifer tarandus (Linnaeus) 1758.

GROUP: Cylindricornis Jacobi 1931. Tundra Reindeer.

R. t. tarandus (Linnaeus). Eurasian Tundra Reindeer.
R. t. groenlandicus (Linnaeus). American Tundra Reindeer.
R. t. granti J. A. Allen. Grant's Reindeer (Alaska).
R. t. pearyi J. A. Allen. Peary Reindeer.
R. t. eogroenlandicus Degerbol. East Greenland Reindeer.
R. t. platyrhynchus Vrolik. Spitsbergen Reindeer.

GROUP: Compressicornis Jacobi 1931. Woodland Caribou or Forest Reindeer.

R. t. caribou (Gmelin). American Woodland Caribou.
R. t. dawsoni Seton. Queen Charlotte Island Caribou.
R. t. fennicus Lonnberg. Eurasian Forest Reindeer.

The domestic caribou, or reindeer, have not been treated in this work; they are derived primarily from R. t. tarandus and R. t. fennicus stock.

Unfortunately, the taxonomy of Alaska's caribou still remains unsettled. Until the recent study by Banfield (1961) Alaska was considered to have two sub-specific forms: R. t. granti and R. t. stonei (Murie, O. J., 1935; Hall and Kelson, 1959). Banfield's work placed the former subspecies into the tundra group and the latter into the woodland group. Both had been described by J. A. Allen (1901; 1902) at the turn of the century on the basis of a few specimens obtained from the Alaska Peninsula (R. t. granti; 15 specimens) and the Kenai Peninsula (R. t. stonei; 1 specimen). Banfield felt that the Kenai speciment was indistinguishable from the woodland caribou specimens obtained in British Columbia. His comments (1961: 59) regarding Alaska were as follows:

> The identification of the caribou populations in Alaska and the Yukon district has been the most difficult problem in the present investigation. Originally, nine geographic groups were analyzed in the region. Those groups were gradually amalgamated, as statistical analyses indicated that the differences were insignificant. Eventually four groups remained exclusive of the Kenai and Alaska Peninsula groups, which have been previously treated. [by J. A. Allen, 1901 and 1902.] Those were as follows: the Nelchina herd, the Steese Highway herd, the northern Yukon herd, and the Brooks Range herd....South to North clines are evident in most characters [skull measurements] treated [for those Alaska-Yukon demes]....Other factors, such as pelage colour, external measurements, and antler formation, bear out the same clines.

Other statements made regarding Alaska's caribou included the following:

> In Alaska this subspecies [referring to R. t. caribou] as a recognizable form was restricted to the southeastern portions of the State from the Kenai Peninsula to the Copper River Valley and the southern Alaskan "panhandle". (p. 76) [Presumably this area designation does not include the Talkeetna or Wrangell Mountains, i. e., the Nelchina, Mentasta, and the Chisana herds.]
>
> The present study has shown that tundra caribou of the Alaska Peninsula and the Brooks Range of northern Alaska resemble each other closely. Although granti is generally slightly larger, the differences are not statistically significant. (p. 58)
>
> Subsequent statistical analysis indicated that the Brooks Range population could not be separated adequately from groenlandicus, and the southern groups could not be separated from granti....Since the only statistically valid Alaskan race is granti of the Alaskan peninsula, one is faced with the possible choice of referring to all central and northern Alaskan populations as granti intergrades. (p. 59)

The confusion that seems to exist in the taxonomy of Alaska's caribou is of interest, especially in view of the statewide interchange of animals that has occurred during the past 100 years (see later section, "Population Shifts"). The only group that has remained essentially isolated has been that of the Alaska Peninsula.

Paleontological evidence reveals that caribou were present in Alaska throughout the Wisconsin stage of the Pleistocene epoch. In reference to interior Alaska, Banfield (1961: 35) quoted Dr. Troy L. Pewe of the U. S. Geological Survey in Alaska (a personal communication in 1960) as stating:

> All the caribou specimens that I have seen, except one,...come from the Wisconsin deposits. I would say that they go back at least 50,000 years....It is my impression that the caribou was indeed present here all through Wisconsin time and the remains are fairly abundant.

Other references to the presence of caribou in Alaska at that time include Frick (1937), Simpson (1947), Geist (1953), Pewe (1958), and Rousch (1963). Three major unglaciated refugia in North America were evident during the Wisconsin glaciation: 1) Beringia--encompassing much of the interior and arctic-slope regions of Alaska, plus the Bering land-bridge as well (Hopkins, 1959); 2) Pearyland--encompassing the northern portions of the Canadian arctic archipelago and adjacent parts of northern Greenland (Manning, 1960); and 3) the periglacial region south of the ice-sheet (Wright and Frey, 1905).

Banfield (1963) has pointed out that "The finding of the late-Pleistocene caribou remains in each of these refugia confirms their occupation during the Wisconsin stage." The subspecies he associated with each of these refugia as having common ancestry are, respectively, 1) the mainland tundra taxa, R. t. granti and R. t. groenlandicus; 2) the arctic insular taxa, R. t. pearyi and R. t. eogroenlandicus; and 3) the forest taxa, R. t. caribou and R. t. dawsoni. He postulated further that "...certain anomalies in the distribution pattern...can best be explained by emigration into corridors which are known to have become ice-free early in the deglaciation process." Thus it would appear that as the ice-sheet retreated the woodland caribou extended northward along the Mackenzie

River and Yukon River corridors. Presumably if the woodland caribou reached the Kenai Peninsula (as represented by R. t. stonei; Allen, 1901) it would have done so via this route. This northward dispersal of the woodland caribou, and subsequent interbreeding with the tundra caribou, supposedly resulted in the so-called granti intergrades that are present in Alaska today. (See Manning, 1960, for a discussion of the intergradation of R. t. pearyi and R. t. groenlandicus).

Populations shifts among Alaska's various caribou herds probably have occurred throughout history, as seems evident since the late 1800's (see later section, "Population Shifts"). Apparently the exchange of genes between "populations" has been a rather common phenomenon, and thus the assumption of but one subspecies for Alaska would appear most logical. Perhaps the clines noted by Banfield in the various measurements compared resulted more from the effects of small sample sizes (61 specimens for the four Alaska-Yukon demes recognized; Banfield, 1961: 135-136) and/or the effects of transient (e. g., the quality of available forage) and intransient (e. g., climate) environmental differences between the four geographic regions involved, than from actual genetic differences in those "populations". Unfortunately, most of the taxonomic work with Rangifer has been based strictly upon morphological criteria, and mostly upon skeletal measurements. Little attention has been given to determining whether or not the differences existing among the designated subspecific populations are in fact genetic. Such a determination has been lacking in most taxonomic work concerned with intra-specific variation.

It would seem logical that average skeletal measurements in populations occupying different regions could vary significantly simply as a result of differences in the energy-flow patterns of the ecosystems involved. One can visualize readily the extent of such differences by comparing the habitat, say, of the Queen Elizabeth Islands' caribou in the high arctic with that of the Nelchina caribou in southcentral Alaska. Obviously the ultimate size attained in adult animals is affected strongly by the nutritional regimen of the young animals during the growth period.(In caribou, mostly the first, second, and third summers.) The largest animals can be expected in those areas where the growing season is the longest, the forage the most nutritious, and the maintenance-energy requirement the least--contingent, of course, upon the limitations imposed by the species' genetic variability. Thus, the smaller size of caribou in arctic regions as compared with those in the subarctic could reflect merely a low-energy intake relative to the maintenance-energy cost during the growth period.

The relation of skeletal size to range quality, nutrition, and other environmental influences is well known among workers in the fields of animal husbandry and wildlife management. Klein (1964) has shown this relation with respect to deer populations in southeast Alaska. In addition, his work (Klein, 1959; 1964; 1968) with the reindeer of Saint Mathew Island in the Bering Sea demonstrated well the changes in skeletal growth occurring concurrently with changes in the range vegetation--a decrease in size as the population

expanded and the forage deteriorated. In 1957, 13 years after the original introduction of 29 reindeer to the island, the animals averaged considerably larger (both in skeletal measurements as well as overall body weight) than the original stock from which the animals were derived. By 1963, however, the average size of the young animals had decreased. Presumably this effect would have been continued into adulthood had not an extensive die-off intervened and reduced the population during the winter of 1963-64 from an estimated 6,000 animals to less than 50. Above-average size of both young and adult animals has been noted as well among descendants of caribou taken as calves from the Nelchina herd and introduced to Adak Island in the Aleutians (Jones, 1966) and of reindeer introduced to various other islands in that group.

There seems to be little justification for splitting the Alaska-Yukon caribou into various subspecific groups. What evidence exists suggests that the animals have a common gene pool, at least in terms of the time required for subspeciation in a long-generation mammal such as caribou. For the present, the subspecific name of *Rangifer tarandus granti*, as suggested by Banfield (1961), seems adequate.

MORPHOLOGY

The Alaska-Yukon caribou can be classed as a deer of moderate to large size. The body of an average, full-grown (6-years or older), adult male will measure approximately 210 centimeters (82 inches) total length, stand 125 centimeters (50 inches) at the shoulder, and weigh (in September) 190 kilograms (400 pounds). An adult female (3-years or older) is considerably smaller, averaging only half the weight of the male. The trunk and head of this species are rather elongated; the muzzle is thick and expanded. A profile of the nasal region is mostly convex ("Roman-nosed") in the adult bulls and the old cows, but straight in most adult cows and the juveniles (Skoog, 1956: 94-96).

The eyes are relatively small. The neck is of moderate length with a strongly developed ventral white mane in the adult male, but with a much less conspicuous mane in the adult female. The withers are somewhat elevated in the form of a small hump, but are not much higher than the rump. The back is straight, and the rump is almost straight or slightly rounded. Both the ears and tail are rather short and well furred, the ears averaging about 14 centimeters (5.5 inches) from notch to tip, and the tail, 15 centimeters (6 inches). The hooves are large, very wide and flattened, crescentic in shape. The lateral digits, or dewclaws, are long and wide, and actually are functional in supporting the animal.

Both sexes grow antlers each year, and in the adult male they are quite large, measuring up to 150 centimeters (60 inches) or more in length. The general coloration of the body in early September is dark brown, with a white ventral neck mane, white "stockings" above the hooves, a white perineum, and a white underside of the tail. In winter the brown color of the body fades, as the pigmented tips of the growing hairs break off to expose the lighter underparts; by spring the animals are rather grayish in color. In general, the caribou appears more rangy in form than the reindeer, having longer legs and a slimmer body. In comparison, where selective breeding has been practiced, reindeer often appear thick-bodied and short-legged.

This section is not meant to be an exhaustive treatment of caribou morphology, and therefore the discussion has been limited to those aspects which have been important in this study of the animal's population ecology. The body weights and measurements point out the differences between the sexes and the age classes, as well as those existing between the various sub-populations in Alaska. Antlers have proved to be important characters in sex and age identification, and also as an indicator of natality. To certain extent the caribou's pelage can be considered as the main physical character enabling this species to survive in the generally inhospitable boreal environment; the annual cycle in the growth and replacement of hair plays an important role in the species' bioenergetics. Aging techniques have been based mostly on the dentition,

and therefore a discussion of tooth development and sequence of eruption would seem pertinent. An understanding of these aspects of caribou morphology will provide an important background for what follows.

Body Size

Differences in mean body-size are evident between various sub-populations of Alaska caribou. Such differential growth within the subspecies probably results mostly from regional differences in the nutritional regimens, rather than from genetic factors. Gene-flow between herds has occurred commonly during the past 100 years (see Part II, "Population Changes"), and it seems likely that Alaska's caribou are comprised of a rather uniform genetic stock. The physiological response of ungulates to nutritional differences in the forage has been studied extensively by a variety of workers, and there is little doubt that the ultimate size attained by an animal depends greatly upon its nutrition during the juvenile years, limited, of course, by the genetic potential of the species. The literature in animal husbandry pertaining to this subject is voluminous; that in the field of big-game management is scarcely less so. Klein (1964a and 1965) has presented an excellent discussion regarding this aspect of nutrition, and his work with the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) of southeast Alaska demonstrates well the principles involved. More detailed information can be had from the works of Brody (1945) and Mitchell (1962).

Newborn calves--Caribou are born at a rather advanced stage of physical development. This precocity permits the calves to follow their mothers soon after birth, and undoubtedly has evolved in response to the nomadic behavior of this species. In view of the

continual movements of caribou herds, even during the calving period, selection would favor those calves that could survive the rigorous energy demands of constant travel. Differences in the average total-weights of newborn calves from two herds in Alaska are not significant in the data obtained. Table 1 lists these data for Alaska caribou and for reindeer in Alaska, Canada, and Russia. As shown, the newborn caribou calf weighs approximately 6 kilograms (13 pounds), with a range of 2.7-8.2 (6-18 pounds). Those weighing less than about 3.5 kilograms (8 pounds) appear to be quite weak and underdeveloped, and it is likely that most of these succumb. Work by Hammond (1944), Wallace (1945), and Everitt (1964) with sheep has shown that lambs born to undernourished ewes usually weigh much less than the average. Such underweight lambs are not fully developed morphologically nor physiologically and therefore are of low viability. Conversely, ewes on a high plane of nutrition tend to give birth to somewhat larger-than-average lambs, which are advanced in development.

The differences in weights shown in Table 1 probably reflect such nutritional influences. The two sets of data obtained for the Arctic herd suggest a drop in the average weight of newborn calves. Lent's measurements were taken primarily during 1960 and 1961, whereas those by the author, during 1963 and 1964. By the latter period the physical condition of the animals in this herd had deteriorated considerably due to the increased incidence of disease (Huntley _et al._, 1963; Skoog, 1963a, 1964) and to several prolonged

Table 1. Birth-weights of caribou and reindeer.

AREA	n	AVERAGE WEIGHT	RANGE	INFORMATION SOURCE
CARIBOU:				
Northwest Alaska	32	5.9	3.2 - 8.2	Lent, 1964
	16	5.0	2.7 - 6.8	Field data
Southcentral Alaska	16	6.1	3.6 - 8.2	Field data
REINDEER:				
West Alaska	?	5.5	3.2 - 6.8	Palmer, 1934
*Northwest Canada	9	5.5	2.3 - 7.9	Krebs and Cowan, 1962
U.S.S.R. (various locales)	?	6.5	2.7 - 9.7	" "
Northwest U.S.S.R.	6	7.2	6.5 - 8.2	Alaruikka, 1959
North Finland	?	5.0	?	" "

Note: Measurements in kilograms; no significant difference in size between the sexes has been noted, hence both are considered together here.

* These figures include 5 calves found dead on calving grounds.

winters. The latter condition prevailed especially during 1963 and 1964. Such adverse weather during early spring delays the new growth of vegetation, which is needed by the pregnant cows to satisfy the greatly increased nutritional demands of the growing fetus during the final two months of prenatal life. During those two years many of the pregnant cows probably were unable to obtain adequate forage during April and May, as evidenced by the extreme minimum of fat present in all animals examined in early June, the number of small calves observed, the prevalence of retained placentae among parturient cows (both poor nutrition and the disease brucellosis were factors here), and the relatively high mortality among neonate calves (Skoog, 1964). It seems likely that the lower average-weight obtained by the author for newborn calves reflected the overall rather poor condition of the animals in this herd.

The newborn-calf weights noted for reindeer in Alaska and Canada are comparable to those for caribou. Those from Russian reindeer herds average heavier (Krebs and Cowan, 1962); weights up to 9.7 kilograms (21.4 pounds) have been recorded, with the average being about 6.5 (14.0-14.5 pounds). These greater weights probably reflect the fact that Russian herds are well managed, the herders practicing selective breeding and keeping the ranges in good condition. Alaruikka (1959: 18) observed that the reindeer calves in northwestern USSR were considerably

larger at birth and at five months than those in northern Finland. In Herre's (1955) opinion, however, birth weights are not completely indicative of the final mature weight attained; the level of nutrition during the first few years of life plays an important role. Work by McEwan and Wood (1966) has suggested that growth continues in the caribou for about six years. This conclusion is supported by data presented later relative to measurements of Alaska caribou.

There is little indication that the birth weights differ between male and female calves. Such a difference, if present, probably would be so small that an exceptionally large sample would be needed in order to reveal it. Krebs and Cowan (1962: 867), however, noted a Russian investigator giving the mean birth-weight of male calves as 14.8 pounds and of females, 14.3 pounds; no further data were presented. In lieu of adequate information to the contrary, the writer has assumed that among Alaska caribou there is no significant difference in size between the sexes at birth (see also Lent, 1964: 44). Furthermore, considering the supposed common genetic stock within Alaska's population, the writer also has assumed that each herd has about the same potential for producing calves weighing about 6 kilograms at birth. Thus, variances from this average would suggest either differences in the body-size of the parturient cows and/or in the animals' physical condition during the pregnancy period.

Subsequent Age-classes.--As with the young of most ungulate species, caribou calves grow rapidly after birth. The animals double their weight in 10-15 days, depending on the initial size, the small ones gaining more rapidly (Palmer, 1934; Krebs and Cowan, 1962). Thereafter, assuming a normal physiological development, the growth-rate depends basically upon the quantity and quality of food ingested relative to the maintenance-energy expenditure. The latter is influenced by certain physiological periodicities (antler and hair growth, reproduction, etc.), by weather, and by a variety of factors affecting physical exertion, such as distance traveled, type of terrain traversed, harassment from predators and flies, etc. Krebs and Cowan (1962), for example, found that mosquito harassment during July actually caused a cessation of growth in one of the reindeer calves being studied. In addition, it has been found that an innate periodicity of growth occurs in species of *Rangifer* and *Odocoileus*. Thus, reindeer have a greatly reduced maintenance-energy requirement during the winter months, with a reduction in food-consumption as well (Kvitkin, 1950). Animals raised in captivity under optimum conditions--caribou (McEwan and Wood, 1966), black-tailed deer (Woods *et al.*, 1962), and whitetailed deer (French *et al.*, 1955; Magruder *et al.*, 1957)--still underwent a reduction in food-consumption during the winter months, with the retardation of growth in young deer and the loss of weight in adults. Such a physiological adaptation has obvious survival value: the maintenance-energy requirement reaches a low point when the food supply becomes

limited during the winter months; conversely, the greatest physiological energy demands (late pregnancy, parturition, lactation, breeding, antler and hair growth, skeletal growth, etc.) occur when food is abundant.

In free-ranging populations of these animals it seems likely that growth actually ceases during most winters, although mild weather and food abundance in some years probably would prevent a complete cessation. Thus, McEwan and Wood (1966: 408) found that caribou in the wild required about 6 years to achieve the same size reached in 2 years by captive animals under optimum nutritional conditions. The latter animals continued to grow during the winter months, but at reduced rates. Georgeson (1904) stated that caribou and reindeer did not reach their prime until 6 or 7 years of age; Palmer (1934) indicated that Alaska reindeer attained full size at about 5 years. Data presented later (Tables 2-7) for Alaska caribou show that the males do not reach full size until at least 6 years of age, and the females, until at least 3 years. Lent (1964: 45) noted the apparent cessation of growth during winter in caribou calves of the Arctic herd in northwest Alaska. On the other hand, Gul'chak (1950) reported that in Russian reindeer herds young animals can increase their body weight in winter by 15 percent on good pastures, but will lose 20 percent on poor.

There is little doubt that abundant, high-quality forage is necessary for caribou to attain their genetic potential for maximum size. For this to occur, the food supply must be readily available during much of the year, and it is especially important during the first and second years of life when the greatest percentage of the total skeletal growth occurs. Obvious differences in the quantity, quality, and availability of forage occur in the regions occupied by caribou; many of these differences can be related to climate. In sub-arctic Alaska, for example, forage is abundant and generally of high quality during May-September; thus, calves have a full 4-month growth-period before the winter weather arrives. In the Arctic, the growing season for plants is much more restricted (Britton, 1957); calves are born one to two weeks later (Lent, 1964, 1966a) and their growth-period is limited to about 2-1/2 months, mid-June through August. In the high arctic, such as Ellesmere Island, the growing season for plants is restricted mostly to July, during a period of 40 days or less (Tener, 1965); thus the growth-period for caribou calves must be even more restricted. The same relative differences between these various regions also would obtain for the older age-classes. Of course, weather conditions during some years could alter the situation significantly. On the average, however, one might expect larger animals in those areas having the longer growth-periods.

In the course of my field studies in Alaska, I have been able to gather a series of body weights and measurements from 724 caribou. These represent four herds: Alaska Peninsula, Arctic (northwest Alaska), Fortymile (east central Alaska), and Nelchina (south central Alaska). Tables 2-7 present the measurements taken with respect to total-weight, total-length, hind-foot, metacarpal/femur lengths, and the length of the mandible (ramus). I examined most of these animals myself, and the measurements were taken by me or by research assistants; the remaining few were examined and measured by various workers at hunter check-stations.

Most of the total-weights are reconstructed from "field-dressed" carcasses (eviscerated only). The complete weighing of 186 animals established that the viscera (including trachea, lungs, heart, liver, kidneys, digestive and reproductive tracts, plus the various mesenteries) averaged 27 percent (range: 22-33 percent) of the total weight and the "field-dressed" carcass 67 percent, with blood loss estimated at 6 percent. The last item is a rather variable item, depending upon where the animal was shot; e. g., a lung-shot removes a large percentage of the blood, as compared with the head- or neck-shot which leaves much more of it remaining in the muscle tissue. All total-length measurements were taken along the body contour of the head and vertebral column, from the tip of the nose to the posterior end of the last tail vertebra; the hind-foot measurements are standard, to the tip of the hoof (c. u.); the lengths of the metacarpal and femur bones are the maximum longitudinal measurements.

Table 2. Total-weights of Alaska caribou, tabulated according to age-class and season—Arctic and Nelchina herds.

AGE CLASS	CARIBOU HERD (Location in Alaska)									
	ARCTIC (northwest)				NELCHINA (southcentral)					
	POSTRUT		SPRING		FALL		POSTRUT		SPRING	
	M	F	M	F	M	F	M	F	M	F
Calf:										
Avr.	38.5	33.0	35.5	37.0	57.0		61.0	43.0	56.5	53.5
n	5	1	5	3	3		1	3	11	4
Low	33.5	-	28.5	31.5	54.0		-	38.5	48.0	46.0
High	48.5	-	42.7	40.5	62.5		-	46.0	68.5	59.5
1 Yr:										
Avr.	76.0	59.0	54.5	53.8	100.0	95.0	94.0	71.5	91.5	74.5
n	1	1	5	6	3	1	2	1	7	8
Low	-	-	49.0	45.0	87.0	-	94.0	-	83.5	65.5
High	-	-	62.0	58.2	108.5	-	94.0	-	99.0	94.0
2 Yr.										
Avr.	81.0	81.5	69.0	70.5	134.0	103.5	112.5	102.5	113.5	88.5
n	6	2	5	19	2	2	3	2	6	14
Low	73.0	77.0	57.0	56.0	132.0	102.0	105.0	101.0	96.5	75.0
High	90.0	85.5	77.0	82.5	136.0	105.0	118.5	103.5	133.0	98.0
3-5 Yr:										
Avr.	118.5	87.0	78.0	73.5	181.0	105.0	147.0	108.5	155.0	100.0
n	9	14	13	59	3	6	13	11	7	29
Low	88.5	73.5	61.0	52.5	162.5	98.0	121.0	88.0	140.5	72.7
High	149.5	109.0	93.0	91.0	207.0	118.5	168.0	125.5	172.0	129.0
6 Yr+:										
Avr.	154.5	94.5		77.0	255.0	141.0	181.5	99.5	178.5	110.0
n	15	6		43	9	1	1	3	3	26
Low	133.5	83.0		62.0	200.0	-	-	89.5	167.0	94.0
High	182.5	105.5		90.0	298.5	-	-	115.5	188.0	135.5
Adults 3 Yr+:										
Avr.	141.0	89.5	78.0	75.0	236.5	110.0	149.5	106.5	162.0	104.5
n	24	20	13	102	12	7	14	14	10	55
Low	88.5	73.5	61.0	52.5	162.5	98.0	121.0	88.0	140.5	72.7
High	182.5	109.0	93.0	91.0	298.5	141.0	181.5	125.5	188.0	135.5

NOTE: M = male, F = female; FALL = Aug.-Sept.; POSTRUT = Oct.-Dec.; SPRING = Apr.-June; Measurements in kilograms.

Table 3. Total-weights of Alaska caribou, tabulated according to age-class and season—Alaska Peninsula and Fortymile herds.

AGE CLASS	CARIBOU HERD (Location in Alaska)							
	ALASKA PENINSULA				FORTYMILE (eastcentral)			
	POSTRUT		SPRING		FALL		POSTRUT	
	M	F	M	F	M	F	M	F
Calf:								
Avr.		48.0	68.0	54.0	54.0	52.0	55.5	49.5
n		1	1	1	6	14	5	3
Low		-	-	-	47.5	44.0	44.0	44.0
High		-	-	-	58.0	61.0	64.5	56.5
1 Yr.								
Avr.					94.0	83.5	77.5	76.0
n					21	9	5	7
Low					74.5	74.5	71.5	67.5
High					108.5	91.5	88.0	81.5
2 Yr.								
Avr.	123.5	94.5	112.0	92.0	124.0	104.5	111.0	92.5
n	1	3	3	4	10	7	12	9
Low	-	82.5	102.5	79.5	105.0	88.0	91.5	78.0
High	-	103.5	118.5	108.5	136.0	132.5	136.0	105.0
3-5 Yr:								
Avr.	134.5	100.5	145.0	102.0	158.0		146.5	
n	3	2	1	3	22		26	
Low	126.5	95.0	-	93.5	115.5		113.5	
High	140.0	106.0	-	115.0	186.5		190.0	
6 Yr+:								
Avr.		105.0	141.0	108.5	203.5		188.0	
n		5	2	3	15		5	
Low		88.0	137.0	106.5	183.0		169.5	
High		127.0	145.0	112.0	234.0		193.0	
Adults 3 Yr+:								
Avr.	134.5	103.5	142.0	105.5	176.5	104.5	153.0	101.5
n	3	7	3	6	37	33	31	37
Low	126.5	88.0	137.0	93.5	115.5	88.0	113.5	81.5
High	140.0	127.0	145.0	115.0	234.0	128.5	193.0	136.0

NOTE: M = male, F = female; FALL = Aug.-Sept.; POSTRUT = Oct.-Dec.; SPRING = Apr.-June; Measurements in kilograms.

Table 4. Total-length measurements of Alaska caribou (by age-class).

AGE CLASS	CARIBOU HERD (Location in Alaska)							
	ALASKA PENINSULA		ARCTIC (northwest)		FORTYMILE (eastcentral)		NELCHINA (southcentral)	
	M	F	M	F	M	F	M	F
Calf:								
Avr.	1600	1500	1420	1410	1500	1410	1590	1500
n	1	2	10	4	7	15	20	9
Low	-	1470	1350	1240	1350	1300	1350	1400
High	-	1520	1550	1520	1600	1580	1730	1600
1 Yr:								
Avr.			1610	1610	1740	1650	1830	1750
n			7	6	16	9	17	11
Low			1500	1550	1630	1420	1730	1630
High			1730	1680	1830	1830	1930	1880
2 Yr.								
Avr.	1930	1840	1750	1690	1780	1720	1970	1820
n	4	7	8	24	11	9	14	23
Low	1910	1750	1650	1550	1600	1590	1850	1700
High	1960	1960	1930	1830	1980	1960	2130	1960
3-5 Yr:								
Avr.	2150	1850	1850	1760	1980		2050	1900
n	4	5	25	77	20		29	60
Low	2060	1780	1680	1630	1780		1850	1650
High	2180	1960	2010	1910	2210		2230	2080
6 Yr.+:								
Avr.	2120	1930	1990	1780	2030		2200	1920
n	2	9	16	47	10		12	48
Low	2060	1700	1780	1650	1910		2110	1730
High	2180	2060	2160	1880	2160		2310	2110
Adults 3 Yr+:								
Avr.	2140	1900	1900	1770	2000	1800	2090	1910
n	6	14	41	124	30	36	41	108
Low	2060	1700	1680	1630	1780	1580	1850	1650
High	2180	2060	2160	1910	2210	2030	2310	2110

NOTE: M = male, F = female; measurements in millimeters.

Table 5. Hind-foot measurements of Alaska caribou (by age-class).

AGE CLASS	CARIBOU HERD (Location in Alaska)							
	ALASKA PENINSULA		ARCTIC (northwest)		FORTYMILE (eastcentral)		NELCHINA (southcentral)	
	M	F	M	F	M	F	M	F
Calf:								
Avr.	535	480	475	455	485	475	530	510
n	1	2	10	4	11	16	19	11
Low	-	465	430	435	455	440	490	475
High	-	490	495	475	520	495	560	535
1 Yr.								
Avr.			525	505	555	535	580	555
n			6	6	18	14	17	13
Low			510	495	520	520	565	535
High			535	525	585	570	605	585
2 Yr:								
Avr.	595	560	545	520	570	545	605	570
n	4	7	11	24	19	13	15	23
Low	580	535	510	485	530	535	570	555
High	615	602	560	545	595	585	640	595
3-5 Yr:								
Avr.	595	550	560	525	590		610	580
n	4	5	25	81	35		34	62
Low	580	515	520	485	520		580	545
High	620	570	595	555	630		650	630
6 Yr:/:								
Avr.	570	550	580	530	595		615	580
n	2	9	14	47	13		12	51
Low	560	520	545	495	570		600	545
High	580	570	600	560	635		630	620
Adults 3 Yr/:								
Avr.	585	550	565	525	590	555	610	580
n	6	14	39	128	48	62	46	113
Low	560	515	520	485	520	495	580	545
High	620	570	600	560	635	585	650	630

NOTE: M = male, F = female; measurements in millimeters.

Table 6. Metacarpal and femur total-length measurements of Alaska caribou (by age-class).

AGE CLASS	CARIBOU HERD (Location in Alaska)							
	ARCTIC (northwest)				NELCHINA (southcentral)			
	METACARPAL		FEMUR		METACARPAL		FEMUR	
	M	F	M	F	M	F	M	F
Calf:								
Avr.	176	174	232	237	199	185	271	
n	10	2	5	3	12	4	5	
Low	160	167	220	226	176	175	263	
High	184	181	241	247	205	196	280	
1 Yr:								
Avr.	197	193	266	260	216	207	285	285
n	6	5	6	4	7	6	1	3
Low	182	188	251	248	214	204	-	280
High	208	200	279	269	221	210	-	290
2 Yr:								
Avr.	207	198	283	278	225	212		307
n	8	22	3	26	11	12		3
Low	201	185	270	257	220	205		296
High	211	210	294	298	237	218		315
3-5 Yr:								
Avr.	211	199	297	283	227	217		318
n	25	75	18	70	26	28		7
Low	194	180	284	262	210	205		301
High	229	218	306	303	239	230		335
6 Yr+:								
Avr.	215	202	296	284	229	215	350	315
n	15	44	1	41	6	16	1	1
Low	207	189	-	262	222	201	-	-
High	221	216	-	303	238	228	-	-
Adults 3 Yr+:								
Avr.	213	220	297	284	227	216	350	318
n	40	119	19	111	32	44	1	8
Low	194	180	284	262	210	201	-	301
High	229	218	306	303	239	230	-	335

NOTE: M = male, F = female; measurements in millimeters.

Table 7. Ramus total-length measurements of Alaska caribou (by age-class).

AGE CLASS	CARIBOU HERD (Location in Alaska)			
	ARCTIC (northwest)		NELCHINA (southcentral)	
	Male	Female	Male	Female
2 Yr:				
Avr.	260	252	272	261
n	33	38	207	87
Low	246	237	255	248
High	281	269	289	280
3-5 Yr:				
Avr.	289	264	298	274
n	294	159	487	336
Low	258	241	272	251
High	314	291	322	292
6 Yr+:				
Avr.	300	266	316	282
n	92	60	180	159
Low	276	250	299	267
High	320	290	346	296
Adults 3 Yr+:				
Avr.	292	265	303	277
n	386	219	667	495
Low	258	241	272	251
High	320	291	346	296

NOTE: Measurements in millimeters.

The classification of animals by age-class is based upon the sequence of tooth eruption and replacement until the full dentition has been attained at 2-years of age, and thereafter upon relative wear on the molariform teeth. This aging technique is described in more detail in a later section discussing the age-structure of the Nelchina herd (see Part III, "Population Structure"). The method is accurate for animals less than 3-years old, and is adequate for the groupings designated for older animals. Some error in the aging of these older animals undoubtedly has occurred, however, and the future use of more accurate techniques, such as annuli in tooth cementum (Sergeant and Pimlott, 1959; McEwan, 1963; Gilbert, 1966), probably will remove some of the overlap evident in the present data.

Because of the seasonal fluctuations in body condition, the data on total-weights have been grouped according to three time-periods: fall (August-September), postrut (October-December), and spring (April-June). These best illustrate the changes that occur as a result of breeding activity and of a lowered energy balance during winter. The skeletal measurements presented encompass the same time-periods, i. e., August through June, except that the August data are not included for sub-adults (calves, yearlings, and 2-year olds). Most of all the weights and measurements were taken during October-November and April-May.

The loss of weight occasioned by adult bulls during the breeding season is a well known phenomenon among cervids. Klein (1965: 278) has stated that adult black-tailed deer bucks experience an average weight-loss of approximately 20 percent during the rut, and that food intake may cease entirely. Palmer (1934: 9) observed in adult reindeer that "During rutting in the fall, the bucks may lose as much as 50 pounds." This represents about a 10 percent decrease in total-weight. Similar losses were recorded earlier (Skoog, 1956: 100) for caribou bulls in the Fortymile herd, and are suggested further by the present data. No significant change in weight has been detected in the adult cows during this same period.

Weight-losses during the winter can vary considerably from year to year, depending upon the severity of the weather and upon forage conditions. Table 2 presents the differences detected between the Arctic and Nelchina herds for this period. It will be noted that among the adult (3-years-old+) animals the average weight losses between the postrut and spring periods were considerably greater in the Arctic herd as compared with the Nelchina. In the latter, the cows essentially maintained their weight and the bulls actually gained. In both herds, most of the spring weights were obtained during late April, before the added energy drain of the last month of pregnancy on the cows. Considerably larger samples are needed, however, before the significance of such differences can be determined. The annual cycle in the physical condition of caribou is discussed in more detail in a later section (see Part I, "Boreal Adaptations").

A significant sexual dimorphism occurs in the body-size of caribou. The skeletal measurements (Tables 4-7) point out strong differences between the sexes for all age-classes. In addition, the data reveal that females have attained most of their skeletal growth by the end of their fourth summer (3-1/2 years of age). The length-of-ramus measurements (Table 7) suggest that some growth also occurs after that age in animals of the Nelchina herd, but not in those of the Arctic herd. In the males, however, all measurements indicated continued skeletal growth till at least 6-years of age. The total-weights (Tables 2 and 3) demonstrate further this sexual dimorphism, although the samples for sub-adults (less than 3-years of age) are not adequate for definite conclusions. Palmer (1934: 18), however, had noted among Alaska reindeer that by 6-months of age the males weighed about 20 pounds more than the females; in yearlings the males were about 30 pounds heavier; and at 2-years of age, about 60 pounds heavier.

On the basis of the data presented, plus other measurements not included (height-at-shoulder, body, ear, and tail), the writer would designate the average body-measurements for adult Alaska caribou in late September as follows:

Measurement	Adult Male: 6-yrs.+	Adult Female: 3-yrs.+
Total-weight	190 kg. (400 lbs.)	100 kg. (220 lbs.)
Total-length	2,100 mm. (82 in.)	1,830 mm. (72 in.)
Hind-foot	595 mm. (23.5 in.)	550 mm. (21.5 in.)
Height-at-shoulder	1,260 mm. (50 in.)	1,100 mm. (43 in.)
*Body	1,270 mm. (50 in.)	1,070 mm. (42 in.)
Ear	140 mm. (5.5 in.)	130 mm. (5 in.)
Tail	180 mm. (7 in.)	150 mm. (6 in.)

* Body measurement: straight-line, from head of humerus to posterior end of ischium.

Animals from the Arctic herd average somewhat less than the above measurements; those from herds to the south, somewhat more.

Comparisons.--An examination of body-measurements from four herds has revealed that the Nelchina animals average the largest, although not much more so than those in the Alaska Peninsula and Fortymile herds. Individual animals, however, are known to reach the greatest size in the Nelchina group. Two adult bulls (6-years+) have been weighed in late September at 298.5 kilograms (655 pounds) total-weight; such large animals are not common, however. Unfortunately, it has been difficult to obtain many measurements from adult bulls in any of the herds, but field observations suggest a wide variance in size among these animals. A similar large variance occurs among the adult females. Nevertheless, it is quite evident from the data presented that animals from the Arctic herd average smaller in every category of the measurements taken. Except for the length-of-ramus data, some of the sample sizes for certain age-classes are rather small, yet all measurements indicate the same differential in size. Differences between the sexes and between herds are evident after the first summer of growth. The total-weights (Tables 2 and 3) listed for calves serve as an example: 26 male calves from the Fortymile and Nelchina herds averaged 56.0 kg. (123 lbs.) and 18 females, 50.5 kg. (111 lbs.); comparable weights in the Arctic herd were 37.0 kg. (81 lbs.) for 10 males and 36.0 kg. (79 lbs.) for 4 females. The skeletal measurements (Tables 4-7) substantiate these

differences, which become accentuated in the yearlings, but then continue at about the same magnitude for subsequent age-classes.

Interestingly enough, the sizes of the Alaska Peninsula animals compare favorably with those obtained from the two Interior herds (i. e., Fortymile and Nelchina), in spite of the fact that this group has remained isolated from other caribou since prior to 1900 (see Part II). In 1902, J. A. Allen described the Alaska Peninsula caribou as a new species (Rangifer granti), quite small as compared with animals from interior Alaska; skeletal measurements taken from 5 adult bulls and 2 adult cows (Allen, 1902: 125) were mostly below those obtained in this study (1963-64), and were characteristic of those obtained for Arctic animals. For example, the total-length measurements ranged from 1,727 mm. to 1,905 mm. in the bulls, and the cows measured 1,651 and 1,664 mm. The only known change in breeding-stock that has occurred since 1902 has been the addition of "hundreds" of reindeer from Alaska Peninsula herds abandoned during the late 1930's and early 1940's.

Skeletal measurements are not available for Alaska reindeer (eastern-Siberia stock), but body-weights indicate that these animals compare closely with Arctic caribou in size. Rood (1942), who was the Reindeer Supervisor for the Alaska Native Service during the early 1940's, reported in an informational leaflet that the average dressed-weight of 15,396 adult reindeer from western Alaska was 107 pounds (48.6 kg.) during the period 1931-1941. He noted further that the dressed-weight (minus viscera, head, hide, feet)

averaged 52 percent of the total, the latter thus averaging about 206 pounds (93.6 kg.). Prior to 1925, when the ranges were in better condition, the dressed-weight had averaged 150 pounds (68 kg.) and comprised 58 percent of the total (Palmer, 1926); the total-weight then averaged 260 pounds (117 kg.). Presumably the decrease in body-size was attributable to depleted ranges and a lowered quantity and/or quality of forage. All the above weights pertained mostly to females and steers in late summer; the "intact" bulls, which are saved for breeding, averaged much larger (300 to 400 pounds; Palmer, 1934).

The influence of range quality upon the size of reindeer has been demonstrated in work done by Klein (1959, 1964b, and 1968) on St. Mathew Island in the Bering Sea. In August, 1944, Alaska reindeer (24 females and 5 males) from Nunivak Island were released on St. Mathew. By 1957 these had expanded to 1,350 animals (11/sq. mi.); in 1963, there were 6,000 (47/sq. mi.); but during the winter of 1963-64 the population crashed to less than 50 animals-- the result of overpopulation, depleted winter forage, and severe winter weather. Based on his population and range studies in 1957, 1963, and 1966, Klein has stated (1968: 356), "In 1957 the St. Mathew Island reindeer were in excellent condition, exceeding weight ranges of reindeer in domestic herds....decrease in body weight and skeletal size in 1963 was undoubtedly the product of poorer nutrition, as a result of the increased population pressure....adult weights in 1963....

were nonetheless comparable with those from domestic herds...." Weights obtained from two calves in early August, 1957, were 97 and 107 pounds (44 and 49 kg.); in late July, 1963, three calves were weighed at 62, 64, and 70 pounds (28, 29, and 32 kg.), significantly different, yet comparable to the weights obtained for calves of the Arctic herd (see Table 2). Total-length measurements for the adults examined during all years (males, 1700-2023; females, 1623-1743 mm.) were within the range listed for the Arctic herd; hind-foot measurements, however, were considerably lower (adult males, 476-515; adult females, 456-464 mm.), being typical of the characteristically shorter-legged reindeer. The differences obtained in skeletal measurements between 1957 and 1963 were considered to be statistically significant, the lower measurements of 1963 being attributed to poorer nutrition during the main growth years (first, second, and third summers of life).

A comparison of Nelchina caribou on different ranges also shows size differences that probably can be related to nutrition. In 1958 and 1959 I participated in the transplant of 23 caribou calves from the Nelchina herd near Anchorage, Alaska, to Adak Island (290 sq. mi.) in the Aleutians. By 1966 the population was in excess of 130 animals (D. R. Klein, personal communication). The Refuge Manager, R. D. Jones, Jr., of the Aleutian Islands National Wildlife Refuge has told me that the animals seem to be significantly larger than the average Nelchina stock. One

adult bull measured as follows: total weight, 666 pounds (300 kg.); total-length, 2,565 mm.; body-length (humerus-ischium), 1,670 mm.; and height-at-shoulder, 1,422 mm. (Jones, 1966). This animal greatly exceeded in size any that have been measured from the Nelchina range. Only a few animals from the Adak population have been autopsied thus far, but all have been close to the maximum sizes obtained for Nelchina caribou in the age-classes represented. Forage on this island is abundant throughout the year, and is comprised of excellent stands of grasses, sedges, and fruticose lichens (Jones, 1966); the weather is rather mild, and the snow-cover seldom becomes deep enough to restrict grazing, although freezing rain and crusted-snow conditions might be a problem during some years. Thus, the area is near optimum at present for the rapid, maximum growth of individual animals, as well as of the population as a whole. It will be interesting to observe the future changes that occur in both range and animal as the population increases.

Unfortunately, relatively few data concerning the body-size of Alaska caribou are available from past records. A few animals from east central Alaska were measured by W. H. Osgood in the early 1900's and O. J. Murie in the mid-1920's, however, and these permit some comparison with the present data. Osgood (1909: 18) listed body measurements for one adult male and three adult females; total-length and hind-foot measurements were close to the averages presented in Tables 4 and 5 for the Fortymile herd--i. e., male, 2,000 and 590 mm.; females, 1770-1880 and 540-560, respectively.

Some 20 years later, Murie (1935: 13) measured 11 adult males from interior Alaska; these, too, approximated the present-day averages--1,905-2,121 and 584-623 mm. These comparisons reveal no indication of a decrease in size among Interior caribou during the past 60 years. The implication is that the nutrition of present-day animals remains comparable to that of animals in past years,despite the supposed reduction in range quality that has occurred (see Part II, "Population Changes"; the effects of fire).

These various examples serve to point out the influence of environment upon the ultimate body-size attained by animals of the genus Rangifer. Presumably this influence is mediated primarily through the nutritional regimen during the first few years of life, when most of the skeletal growth occurs. Such conclusions appear valid, in view of the similar findings in the numerous studies of nutrition/ungulate relationships carried out by livestock and wildlife researchers (see e. g., French et al., 1955; Klein, 1964, 1965; Magruder et al., 1957; Palsson and Verges, 1952; Taber and Dasmann, 1958; Wallace, 1948). From the data and discussion presented in this section the writer concludes as follows with regard to body-size in Alaska caribou:

1) The main period during which body-growth occurs extends from May through September for animals south of the Brooks Range; for Arctic animals, however, this period probably is restricted to June-August. Skeletal growth presumably stops during the winter months.

2) A strong sexual dimorphism exists, evident after the first summer growth-period and accentuated in later years until physical maturity is reached. Growth essentially stops in females after the fourth summer growth-period, but continues in the males until at least 6-years of age.

3) Animals from the Alaska Peninsula, Fortymile, and Nelchina herds attain comparable body-size, although Nelchina individuals average slightly larger and attain the maximum size; animals from the Arctic herd, however, average significantly smaller. Alaska caribou presumably are of the same genetic stock, and hence the differences noted between herds are thought to be a reflection of different nutritional regimens.

Antlers.

The caribou is unique in that it is the only species of the Family Cervidae (the deer) in which both sexes grow antlers. This phenomenon presents a problem to the biologist attempting to obtain sex-ratios from field observations of live animals. The difficulty relates mainly to the sub-adult animals, however, for the size differential in adults permits rapid identification of the sexes. Antlers of adult bulls are large and massive, with many points; those of adult cows are much smaller, a few being miniature replicas of the bulls', but most, rather spindly and of irregular growth-form. Strangely enough, even the calves bear antlers.

Some adult cows remain antlerless, however. The percentage of such animals varies between populations, and possibly reflects genetic differences or perhaps differences in range quality. Among the American woodland caribou (*R. t. caribou*), for example, Moisan (1959) noted that 30 percent of the adult cows in the Gaspe Peninsula region of Quebec were antlerless. In Newfoundland, Dugmore (1913) had reported that about 10 percent of the females were without antlers; by 1957-58, however, Bergerud (1961a) noted that this figure had increased to 52 percent. The factors responsible for this change are not known. Stefansson (1913: 151) found only 3 antlerless cows among 1,000 checked along the arctic coast of Canada west of Hudson's Bay.

Among Alaska caribou (R. t. granti) this percentage is quite low. In the Arctic herd (northwest Alaska), 1 (0.9 percent) of 114 adult cows autopsied by the writer during 1962-1964 was antlerless; in the same herd, Lent (1965a) reported a figure of 3 percent among 1,100 cows observed in the field during October, 1961. In the Fortymile herd (east central Alaska) 2 (0.6 percent) of 314 carcasses examined by the writer during 1952-1955 were antlerless. In the Nelchina herd (south central Alaska), the figure was 2.3 percent (26 of 1,147 animals) for carcasses examined at hunter check-stations during 1957-1964; a field-count by the writer during October 1-2, 1962, indicated 1.4 percent (14 of 1,009 adult cows). In view of these data, one can state that about 2 percent of the adult cows in the Alaska population do not grow antlers. There has been no indication among the few (13) antlerless cows I have examined in detail that this condition was related to poor physical condition, to senility, or to sterility.

Structure.--Caribou antlers are characterized by great individual variation. No two sets of adult bulls' are exactly the same, and it is even rather difficult to find a set in which one side matches the other. Despite extreme variation, a general pattern is apparent in all antlers. Upward from the burr the beam first turns rearward and laterally, and then curves forward in an arc, so that the tip usually points forward. Generally there are two main anterior tines that branch off close to the burr. The first is called the brow tine; it points forward over the forehead, and among

adult bulls the tip generally is palmated with several small points. One of the brow tines frequently is absent or reduced to a short or long spike. Also, these tines frequently are missing in calves, yearlings, and 2-year-olds of both sexes, and in many adult cows. The second tine, called the bez, branches off the beam a short distance above the brow, swinging forward in a lateral, flattened arc, containing several points and sometimes a moderate palmation. At the most rearward bend of the main beam there frequently is a short tine branching rearward from the posterior side of the main beam. In adult bulls the terminal portion of the beam is usually flattened or palmated, divided into a variable number of rearward-facing tines; this structure is much less evident in young animals and in adult cows.

Murie (1935) classed caribou antlers into three categories: 1) Round, with a minimum of palmation throughout; 2) Flat, in which the palmation occurs in a general flattening of the beam throughout; and 3) Palmated, in which a definite somewhat circular "palm" appears at the end of the beam and principal branches. A front view of caribou antlers indicates there are two general profiles: those which have a "V" or triangular appearance, and those which are more widely diverging and less angular, resembling more or less a flattened "U".

Individual variations are found in the length of the beam; presence or absence of the brow, bez, and posterior tines; structure of the brow, bez, and terminal tines; and spread of the antlers.

Usually only one brow tine is dominant and it extends vertically over the facial region, widely palmated (in adult bulls) with numerous terminal points, while the corresponding tine on the opposite side is greatly reduced or absent, frequently in the form of a single spike. Banfield (1954, 10B: 4) found that in 35 sets of antlers of adult bulls, 69 percent had the left brow tine dominant, 23 percent the right, and in 8 percent they were equally developed. Corresponding figures for Alaska caribou (Arctic, Fortymile, and Nelchina herds) are presented in Table 8. It was found that in 180 sets of antlers of bulls 3-years and older, 3 percent had no brow tines; 49 percent had the left brow tine dominant, 44 percent the right, and in 7 percent the tines were equally developed. In 175 sets of adult cow antlers examined 56 percent had no brow tines; of those with brow tines, 45 percent had a dominant left, 48 percent a dominant right, and 7 percent were equally developed. Bez tines were present in all adult males, but were absent in 15 percent of the adult cows. The antlers of female caribou follow the same general pattern as those of the males, but are much smaller, simpler in development, and often quite unsymmetrical. Sometimes only one antler is present, sometimes the antlers are mere spikes, and on occasion, as already discussed, the antlers do not develop at all. These differences have been an aid in the field identification of animals according to sex and age; the technique is discussed later (see Part III, "Population Structure").

Table 8. Development of brow and bez tines in antler of Alaska caribou (by age-classes).

TINE DOMINANCE	SEX/AGE						
	MALE				FEMALE		
	1 Yr	2 Yr	3-5 Yr	6 Yr+	1 Yr	2 Yr	3 Yr+
BROW TINE:							
n	36	46	124	56	27	37	175
None Present	25	11	5	0	22	32	98
%	69.5	23.9	4.0	0.0	81.5	86.5	56.0
One Present	4	6	25	12	1	3	27
%	11.1	13.1	20.2	21.4	3.7	8.1	15.4
Both Present	7	29	94	44	4	2	50
%	19.4	63.0	75.8	78.6	14.8	5.4	28.6
R Dominant	7	8	56	21	1	2	37
%	63.6	22.9	47.1	37.5	20.0	40.0	48.1
L Dominant	1	22	56	30	4	2	35
%	9.1	62.8	47.1	53.6	80.0	40.0	45.4
Equal	3	5	7	5	0	1	5
%	27.3	14.3	5.8	8.9	0.0	20.0	6.5
BEZ TINE:							
n	40	50	149	74	22	29	138
None Present	6	0	0	0	7	4	21
%	15.0	0.0	0.0	0.0	31.8	13.8	15.2
One Present	2	1	1	0	4	5	23
%	5.0	2.0	0.7	0.0	18.2	17.2	16.7
Both Present	32	49	148	74	11	20	94
%	80.0	98.2	99.3	100.0	50.0	69.0	68.1

Growth.--It has been recognized for a long time that the annual growth and development of antlers is related closely to the periodicities in reproductive physiology (see e.g., Caton, 1877). The precise controls for this growth have not been determined yet, but work by Wislocki (1942, 1943), Wislocki, et al., (1947), and Waldo and Wislocki (1951) on whitetailed deer (Odocoileus virginianus) has suggested the interaction of adenohypophysial hormones and the sex-hormone testosterone. Photoperiodism is implicated also. In caribou, the fact that calves and females also bear antlers indicates that other hormones probably are important as well. Other factors that influence antler development are the genotype, health, and nutritional state of the individual animal. The effects of differences in nutrition have been documented well for deer by a variety of workers (Severinghaus, et al., 1950; French, et al., 1955; Magruder, et al., 1957; Taber and Dasmann, 1958; and others). Inadequate food or metaboloic disturbances (disease, vitaminosis, etc.) can prevent or severely restrict antler growth.

In central and south central Alaska, new antlers begin to grow first upon the large adult bulls (6-years+), starting in late March. A tally of nearly 500 antlerless animals (mostly bulls) of the Nelchina herd March 13-14, 1958, revealed none with new antler growth. The earliest date noted by the writer has been on March 28: a large Nelchina bull had velveted, 5-centimeter knobs. Bulls in the 3-5-year-old age-class start to grow new antlers at a later date.

but usually have 3-8 centimeter knobs by the last week of April. Other animals shed the previous year's antlers mostly after mid-April and start to grow new ones within a few days. In the Nelchina herd this new growth commences in late April or early May for non-pregnant adult cows (3-years +), in early and mid-May for rising 2- and 3-year-old males and non-pregnant females of those ages, and in late May for rising yearlings; most parturient cows retain their hard antlers till parturition and do not have new antler growth until about one week after the birth of the calf. These generalizations are based upon extensive field observations by the author during the April-June periods of 1956-1963. Individual variations and differences between years no doubt occur.

By late August the antlers of the adult bulls are fully grown (among animals of the Fortymile and Nelchina herds). The velvet then loosens and is cleaned off by the animal by rubbing on brush and small trees. The earliest date I have recorded for a Nelchina bull having hardened antlers, polished and free of velvet, was August 23. By mid-September most adult bulls (3-years +) have cleaned, hardened antlers. The yearling and 2-year-old bulls are approximately one-two weeks later in shedding the velvet. The cows lag three-four weeks behind the bulls, and usually it is the end of September before many of the cows have hard, polished antlers; some may have velvet strips remaining well into October. Most calves of the year, growing antlers for the first time, do not

shed the velvet, which simply dries and is retained throughout most of the year. Presumably the control for the shedding of velvet is related to the production of sex-hormones.

Hadwen and Palmer (1922: 7) noted that adult male reindeer castrated during the growth of antlers failed to shed the velvet and retained the antlers until late spring; those animals castrated after growth was completed and the velvet had been shed dropped their antlers within two-three weeks later. Sheldon (1930) reported an unusual circumstance in which he shot a large adult bull on September 28 in Mt. McKinley National Park, Alaska, whose antlers were in full velvet, with blood remaining in the tips. He observed no other abnormalities. I have noted the retention of velvet in five bulls, all examined during late October when all should have had cleaned antlers. Four of these animals were diseased, having a mange-like condition; the fifth was suffering from malnutrition as a result of an intestinal blockage at the pylorus. These various examples serve to point out how physiological disturbances can disrupt the normal development of antlers.

During the period of this study I obtained measurements of the length of antler-beam from 696 animals--representing the Alaska Peninsula, Arctic, Fortymile, and Nelchina caribou herds. The longest antler of each animal was measured along the outside curve from the burr to the tip. Table 9 lists these measurements

according to sex and age-class, relative to the herd to which the animals belonged. The data serve to illustrate antler development in this species, and also permit a comparison between different regions in Alaska.

Calves start to grow antlers when about four weeks old. By 4-months of age most have short spikes ranging from 100 to 200 millimeters in length; 72 animals examined averaged 150 (6 inches). Some of the calves will have forked antlers and a few will have no antlers or merely velveted knobs. Murie (1935) stated that he had never seen more than a single spike on caribou calves, but noted that forked antlers were rather common among the young of reindeer.

As yearlings, both the male and female bear antlers comparable in size and appearance. These range from about 200 to 600 millimeters in length; 71 animals averaged about 400 (16 inches). Brow tines usually are absent, or if present are merely small spikes; the bez tines generally are present, but may be absent in some. As noted in Table 8, about 70 percent of the males and 80 percent of females lack brow tines; these figures are 15 and 30 percent, respectively, for the bez tines.

In 2-year-old animals the antlers begin to look more adult-like in appearance, and the differences between the sexes start to become more apparent. In 54 males examined the antler-beam length ranged from 317 to 813 millimeters, averaging 575 (23 inches); in 46 males, 24 percent had no brow tines, but all had bez tines. In 50 females examined the length ranged from 254 to 660 millimeters,

Table 9. Length of antler-beam in Alaska caribou, as related to sex, age-class, and herd.

AGE CLASS	HERD/SEX									
	ALASKA PENINSULA		ARCTIC		FORTYMILE		NELCHINA		TOTALS	
	M	F	M	F	M	F	M	F	M	F
Calf:										
Avr.		144	114	165	157	170	169	122	155	145
n		3	9	1	10	11	24	14	43	29
Low		127	25	-	76	63	70	13	25	13
High		178	191	-	229	305	317	203	317	305
1 Yr:										
Avr.			343	302	439	380	393	343	410	355
n			4	4	21	11	22	9	47	24
Low			267	279	203	254	203	203	203	203
High			432	330	610	508	533	457	610	508
2 Yr:										
Avr.	642	430	447	379	616	409	568	363	575	390
n	4	7	9	18	22	10	19	15	54	50
Low	610	305	317	273	419	292	356	254	317	254
High	711	482	559	470	813	660	698	457	813	660
3-5 Yr:										
Avr.	937		837		838		819		835	
n	4		20		38		54		116	
Low	838		508		610		482		482	
High	1092		1372		1295		1295		1372	
6 Yr+:										
Avr.	914		1190		1264		1170		1215	
n	1		6		21		17		45	
Low	-		673		1079		642		642	
High	-		1397		1460		1460		1460	
3 Yr+:										
Avr.		493		423		436		436		435
n		15		113		60		100		288
Low		381		222		330		248		222
High		584		711		673		686		711

NOTE: Measurements in millimeters.

averaging 390 (15 inches); 87 percent had no brow tines and 14 percent, no bez. Nevertheless, much overlap occurred in these measurements, and it is quite difficult to identify the sex of animals in this age-class by the antlers alone. The brow tines are still only spikes, if present.

At 3-years of age a distinct separation of the sexes occurs in antler size and structure. The antlers of cows have changed little from the 2-year-old stage. Those of most bulls, however, now have a distinctive brow tine, still small, but having a small palmation; some still have only spikes. The male antlers are longer and more massive than those of the female, however, and field identification of the sexes by this means becomes possible.

Antler conformation in cows older than 2-years of age changes little. There is great variability, however, and one cannot identify the old cows from the young ones on the basis of antler growth. For the most part the antlers remain rather small and poorly formed, but a few approach in size and development those of some of the smaller 3-year-old bulls. Murie (1935) noted that reindeer cows tended to grow rather large antlers, with highly developed brow tines, in contrast to the caribou. Presumably this greater antler growth observed by Murie in the 1920's among reindeer calves and cows reflected better nutrition, due to, perhaps, better forage and a more sedentary existence. The reindeer ranges

at that time still were in good condition. Sheldon (1930) reported a strange occurrence in an adult cow he killed in Mt. McKinley Park on November 24, 1907: the animal had exceptionally large antlers, measuring 51 inches (1,300 mm.) in length. He noted further (p. 222) in a band of antlered cows and calves sighted a few days later that three cows had antlers as large as the animal killed. These observations are quite unusual, however, and I can offer no explanation, unless these animals were strays from reindeer herds far to the west. Reindeer cows are known to have large antlers rather commonly (Murie, 1935).

The antlers of bulls continue to increase in length and massiveness, and reach a peak between 6-9 years of age. After that, as with most deer, the antlers become reduced in size, and frequently the two beams are greatly disproportionate. It is not uncommon to see old Nelchina bulls with one antler about half the size of the other.

The data presented in Tables 8 and 9 point out these differences between the antlers of males and females. Variability between herds is not so readily evident because of the relatively small samples in some age-classes. Nevertheless, the data suggest that bulls in the Fortymile herd tend to have the largest antlers. Measurements of Alaska Peninsula bulls indicate even larger antlers in this sub-population, but the sample size is quite small. On the other hand, Boone and Crockett Club records (based on antler size and symmetry) for trophy barren-ground caribou taken by hunters show that

70 percent of the 469 animals listed come from the Nelchina herd (Baker, 1964). To great extent this record is biased by the fact that most trophy hunters in Alaska concentrate their efforts in south central Alaska. Recent interest in the Alaska Peninsula for hunting during the past ten years, however, has confirmed the presence of many large antlered bulls in that area. The data for adult cows in Table 9 also suggest larger antlers for Alaska Peninsula animals. The antler-lengths listed for cows from the other three herds are quite comparable to one another. Antlers of Arctic caribou seem to be slightly smaller than those in the other herds, expecially in the sub-adults, but the difference is not significant in the samples taken. I had expected to find greater differences, because of my belief that the Arctic animals have a poorer overall nutrition than do those to the south. Larger samples might reveal greater differences. It seems quite probably as well that volume and/or weight would be a better measure for antler size than length, and certainly a better index of the amount of energy expended for growth.

Shedding.--Antlers are shed each year and new ones are grown prior to the following fall. The sequence of antler-drop varies considerably, depending upon age, sex, and physiological state. In adult male reindeer this process coincides closely with the decrease in urine androgen levels following the rut (Meschaks and Nordkvist, 1962). Work by Wislocki (1943) on the whitetailed deer indicated that the shedding of antlers seemed to be related closely to the lowered levels of testosterone secretion.

Such a relationship seems to be present in Alaska male caribou as well, for the large mature bulls (6-years +) drop their antlers shortly after their rutting activity ceases. The earliest date on which I have observed antlerless bulls has been October 14 in the Nelchina herd. By then the rut is over for the bulls in this age-class, although it continues till the end of October for the younger bulls (1-5 year-olds). Between mid-October and the end of November most of the large bulls shed their antlers. By the end of December few older than 3 years of age still are antlered; many of the latter age retain theirs into February, and a few, as late as mid-April. (One animal autopsied April 15, 1963, still had antlers firmly attached.) Rarely, a 4- or 5-year old bull will be seen with antlers during February. Apparently delayed shedding of antlers in mule deer (Odocoileus hemionus) can be related to the more poorly nourished individuals, those in better condition shedding early (Dixon, 1934; Einarsen, 1956). A similar effect probably holds for caribou as well. The above statements for adult bulls are derived partly from autopsies, but mostly from field observations, many made from low-flying airplanes. The animals were assigned to approximate age-groupings on the basis of relative body and antler size.

Two-year old bulls shed during late April and early May. Six animals examined by the writer during the first two weeks of April and twelve during the third week were found to have antlers

still firmly attached. One animal autopsied on April 21, 1961, had shed one antler recently; the remaining antler was attached lightly. Based upon this information I assume that bulls of this age-class do not shed their antlers much earlier than mid-April. Palmer (1946) indicated that reindeer bulls of this age shed during the first part of March; Alaska reindeer are approximately one month earlier in their physiological cycles (antler growth, hair molt, breeding, and natality) than their wild counterparts.

A ground composition count on April 1, 1960, of several bands of Nelchina caribou further substantiated the late antler-drop among young bulls. Of 241 caribou tallied, 52 were males older than calves of the year; 9 of the males were large antlerless bulls (3-years and older); 2 of the remaining 43 antlered animals were judged as 3-year olds (based on body- and antler-size), and the rest were one-two year olds. By mid-May these young bulls probably all have shed. A tally on May 10, 1957, however, indicated that about 21 percent still had antlers. Of 106 bulls in a count of 2,152 Nelchina animals filing into the calving grounds, 100 were classed as 1- and 2-year olds (short 2- and 3-year olds), based upon body-size and antler-development--these animals being "cow size" and having small hard antlers, no antlers, or velveted knobs; 21 of these still retained hard antlers at this late date. The other 6 bulls were classed as "over 3-years old", based on velveted antlers in excess of 100 millimeters (4 inches) and on a body-size significantly greater than a "large cow". The sex of the animals in all of

the above counts was determined by the direct observation of the genital organs.

Calves of both sexes shed their antlers mostly during the first three weeks of May, just about the time they become yearlings. Counts by the writer on May 17, 1957, of Nelchina animals showed that 17 (23.6 percent) of 72 in this age-class still carried the previous year's antlers. In the Fortymile herd, similar counts during May 18-20, 1954, revealed only 1 (2.4 percent) still with antlers among 42 animals observed closely; 4 of the antlerless ones had dropped theirs within the previous week, based on the appearance of the pedicel scabs. Similar counts in the Arctic herd on May 21, 1963, indicated 1 (3.2 percent) antlered animal among 31 observed closely. During May 24-30, 1956, a tally of 230 Nelchina animals of this age-class ("new" yearlings) showed that only 2 (0.9 percent) still had antlers. Nevertheless, a few retain their old antlers into June, and I have sighted several in the first week of June during low-level aerial reconnaissance.

The antler drop in female caribou varies considerably from that in the male, and depends to great extent upon the animals' physiological state with respect to reproduction. All cows carry their antlers at least into early spring.

Adults (3-years +) which are not pregnant shed first. Flerov (1952) stated that among caribou of the Kola Peninsula in the USSR these animals drop their antlers during March and April. The present study indicated the earliest among Alaska caribou to be

about mid-April. One non-pregnant cow (age judged at 7 or 8 years) autopsied on April 18, 1958, had shed both antlers recently; another (similar age) on April 18, 1961, had shed one antler and the second dropped off during the autopsy work. In 18 other non-pregnant adult cows examined during the period April 15-19 all bore antlers which were firmly attached. During the Nelchina calving-ground studies in May, 1956, 1957, and 1958, I made a special effort to collect antlerless adult females without calves. These animals are not very common in the main calving area where most of the work was done, but tend to remain on the peripheries; hence, the sample obtained was small. Nevertheless, among 20 such animals autopsied 17 were found to be non-pregnant; based upon the pedicel scabs or the amount of new antler growth, it was judged that 5 of these had shed their old antlers during April and 12, during the first two weeks of May. The latest indication of shedding was of a female collected on May 17, 1957, which probably had dropped its antlers not more than two days previously. How many non-pregnant cows retain their antlers later than this is not known, but the number must be quite small. Further discussion of this aspect is presented later.

The remaining 3 antlerless cows examined during May (autopsied May 23-25) were pregnant; 2 had shed within a few days previous to the examination; the third, had shed at least two weeks earlier, judging from the amount of new antler growth present (30

millimeters). Earlier shedding in pregnant animals was found in two cows autopsied on April 21 (1961 and 1962). Each had recently shed one antler; in both, the second antler was only lightly attached. Antler-shedding by pregnant females prior to calving is exceptional, however, for by far the majority retain their antlers at least to parturition, and most for several days beyond that. This delayed antler-drop has been known for centuries among reindeer-breeding peoples, and in recent years has been commented upon by a number of workers (Hadwen and Palmer, 1922; Collinder, 1949; Skoog, 1957; deVos, 1960; Lent, 1964). I have used the retention of antlers by pregnant cows as a measure of natality (Skoog, 1957; also, see Part III, "Reproduction"). Palmer (1934) noted that pregnant reindeer cows retained the old antlers for 5-7 days after parturition; Flerov (1952) gave 3-7 days. Lent (1965: 557) concluded from his data that antler retention in these animals....approached but did not exceed 1 week post partum."

The reason for the late shedding of antlers among pregnant cows has not yet been established. Lent (1965: 558) reasoned that "....antler shedding in cows after parturition and antler shedding in bulls after testicular regression can both be explained by a rapid decrease in sex hormone production." Yet, such reasoning does not account fully for the wide variation encountered between sexes and age-classes, i. e., the later shedding of 2- and 3-year old bulls and of calves and yearlings, and the shedding of some

pregnant cows several days or weeks before parturition. Once again nutrition possibly can be evoked as an important influence. As noted earlier, the health and physical condition of deer have been shown to influence antler development to considerable extent (Dixon, 1934; French, et al., 1955; Einarsen, 1956; and Magruder, et al., 1957). Pregnant cows are subjected to rather heavy energy demands during the latter half of the winter. Energy stores in the body often become severely reduced, and the animals' nutritional condition frequently reaches a low level. It seems likely that this condition could have important effects upon the physiological factors causing antler-drop. Similarly, severe winters during some years could result in non-pregnant cows carrying their antlers later than usual. Belanger, et al.,(1967) suggested that the antlers of cows may serve as a calcium "bank".

The importance of antler-shedding among cows in studies of caribou populations lies in its use as an index of natality. In this respect then, it is important to have some knowledge as to what percentage of the pregnant cows retain their old antlers to the time of parturition, as well as what percentage of the non-pregnant cows carry them into the calving period.

I found the first figure to be easily obtained by an aerial count of cows having calves less than 2 days old. Such calves are readily identified by their long, bent hind-legs, their arched back, and their stumbling gait (see Lent's description,

1966a: 702-703); the calves do not lose these characteristics until after 2 days of age. In this case, it was necessary to be assured only that the calf had been born within a few days previous to the count; thereafter the cows shed their antlers rapidly. This type of count necessarily must be made from the air, for a large sample would be difficult to obtain from the ground. I made such counts on the calving grounds of the Arctic herd in northwest Alaska: June 3-7, 1963, and June 7-11, 1964. The first year, 3 cows (1.0 percent) among 314 tallied were without antlers (either shed or not grown); the next year, 22 (4.9 percent) among 451; and in the combined totals, 25 (3.3 percent) among 765 animals checked. As noted earlier, about 2 percent of the adult cows of Alaska caribou can be expected not to grow antlers at all. Thus, the data suggested that about 97 percent of the pregnant cows (in the Arctic herd, at least) will have hard antlers until after parturition.

Data concerning the number of non-pregnant cows which retain their antlers into the calving period are not obtained so easily. Lent (1965) attempted to determine this figure with his 1961 work on the progression of antler-shedding among cows of the Arctic herd. He concluded (p. 556) that "The high proportion (mean of 20%) of antlered cows among those without calves but not pregnant in the June 2 and June 3 counts shows that not all barren cows had shed their antlers by the start of the calving season." It is possible that this conclusion was true, yet certain doubts

exist as to the validity of the figures presented. I have presented Lent's 1961 data (reworked into a slightly different form) and my own 1957 data from the Nelchina herd in Table 10. This tabulation permits a critical examination of field data used to compute antler-retention in non-pregnant cows.

It is evident from the figures presented that discrepancies exist in both sets of data. Such is to be expected because of the changing composition of caribou bands from day to day and hence the difficulty in obtaining samples that are completely comparable. Yet it is possible to evaluate such data to certain extent. My basic assumption used in this analysis is that the vast majority of pregnant cows retain their old antlers until parturition. Thus, the proportion of antlered animals present among adult (2 years and older) cows just prior to the calving period would represent a close estimate of the pregnancy rate at that time (Table 10, Column 2). This proportion would be too high if significant numbers of antlered non-pregnant cows were present. Subsequent counts after the start of calving should reveal a lower pregnancy rate, when based on a count of the parturient cows which can be identified (i. e., those with antlers and/or with live calves). A lower rate results because certain cows lose both their antlers and their calves, and hence cannot be readily identified as parturient cows. In addition, any antlered non-pregnant cows included in the first tally (prior to calving) would be excluded from any subsequent

Table 10. A comparison of data relating pregnancy and antler-retention among caribou of the Arctic and Nelchina herds, Alaska.

DATES OF COUNTS	TOTAL COWS IN COUNT	EST. NO. PREG.	COWS w/LIVE CALF	EST.NO. STILL PREG.OR w/DEAD CALF	COWS TALLIED w/o CALF w/ Antlers	COWS TALLIED w/o CALF w/o Antlers	NON-PREG. COWS w/ ANTLERS	PARTURIENT COWS (w/live calf or assumed preg.) No.	PARTURIENT COWS (w/live calf or assumed preg.) %	CALF MORTALITY INDICATED No.	CALF MORTALITY INDICATED %
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
A. NELCHINA:											
May 21-23	90	76	20	56	52	18	0	74	82	2	2
24-26	242	203	78	125	110	54	0	191	79	12	5
27-31	647	544	449	95	58	140	0	509	79	35	5
B. ARCTIC:											
June 2	241	128	8	120	142	91	22	154	64	0	0
5	261	138	35	103	72	154	0	109	42	29	21
7	148	78	40	38	18	90	0	59	40	19	24
14	1128	598	717	0	30	381	30	748	66	0	0
16	2705	1434	1010	424	12	1683	0	1022	38	412	29
18	1178	624	542	82	1	635	0	543	46	81	13

NOTE: A. 1957 data obtained by writer; calving peak May 25.
B. 1961 data from Lent, 196 (Table 1); calving peak June 5.
2. Estimation of pregnant cows obtained from tally of antlered cows prior to calving:
A. Nelchina, May 7-10, 1957—84% (1,428 of 1,710 cows);
B. Arctic, May 16-24, 1961—53% (5,032 of 9,428 cows).
4. Column 2 minus 3.
7. Column 5 minus 4; minimal if assumed that all those in Column 4 still had antlers.
8. Total of Columns 3 and 5, plus the addition of 3% to latter for pregnant cows w/o antlers (assuming no non-pregnant cows w/antlers).
9. % of Column 1.
10. Column 2 minus 8, assuming both are valid.
11. % of Column 2.

count as soon as they dropped their antlers, and thus the difference between counts would be accentuated further. Nevertheless, all counts of parturient cows (Table 10, Columns 8 and 9) made after the start of calving should reveal a lower percentage than that obtained in the initial count (Table 10, Column 2), provided the sample counts were obtained from caribou bands comparable in composition.

Obviously, the data for the Arctic herd show considerable variation, and indicate that the caribou bands under observation were shifting in composition between the count periods. Thus, the data concerning antlered non-pregnant cows (Table 10, Column 7) cannot be relied upon. If the proportion of parturient cows for June 2 were in fact 64 percent as indicated (instead of the pre-calving estimate of 53 percent), then there could have been no antlered non-pregnant cows in the tally. On the other hand, there could have been more than the suggested 22 antlered non-pregnant cows, if parturient cows that had lost calves also had lost their antlers. In addition, the figure of 30 antlered non-pregnant cows obtained for as late a date as June 14 seems quite unrealistic. It is doubtful that any would carry the old antlers that long. This discussion is not meant to be a criticism of Lent's work, but intends merely to point out that the problem of ascertaining this information is not an easy one. Reliable samples are difficult to obtain.

The data concerning the Nelchina caribou, however, suggest that very few non-pregnant cows retain their antlers into the calving period. Although the samples obtained were rather small, the parturient-cow proportions were quite consistent with that in the large pre-calving count made during May 7-10. Based upon this information and that presented earlier relative to antler-retention among cows with new-born calves, I concluded that the proportion of antlered animals among adult cows just prior to the calving-period can be used as a reliable estimate of natality. In addition to this use, a knowledge of antler development can provide valuable assistance in the field identification of animals as to sex and age. This aspect is discussed later (see Part III, "Population Structure").

The sequence of antler growth, velvet shedding, and antler shedding varies with different populations of caribou and reindeer, depending to a great extent upon the time of breeding and parturition. In Alaska the sequence for the Arctic herds is approximately one week <u>later</u> than for those groups farther south; in northern Canada, two or three weeks <u>later</u>. For reindeer in Alaska, and for many of the populations in Eurasia, the sequence for the annual growth and shedding of the antlers occurs about four weeks <u>earlier</u> than in central Alaska. Presumably the differences noted for Alaska caribou between the sexes and certain age-classes pertain as well to other populations of this species.

Pelage

The hair of the caribou is dense and relatively long, as compared with other deer. It consists of two types: long guard-hairs (and bristles), which constitute most of the hair, and dense underwool lying close to the skin, hidden by the guard-hairs. It is commonly believed that the guard-hairs are hollow, but actually they consist of large, greatly vacuolated, keratinized cells. As with all northern mammals, the caribou has an annual molt which occurs during the summer months. This change of pelage generally starts during April with the mature bulls, followed by the young animals (one-two year olds) and non-pregnant cows. The molt in pregnant cows is delayed until after parturition.

Immediately after the molt has been completed, the animals are a dark brown (clove-brown) color throughout most of the body; at a distance and under some light conditions they look almost black. The few white areas present are startling in contrast, and these include the ventral surface of the tail, the entire perineum, and the "stockings" around each foot immediately above the hooves. White hairs also occur on the inside of the thighs and the belly, and a few on the muzzle and in the neck mane. The cows generally are lighter brown in color than the bulls. Calves born that spring begin their first molt during July (about 1 month of age) and by September they have assumed the dark-brown color phase.

Banfield presented information taken from Sokolov (1959) in which he described an autumn change of coat in addition to the summer molt. The Russian stated (Banfield, 1961: 19), "The lightening takes place due to the fact that beginning with the end of summer longer hairs of white colour grow through the summer hair, which is brown colour, in an ever increasing number and cover up the summer colour. The transitional grey colour of the autumn fur depends on the mixture of white and brown hairs." From this description it would seem that an actual second molt does not occur, but rather a delayed growth of white guard-hairs.

Flerov (1952) indicated that the underwool begins to fall out in March, and the new underwool appears in May, followed by the bristle. (The reader will recall a previous notation that physiological periodicities in most reindeer herds occur about one month earlier than in Alaska caribou.) Traces of the old "wool" sometimes remain in September. Occasionally during the summer the underwool becomes longer than the other hair, and the animal appears to be covered with down. By late August, however, the brown guard-hairs have covered the underwool.

By the end of September the adult bulls have developed a conspicuous white ventral mane on the neck, and frequently have a white band that proceeds posteriorly across the shoulder and along the flank. The pelage of the adult cows and the young bulls is similar to that of the adult bull in general pattern,

but the brown seems to be lighter and the white more grey. As the winter progresses, the hair of all sex and age classes lightens in color, until by late winter the animals appear quite pale. This change is caused by the gradual exposure of the grayish-white bases of the guard-hairs as the hair continues to grow and the brown tips break off.

Individuals are likely to vary greatly, of course, and some are very dark in coloration in comparison with others who are much lighter. Generally, the cows are lighter than the bulls, and the young animals lighter than the old. All animals have a white rump and tail, however, and these are very conspicuous when an alarmed animal raises its tail. By May most of the caribou are rather sorry-looking animals,for patches of hair are falling out and the warble larvae encysted under the skin give a rough, irregular appearance to the hide.

Newborn calves vary greatly in their coloration, ranging from a pale beige to a reddish-brown and dark-brown. Reindeer calves, however, are very noticeably dark brown, nearly black in appearance, with but a few of them having the lighter colors. Although very light-colored animals are not unusual among caribou, especially in late winter, white animals are quite rare. Among reindeer the white animal is fairly common in some herds, as is the spotted or pinto.

The exact time of the molt and the subsequent progress of pelage renewal varies with the sex, age, and physical condition of the animal, and seems to be correlated closely with the development of antlers. Diseased animals or those in poor condition sometimes are still in the process of molting during September. Bogoraż (1904: 75) commented with regard to the reindeer of the Chukchi in eastern Siberia that "Well-fed animals start shedding before lean ones, and grown animals before younger ones. A herd in good condition will finish two weeks earlier than a lean one." Similar comments were made by Hadwen and Palmer (1922) with regard to Alaska reindeer. One can perceive readily that the progression of hair molt can serve as a supplementary aid to the sex-and-age identification of animals in the field.

Dentition

The dentition of the caribou may be classified as sub-hypsodont selenodent (Banfield, 1961), which indicates that this animal is mainly a browser in food habits. As is typical with all deer, caribou do not show the selenodent modifications reached by the bovids, which are almost completely grazing animals. The normal dental formula for this species is (I)0/3:(C)1/1:(P)3/3:(M)3/3 = 34. The incisors are small, graduated in size, I1 being the largest and I3, the smallest. The upper incisors are absent, but the upper canines generally are present in both sexes, although they do not pierce the gum. The lower incisors and the lower incisiform canines are loosely set in their alveoli and are flexible; thus, they seem admirably adapted for the rather soft, finely structured plant-food of the caribou (e. g., lichens, sedges, and forbs). The upper molars are relatively small and extended, the length being greater than the width; the lower molars are small but also more narrow. The permanent premolars are relatively large, hardly different from the molars in width, or even equal to them, and rounded in outline. The deciduous lower P4 has three lobes; the last lower molar, M3, has a weak posterior third lobe.

The eruption and replacement of teeth among the ungulates follow a definite chronological sequence, leading eventually to the full permanent dendition. In caribou and reindeer the latter is completed at approximately 25 months of age. A knowledge of this

sequence provides the means for aging these young animals. After two years, however, other techniques are used, and these are discussed in detail later (see Part III, "Age Ratio"). In an attempt to quantitate the pattern of tooth eruption among Alaska caribou, I examined a series of 187 mandibles from animals of the Arctic and Nelchina herds. Previous work of this sort has been reported by Skunke (1952) for Scandanavian reindeer and Banfield (1954) for Canadian barren-ground caribou. The following discussion pertains only to the lower jaw, although the sequence in the maxillary teeth probably is comparable.

The newborn calf starts life with the incisiform teeth already erupted, consisting of 6 deciduous incisors and 2 deciduous canines. All individuals of 13 calves less than 2-days old and of 6 full-term fetuses had reached the above stage. The deciduous premolars were protruding through the gum, but still had not broken through their epithelial covering. These probably erupt shortly, for 5 calves estimated at 2-weeks of age all had a full set of deciduous teeth (6 I's, 2 C's, and 6 P's).

The first permanent molar is beginning to erupt in some of the calves by mid-August (in 3 of 4 animals checked). This tooth was completely erupted in 5 of 7 animals examined during the last week of September, and in all of 14 animals checked during the first two weeks of October. (In one October animal M2 was beginning to erupt, also.) Thus, for Alaska caribou the eruption of M1 can be placed at approximately 4 months of age.

During the winter growth-retardation period (October-February), apparently no replacement of teeth occurs, judging from 11 animals examined. The deciduous incisors are shed between 10 and 13 months of age, starting in late March. The sequence starts with I1 and continues posteriorly until C is shed, but individual variation in timing seems considerable. Among 12 animals examined April 13-26, 6 had obtained permanent I1's, and one of these also had permanent I2's. In all, M2 was beginning to erupt. Two calves (short yearlings) examined on May 1 had a full set of permanent incisors and canines; both also had fully erupted M2's. In 15 animals examined May 7-20, however, only 3 had a full set of incisiform teeth, and one of these had the M2's. Furthermore, in nine animals examined June 5-10 only 4 had permanent incisiforms; 2 of the latter had permanent M2's. One animal examined on June 15 and one on June 18 each had the incisiforms, but the M2's were only about half erupted. The conclusions from these observations are that the average Alaska caribou has obtained its permanent I1's by 11 months, all 8 incisiform teeth by 12 months, and its M2's by 13 months.

The deciduous premolars are retained through the second winter. The third molar starts to erupt in the fall at about 15 months of age (one in twelve examined August 15-September 16). By 17-18 months all animals have M3's in various stages of eruption, but none were more than half erupted in 34 animals checked October 8-November 15. The growth of this tooth then must cease during the

winter months, for in most animals examined the following April, at 22 months of age, the third molar was just starting to erupt or was only half erupted (11 of 13 animals checked April 13-26). In one animal, taken on April 26, the third molar was completely erupted. Most animals (27 of 29) examined throughout May, however, still did not have a fully erupted M3; in 6 animals examined June 4-9, M3 was three-fourths erupted in all. This tooth was fully erupted in 4 animals examined June 20-22, at approximately 25 months of age.

The deciduous premolars are starting to be replaced in early April (22 months), the earliest record in Alaska being from an animal taken on April 13 in which all deciduous premolars had been shed, with P2 and P3 mostly erupted, and P4 fully erupted. Most of the animals examined (the same as noted above) did not have a full set of premolars until the end of May, however, at approximately 24 months of age. During May 11-20, only 6 of 13 examined had a full set of permanent premolars; June 4-9, all 6 animals had full sets. Conclusions from these data are that the permanent premolars are obtained at 24 months of age. The third molars, and therefore the full dental complement, are obtained at about 25 months of age. Table 11 summarizes the data presented, and compares the results with other sources (i. e., Skunke, 1952, and Banfield, 1954). The Alaska data were derived from the examination of 187 mandibles of caribou during 1957-1964 from the Arctic and Nelchina herds. Of these, 96 were simply cleaned jawbones from various sources and time-periods; the remaining 91 were

examined in the field either from autopsied animals or from hunter-kills. The sample revealed no difference between the sexes in tooth eruption and replacement. Ages were designated on the basis of the date each specimen was examined relative to an assumed birthdate of June 1.

In the course of examining and measuring mandibles from over 5,000 caribou of the Arctic and Nelchina herds, I encountered various dental abnormalities. Those recorded have included extra teeth, missing teeth, retention of deciduous teeth, and the rotation of certain teeth. More specifically, one adult cow had a fourth premolar, either P1 or deciduous P2, on both sides of the mandible; an adult male had two lower canines on each side, both of which appeared to be permanent-type teeth; one adult male and one adult cow had the third molars missing; an adult male had both canines and P2's missing; an adult male was missing both I2's; another male was missing the left P2; both canines were missing on an adult female; both I3's and C's were absent on an adult male; in another adult male both P4's were rotated 90 degrees; an adult female had the left P2 rotated 90 degrees. Banfield (1961) in the course of his taxonomic work found similar abnormalities in the specimens he examined. He considered some of them to be important enough to be exceptions to family and generic definitions, such as the absence of the posterior cusp on the lower 3rd molar. The presence of super-numerary teeth and the absence of teeth have been noted regularly among mammals, however, and the significance of such observations in most cases is not clear.

Table 11. Approximate ages (in months) at which permanent teeth become fully erupted in mandibles of *Rangifer tarandus*.

PERMANENT TOOTH	ALASKA CARIBOU Starts to Erupt	Eruption Earliest	Completed Aver.	CANADA CARIBOU (Banfield, 1954)	LAPPLAND REINDEER (Skunke, 1952)
I1	10	10	11	10	12
I2	10	11	12	10	12-14
I3	11	11	12	10	12-14
C	11	11	12	11-15	12-14
P2	21	22	24	18	30
P3	21	22	24	18	30
P4	21	22	24	18	28
M1	3	4	4	3	4
M2	5	11	13	10	15
M3	15	22	25	17	20
FULL SET	-	22	25	18	30

BOREAL ADAPTATIONS

The caribou ranges farther north than any other deer, reaching into the Arctic as far as the northwestern portion of Ellesmere Island (ca. 82 degrees N. latitude) and adjacent parts of Greenland (Banfield, 1961). The only other ungulate currently living in the high arctic is the muskox (Ovibos muschatus). Both animals probably evolved in the arctic regions, and each exhibits a number of adaptations that permit it to exploit this rigorous environment. Of the two, the caribou seems to have been the more successful, for it has dispersed across a broad spectrum of vegetation types throughout the Boreal Region, and has coexisted and successfully competed with a wide variety of herbivore species. Its great plasticity in habitat utilization can be attributed to certain morphological and physiological adaptations. Some of these are discussed below. The more obvious adaptations which evolve in all mammals, such as age of sexual maturity, maximum longevity, litter size, etc., are not considered; nor are the behavioral adaptations which might be applicable to this section.

A discussion of the evolutionary aspects of behavior is fraught with many problems. How does one distinguish between that which is learned from that which is truly innate? Does an animal actually inherit behavior or only the capability of behaving in certain manner? In reality, all behavior can be considered as merely the outward manifestation of the many physiological processes active within the body. Certainly, the behavior of any

animal depends as well upon its motor capabilities as the morphological structures which have evolved. The concepts of learned versus innate have been discussed thoroughly by Lorenz (1965) and by Skinner (1966). The conflict remains to be resolved, and I do not presume to have an answer. Caribou behavior, therefore, is discussed throughout the manuscript whenever pertinent, generally without regard to its possible innate or learned qualities.

Morphological.

One of the most important adaptations to life in cold regions concerns the conservation of heat. Under extreme winter conditions a caribou may be required to maintain its body temperature against a thermal gradient of as much as 100° C. (a body temperature of ca. +39° C. versus an air temperature of ca. -61° C.). Prolonged periods with air temperatures of -45° C. (ca. -50° F.) or colder are common during mid-winter in many parts of the arctic and sub-arctic. In addition, wind can accelerate greatly the amount of heat lost, as indicated by the studies of Siple and Passel (1945) and of Hart *et al.* (1961).

One means for conserving heat is by the reduction in the relative amount of body surface area exposed to the external environment. Thus, within certain species of mammals, there is a tendency for those races inhabiting colder regions to be larger in size than those in warmer areas (Bergmann's Rule). To a certain extent this generalization appears valid within certain species of the Cervidae, e. g., moose (*Alces alces*; Paterson, 1955) and white-tailed deer (*Odocoileus virginianus*; Taylor, 1956). The various subspecies of caribou do not seem to fit this rule, for the smallest forms are found to the north (Banfield, 1961).

The extremities of northern homeotherms tend to be reduced in size (Allen's Rule), and in this respect the caribou conforms somewhat. Both the tail and the ears are rather short and

well furred. The legs, however, are rather long and not particularly well insulated with hair, although the feet are well covered. (Heat loss with respect to the legs will be discussed in the next section.) The muzzle, too, is large and squarish, but completely covered with hair. The nasal cavities have a much greater volume than in most deer, and it is thought that this is an adaptation associated with the breathing of cold air (Flerov, 1952).

Hair.--Insulation against heat loss is provided by the caribou's dense hair, comprised of long, brittle guard-hairs and short, fine, curly under-fur. The guard-hairs are enlarged toward the tip and thus form a particularly tight, dense coat during the winter when the hairs are long. Hairless regions are extremely few, being limited to small areas around the lips, eyes, and anus. These same areas are those which are most vulnerable to the attacks of flies and mosquitoes during the summer. Added insulating quality results from the large, greatly vacuolated, keratinized cells of the guard-hairs and from the dense, well-developed under-fur. Seton (1937) referred to the "weather-proof-coat" of the caribou. Indeed, the insulating qualities of caribou hair have been known long to man, and the pelts have been used extensively for clothing and for sleeping robes. A common practice among winter caribou hunters who killed more animals than they could handle has been to dress the animals, skin out the legs and tuck them under the body, and prop

the animal on its ventral surface; the carcasses remain unfrozen for 24 hours or more in the coldest of weather. I had occasion to try this technique one winter at temperatures ranging from -45° C. to -50° C. (-50° to -60° F.); the carcasses of two adult cows killed and so handled, remained unfrozen for 20 hours, except for certain areas about the head, such as the lips, eyes, and ears.

Scholander *et al.* (1950a, b, c) attempted to quantify body insulation and heat regulation in some arctic and tropical birds and mammals. In an experiment concerning the insulation quality of the hair of various arctic mammals, they found a good correlation between the thickness of the fur and the insulation, but (in animals from the size of a fox to the size of a moose) no correlation between body size and insulation, i. e., all had about the same insulation per surface area. The arctic terrestrial mammals in this size class examined included polar bear (*Thalarctos maritimus*), grizzly bear (*Ursus horribilis*), reindeer and caribou (*Rangifer tarandus*), Dall sheep (*Ovis dalli*), wolf (*Canis lupus*), Eskimo dog (*Canis familiaris*), red fox (*Vulpes fulva*), and arctic fox (*Alopex lagopus*). The investigators were able to show that these larger arctic mammals were able to maintain their body temperatures without an increase in metabolism in temperatures ranging to -30° C. The critical temperature (that temperature at which the metabolism must be increased) is even lower. They concluded (1950b: 256) " ...from observations on sleeping animals it is probable that their

zone of thermoneutrality extends to -40° C. or -50° C." Thus, the adaptive significance of the caribou's pelage to arctic survival becomes apparent.

Hoof.--Another important morphological adaptation concerns the hooves. These are widely broadened and all four toes are well developed and used. The blunt-toes, crescentic-shaped hoof, with functional lateral digits, is quite different from that found in any of the other deer. Long, bristle-like hairs, which grow very thick during the winter, surround the hooves and form tufts which cover the fleshy pad. The joints of the middle toes can be bent sharply so that the phalanges take on an almost horizontal position. This adaptation provides a considerable increase in the area supporting the animal, and is an aid to winter travel across snow. In winter the edges of the hooves grow quite long, and the footpad shrinks and becomes quite horny; the animal walks on the thin, crescentic, horny rim of its hooves. Caribou can cross crusted snow almost without leaving a trace.

Such a hoof structure provides the caribou with good locomotion on hard surfaces and ice, greatly reducing the chances of slipping; facilitates movement across deep snow and across the bogs and muskegs of the northern regions; and serves as an effective tool for digging in snow for food. The sharp edges of the hoof permit the animal to expose food plants covered with relatively hard, well packed snow. Such digging probably can be done with much less energy

loss than what might be sustained by other animals, such as the muskox and Dall sheep, which have more blunt-edged hooves. Based on hoof structure alone, it would seem that a caribou in feeding could penetrate a harder snow-crust than either of the other two species mentioned, although I have no data to support such an assumption. Finally, by providing the caribou with good traction in difficult terrain, the hoof can be considered an important factor in the survival of caribou against its principal predator, the wolf.

Teeth.--The dentition of caribou reveals certain adaptations also. Its selenodent molar teeth are relatively small, with long crowns, an adaptation believed by Flerov (1952) to be associated with feeding on soft food, such as lichens. The incisors are small, symmetrical, and flexible, not adapted to cutting hard plants, but well suited for picking up lichens and sedges, which do not require any particular strength. Palmer (1944b) noted in his feeding experiments with caribou that they consistently fed upon the finest parts of the forage available, rejecting the coarsest portions, such as the stems of grasses and willows. The small, flexible incisors permit the cropping of the choicest portions of a forage plant with a minimum of damage to the plant itself. In this respect I have noted animals eating willow (*Salix* spp.) catkins and leaves, dwarf birch (*Betula glandulosa*) leaves, and the upper portions of sedges (*Carex* spp. and *Eriophorum vaginatum*) and of fruticose lichens

(*Cladonia alpestris*, *C. sylvatica*, and *C. uncialis*). Such selective foraging results in the gathering of highly nutritious food, in that most nutrients are associated closely with the active tissues, such as leaves and buds (Maynard and Loosli, 1962). The impact upon the range vegetation is reduced also, for it is well known that plants can recover more rapidly (some may even be stimulated to grow at a faster rate) under light grazing than under heavy grazing in which a relatively large portion of the plant is eaten (Sampson, 1952). In addition, the structure of the incisors and the food-selection exhibited permit the utilization of the sparse, low, rather fragile vegetation (mostly certain species of lichens and ground willows) which forms an important segment of certain alpine and arctic communities. Such utilization extends the range of caribou into areas too marginal for most ungulates. Even the muskox seems to require more easily obtained food for its subsistence. Tener's (1963) work in the Queen Elizabeth Islands of the Canadian arctic archipelago showed the caribou there (*Rangifer tarandus pearyi*) were associated commonly with the more primitive plant communities.

Physiological.

There are number of physiological adaptations in caribou that can be related to the conservation of heat and energy. Experiments by Scholander *et al.* (1950c) on various homeotherms suggested that neither body temperature nor basal metabolism is adaptive to environmental conditions; both tend to remain rather constant over a wide range of habitats from the tropics to the arctic. Basal metabolism was found to vary according to the body size of the animal species, as indicated by the formula, Q (in kcal./day) = 70 (wt. in kg.) .75; similar formulae have been derived by Brody (1945) and Kleiber (1947). Hair insulation proved to be the main factor involved in heat conservation. (Work on reindeer metabolism by various Russians is discussed later.)

Thermo-regulation.--An interesting phenomenon was found to exist in arctic ungulates, e. g., the caribou and reindeer, by Scholander *et al.* (1950a). The legs of this mammal present a high surface-area to volume ratio; hair insulation during the winter is only 20-30 percent that of the body. One might expect then a rather high loss of heat from the legs. It was found, however, that the tissue temperatures recorded in the lower legs and hooves were only 10° C. or lower; in addition, fat on the lower legs had a melting point 30° C. lower than the fat of the upper legs. Thus, by being able to maintain normal tissue function in

the legs at temperatures far below the usual body temperature (ca. 39° C.), the caribou is able to reduce the thermal gradient in that area and conserve heat, even though the lower legs are essentially "encased in ice" during most of the winter months. (Table 12 lists the available data on body temperatures in *Rangifer tarandus*.)

Perhaps the most important function of the various adaptations present in the legs, however, concerns body temperature regulation, which becomes possible mainly through a counter-current vascular exchange. Such a mechanism has been found to exist in the flippers of marine mammals, as well, and it functions as an important means for controlling body heat. Scholander (1958) reviewed some of the evidence for this adaptation, and discussed its importance. The anatomical studies by Akaevskii (1939: see p. 221-250; also fig. 119, p. 247) demonstrated the existence of this vascular arrangement in the reindeer. Thus, the legs probably are the principal means for dispersing excess heat, such as might build-up in an animal after a long or strenuous run. Scholander *et al.* (1950b: 256) concluded:

> The very broad zone of thermoneutrality in the larger arctic species, from +30° C. to -40° C., shows their ability to balance an 11-fold increase in gradient and hence the animal can change its heat dissipation by a factor of 11 even when lying down. It is believed that vasomotor control of the poorly insulated legs must play an important role in the general thermoregulation of these animals.

Table 12. Body-temperatures (centigrade) recorded for *Rangifer tarandus*, as obtained from various sources.

AREA	n	TEMPERATURES AVERAGE	RECORDED RANGE	SOURCE
Alaska	280	39.3	37.8-40.6	1. Skoog, this study.
Alaska	19	38.9	37.5-40.0	2. Irving & Krog, 1954.
Canada	4	39.0	±0.78	3. McEwen, et al.,1965.
Russia	8	ca.38.4	37.5-39.2	4. Segal, 1952a.
(Unknown)	?	38.9	37.5-40.0	5. Spector, 1956.

1. All temperatures measured within 30 minutes after the caribou were shot; some of the variance probably resulted from the method of securing the animals; mostly winter-killed animals; all age-classes and both sexes combined; data from Alaska Peninsula (20 animals), Arctic (83 animals), and Nelchina (177 animals) herds.

2. Included 8 caribou and 11 reindeer.

3. All 4 animals were penned caribou calves.

4. Segal found that the body-temperatures in these live reindeer fluctuated about 3 per cent during the day; animals in resting state.

5. Data from both reindeer and caribou.

Metabolism.--The results of recent metabolism studies with reindeer in Russia indicated that maintenance energy expenditures are considerably reduced during the winter. Segal (1962a, b) found that the daily expenditure of energy for a reindeer weighing 100 kg. was 3000-3500 kcal. in winter, as compared with 5000-6000 kcal. in summer; the oxygen consumption was 250-300 ml/kg/hr and 450-500 ml/kg/hr, respectively. Pulmonary ventilation and respiration rate doubled from winter to summer in the animals examined (see also, Makarova and Segal, 1958). Experimenting with 20 reindeer (10 adult males, 5 adult females, and 5 calves), Kvitkin (1950) had obtained similar results. He found the changes in energy expenditures between summer and winter to be most marked in the calves. Such might be expected, because of the normally rapid growth of young ungulates in summer, followed by a growth cessation or severe retardation in northern species during the winter (Wood, Cowan, and Nordan, 1962). Kvitkin suggested that the basic cause for these seasonal differences in metabolism could be related to the quantity and quality of food. Indeed, it seems more likely that the reduced metabolism in winter is an adaptation resulting from the following factors.

First, the interruption in growth mentioned above for young animals occurs in older animals as well, as has been shown for deer by Magruder *et al.* (1957) and Wood *et al.* (1962) and as is implied in the weight data for caribou presented earlier (see

Tables 2-3). This period of growth dormancy occurs irrespective of food supply and sexual activity, and appears to result from an inherent physiological rhythm entrained to photoperiodism (French et al, 1960); a lowered food intake seems to be the main factor.

Second, maintenance energy demands for caribou are much lower during the winter months than in summer. Reduced growth, low energy requirements of the fetus during the first two-thirds of pregnancy (Mitchell, 1962: 547-564), decreased muscle tonus (Segal, 1962a, b), low heat loss (Scholander et al., 1950b), and the general lack of other physiological stresses (e. g., sexual activity, hair and antler growth, fly harassment, etc.) combine to keep the total expenditure of energy to a minimum during that period.

The fat-cycle can be considered a further adaptation of caribou to their energy needs during the year. Although I have not attempted to quantify this cycle, I can describe the seasonal changes in a subjective way, based upon the examination of well over a thousand carcasses. The low point in fat-reserves for adult bulls occurs in late October at the end of the rut. By then these males have expended all or most of the subcutaneous and visceral fat, and start the winter in what might be considered poor condition. The segregation of the sexes and the apparent lethargy of the bulls after the rut suggest an adaptive behavior-ial mechanism which permits the fat-depleted males to replenish

their losses. Certainly the main function of these animals is to inseminate the females, and therefore it is important that they be in prime condition for the rut. In the Nelchina herd the large, most active rutting bulls begin to segregate from the breeding aggregations in mid-October, shortly after the peak of rutting activity. (The younger bulls continue their activity until the end of October.) During this same period the antlers are shed. By November large numbers of antlerless bulls, mostly singles and bands of less than five, can be found scattered over the area where the rut took place and/or along the route followed by the migrating herd. Many of these bulls spend the entire winter near the rutting area; others drift slowly after the main herd and eventually reach the same wintering grounds. By late March, after 4-5 months of mostly eating and resting, these animals have regained sufficient nutrient reserves to start growing new antlers. Fat accumulates rapidly during the spring and summer until the start of the rut in late September, after which the reserves are depleted once again by the rigors of sexual activity. Such behavior tends to characterize the large adult bulls of all the herds in Alaska, and would appear to be of adaptive significance.

In the adult cow, severe energy demands occur during the last two months of the gestation period, and by parturition in late May or early June the animal reaches its low point in the fat cycle. During the summer, lactation requirements, antler

growth, hair molt and growth, and energy expenditures due to fly harassment utilize many of the total calories ingested, and in early September the cow-with-calf still has rather low fat reserves. By that time, however, the molt is completed, the antlers have ceased to grow, and the calf is weaned. Thereafter the cow gradually adds fat through the winter into late March, after which time the growth of the fetus once again begins to deplete the supply. Here too the adaptive significance of a lowered basal metabolism and low maintenance energy demands is evident. The ability of pregnant cows to add nutrient stores during the winter greatly enhances survival (of both the cows and their offspring) during the critical spring period, when energy demands are high and adequate food supplies can be low.

A number of other adaptations are important with regard to nutrition in the caribou. First, the food habits of this species (as discussed later) have evolved so as to provide a maximum, sustained utilization of the food available in the Arctic biome. The range of food items eaten is enormous; the cursory feeding behavior and the periodic shifts in range use insure a continued supply of forage. Second, it seems likely that the caribou rumen has evolved so as to permit the digestion of a wide variety of food types. For example, no other ungulate seems as well adapted to handle large quantities of the very

acidic lichens. Presumably this adaptation necessitated a greater secretion of saliva in order to maintain a proper pH for the ruminal micro-organisms. This aspect requires considerably more study, however.

Third, the digestive processes associated with the rumen produce considerable quantities of heat, which the ruminant animal can use to help maintain its body temperature during cold weather (Annison and Lewis, 1959). The survival value with regard to caribou is obvious. Brock (1966: 201) suggested that this factor probably represented a prime reason for ruminants generally being well adapted to cold climates. Fourth, the recycling of nitrogen via ammonia and urea in the blood, liver, and saliva--a phenomenon characteristic of many ruminants--might well be accentuated in caribou during the winter when the protein intake is quite low, and especially when lichens are the main food. Various research on this important phase of ruminant nutrition has suggested that nitrogen excretion via the urine is reduced when an animal has a low protein diet (Schmidt-Nielson, 1958; Livingston et al., 1962), but more work needs to be done.

Reproduction.--In accord with the caribou's nomadic existence, several adaptations with regard to reproduction have evolved. First, the caruncles of the uterine mucosa have been reduced to only 6 (Range, 3-8; ca. 80% have 6; see Part III, "Reproduction"), as opposed to 88-96 in the domestic ewe and 70-120 in the domestic cow (Harvey, 1962). These structures together

with the fetal cotyledons form the placentomes, which comprise the epithelio-chorial placenta of ruminants. In the domestic ungulates it is common for gravid females to have problems at parturition with retained placental membranes. These tissues become necrotic rapidly, the uterus usually becomes infected, and death can result. Fincher (1941: 400) recorded a 2.3 percent mortality among 3,544 domestic cows with retained placenta, in spite of medical treatment. Obviously there is a selective advantage for wild ruminants to shed the fetal membranes as rapidly as possible. It seems likely that the greatly reduced number of placentomes present in caribou would facilitate the expulsion of both the fetus and the membranes.

A rapid expulsion is facilitated further by the fact that the caribou is monotocous, and thus the single fetus can be expelled while still enclosed in the amnio-chorion, provided the fetal-maternal attachments have loosened. Deliveries of this type occurred in all three births of caribou calves I observed. Expulsion of the complete fetal-sac at parturition occurs commonly in the horse (Hafez, 1962). The natural selection value is clear, but more observations are needed for confirmation in the caribou. Lent (1966a: 714) described in detail two births in the Arctic herd of northwest Alaska; in neither of these was the entire fetal-sac passed, and the placental membranes were expelled 15-30 minutes after birth. In two observations of births in Canada (Lent, 1964: 69) the membranes were expelled 10 minutes and 2 hours, respectively,

after parturition. These few observations are difficult to evaluate, however, for individual variation is commonplace. Various factors can influence the shedding of the placental exuvia. During 1963 and 1964, for example, I found that 15-20 percent of the parturient cows in the Arctic herd were having problems with retained placental-membranes. In a few cows these tissues had been retained for several days, and pathological signs were evident in the uteri examined. The problem in this herd was attributed to a high incidence of the disease brucellosis and also to possible nutritional deficiencies resulting from the late spring thaws during those years (Skoog, 1964). Further work is needed regarding this facet of parturition in caribou.

A second adaptation in reproduction that can be related to the caribou's nomadic tendencies is the rapid development of the calf. The calf is born at a very advanced morphological and physiological state. Field observations by this author and by others (see Lent, 1966a) have indicated that the neonate can stand almost immediately, and can walk for a considerable distance within 30 minutes or so. Such precocity has obvious survival value in a species which moves continually and which inhabits an open terrain where there is little chance of escape from predators except by the animal's own speed. This situation can be compared in part with the East African savanna, where the young of certain plains species (e. g., the wildebeest, *Gorgon taurinus*, and the zebra, *Equus burchelli*) also are extremely

precocious at birth. Talbot and Talbot (1963: 47) considered this precocity of "considerable survival value" with regard to the wildebeest. The caribou calf grows rapidly and in about 10 days has doubled it birth weight (Krebs and Cowan, 1962). Russian work on reindeer has shown that rumination begins in the young calf at about two weeks of age. Calves of that age examined by the author still had but a small rumen, yet the contents were comprised of about one-half vegetation and one-half milk.

In part, the rapid development can be attributed to the high level of nutrition obtained. The chemical composition of reindeer and caribou milk reveals it to be highly nutritious, and thus well suited for the dietary needs of rapid growth. A number of analyses of Rangifer milk have been reported in the literature (e. g., Brody, 1945: 47; Aschaffenburg, et al., 1962: 326; and Bourliere, 1964: 175). Considerable variation is evident in the results presented, but the composition is known to fluctuate widely within most species, depending on the stage of lactation, the portion of the udder sampled, maternal nutrition, etc. (Smith, 1959). An average composition, as derived from the published data, approximates 20 percent fat, 11 percent protein, 3 percent sugar, 1 percent ash, and 65 percent water. Of the mammals which have been examined thus far, apparently only marine mammals' milk exceeds the reindeer's in caloric content. The high fat content also results in much larger quantities (on a per

gram basis) of the fat soluble vitamins A and E, as compared with most mammalian species. Brody (1945: 805) suggested that there may be a close correlation between milk composition and maturing rate. It seems reasonable to assume that each mammalian species probably secretes a milk which is best suited to the particular requirements of their offspring. Thus the highly nutritious milk of the caribou can be considered an adaptation to the rigorous environment into which the precocious calf is born and to the rapid development required for adequate survival.

MOVEMENTS

The extensive, unpredictable movements of caribou are well known. The vast migrations of large herds have been recorded by various people throughout the history of the arctic regions, and such migrations probably were as much a wonder to the ancient peoples as indeed they are to us even in this age. Caribou range widely during the year, and it is quite difficult to keep track of their irregular movements over an extensive area. Sometimes the animals seemingly disappear; sometimes they disperse so thinly that aerial and ground observations are practically useless; and at other times they concentrate into compact herds of thousands. Stragglers may be seen throughout the range at almost any time of the year. Yet an area known for many years to have great numbers of caribou suddenly may be abandoned as the animals change their migration pattern. The caribou seldom remains still for any appreciable length of time. Such restless behavior is a prime characteristic of this animal.

Caribou possess extraordinary powers of locomotion. These, coupled with an inherent nomadic drive, make this a species of great vagility. The usual concept of home-range is not applicable, because over a period of time the herds seem to be continually changing their movement patterns--occupying new ranges and abandoning old. The extent to which this shifting

has occurred in Alaska is discussed in detail later (see Part II, "Population Changes"). This section will examine the factors influencing movements and the periodicity occurring in these movements.

Locomotion

Caribou are well adapted to travel in the northern latitudes, and can traverse great distances swiftly. During the main seasonal migrations they frequently travel throughout the day, snatching up food occasionally as they move along. Field observations obtained from the Arctic, Fortymile, and Nelchina herds in Alaska indicated that the animals will average about 25 kilometers per day during their long migrations. Banfield (1954) reported one herd moving 40 miles (65 kilometers) in a day, and the average of several observations being about 19 miles (31 kilometers). I watched one small band travel about 10 kilometers in 20 minutes with no visible slackening of the pace as they passed from view. The caribou uses a variety of gaits in traveling, all well suited to the animal's nomadic life.

A gallop similar to that of a horse provides the caribou with its fastest means of travel. Banfield (1951) reported the need to drive 45-50 miles/hr. (70-80 km./hr.) to overtake caribou galloping across a frozen lake. He noted another instance when a young bull was clocked at 37 m.p.h. (60 km./hr.). I have had several opportunities to measure the speed of caribou galloping along a road. On one occasion in November, a group of 6 large bulls ran approximately 2 kilometers along a road covered with about 2 inches of hard-packed snow; this group reached 38 miles/hr. (61 km./hr.), as indicated by the truck's speedometer,

and seemed unable to go any faster. On another occasion in November, over a similar surface, a small group af cows and calves was followed; one cow and calf remained on the road for approximately one-half mile (0.8 km.). At 35 miles/hour the calf seemed to be running at its very utmost; the cow apparently could have galloped faster, but seemed to restrict its speed to keep pace with its calf. Caribou tire quickly at a gallop, however, and therefore they use this gait mainly for emergencies. With their heavy coat of hair, the animals become overheated quickly.

The gait used for long-distance running is the trot. The animal using this gait resembles a high-stepping trotter, holding its head high, arching its forelegs, and thrusting them out with precision movements; frequently the hind-legs will be swung in a wide lateral arc. I clocked one animal at 25 miles an hour while trotting over tussocky muskeg. Considering the difficulty that a person has in walking over such country, the caribou's feat seemed amazing. Lomen (1920) recorded reindeer pulling a sled with a man in it over a 5-mile (8 km.) course in 14.5 minutes and over a 10-mile course in 27.5 minutes.

The principal gait for long-distance traveling is the fast walk, used commonly during the seasonal migrations. Judging from the effort required for a human to keep abreast of walking caribou, I believe their speeds must reach 10 km./hr. Pruitt (1960)

recorded an observation of a cow and calf walking on hard, wind-packed snow over a map-measured course of 1.5 miles (1.8 km.) at a speed of 5 miles/hour (8 km./hr.). Such a swift walk allows the animals to cover distances quickly. Indeed, it is almost unbelievable how rapidly a "strolling" band of caribou can disappear from view. Frequently, however, the caribou merely plod along at a slow walk, probably moving no faster than 2 or 3 miles/hour.

Caribou are strong swimmers and take readily to the water. Such behavior is necessary, for the animals must cross many waterways on their long-distance treks. In the water they float higher than most mammals, with the head and back well above waterline. Banfield (1954: p.14) recorded an observation in which a band of caribou swam a distance of 1,000 yards at a speed of about 4 miles/hour (7 km./hr.) without special exertion. When pursued by a canoe they can swim faster for short periods, and under these conditions they probably can attain a speed of about 6 miles/hour (Seton,1927). Calves take readily to water at a very early age, and their mothers do not hesitate to swim rivers with them while they are still only a few weeks old. Personal observations have indicated that the calf usually swims on the downstream side of its mother, but even then the two frequently become separated if the current is strong. In northern Canada some of the river crossings have been sources of high mortality for caribou, because of animals being swept through rapids and over falls (Clarke, 1940; Banfield, 1954). Such mortality

is minimal in Alaska, for there are relatively few streams that have dangerous rapids or waterfalls. The main river crossings take place on the upper Susitna River, the Yukon River at various locations, and the Kobuk, Noatak, and Colville Rivers, plus numerous other smaller streams. I have observed a band of caribou swim across Lake Louise, in south central Alaska, a distance of 5 miles. The caribou commonly swim much longer distances in Canada, where large lakes (e. g., Great Bear Lake) lie close to the path of major migrations. Flerov (1952) stated that reindeer have been observed in the Arctic Ocean swimming from one ice-floe to another. Why caribou would choose to swim among the ice-floes or to traverse great distances in seasonal treks remains unexplained.

Factors Influencing Movements

The caribou's nomadic habit long has puzzled men and has resulted in many explanatory hypotheses. Olaus Murie (1935) reviewed some of these hypotheses and stated his belief that the search for suitable food was the prime cause of migrations, and that the continual searching has resulted in "restlessness" becoming inherent to the race. He suggested (p. 50) that the stimulus for the migrations results from "local failure or seasonal changes of the vegetation" which cause the caribou to search for better food, and that these "local wanderings then take on the nature of a migration....and the animals retrace their ancestral routes."

Banfield (1954, 10 B: 28-30) in discussing causes for migrations stated,

> ...it seems probable that the barren-ground caribou is fundamentally both gregarious and nomadic in behaviour....As a gregarious species the herds are continually in random movement, seeking an adequate supply of food. Superimposed upon these local random movements are annual travel requirements....Local weather and physiography affect routes and periods of movements....Seasonal changes in meteorological factors, food preferences, food production, and reproductive requirements cause a superposition of annual cyclic spatial movements over the territories occupied by the herds.

Banfield's concept elaborates on Murie's idea, and seems able to account for more of the anomalies of caribou movements. That the

nomadic habit, or restlessness, is inherent to the race seems evident. This "drive" causes the caribou to roam continually, and it expresses itself in their daily and seasonal movements. The cursory feeding habit of the animal illustrates well this restlessness. At certain times of the year an apparent intensification of the nomadic drive causes large-scale movements to take place. The exact stimuli for such movements are difficult to determine. Seasonal changes in vegetation alone cannot account for these migrations, and various conflicting movement patterns have been observed both in Canada (Banfield, 1954, 10B: 28) and in Alaska. I observed one such anomaly in 1954. Between April and December of that year, the Fortymile herd moved steadily, making two and a half round trips from the Sixtymile River area in Canada to beyond the Steese Highway--a total of about 1,500 miles. Such a movement had never been recorded in the past, at least during the previous 20 years, according to long-time residents. The factors causing such a movement remain unknown. In most years the herd would have stopped in the Tanana Hills for grazing during the summer months.

Stimuli for large-scale movements could result from exogenous phenomena, such as the amount or intensity of light, or from an endogenous event, such as periodic changes in hormone secretion. Possibly a type of learning similar to that acquired by maze-running animals enables the caribou to follow definite routes during

migration. A homing instinct also is recognized among reindeer, and the animals will return consistently to familiar areas (Lomen, 1920; Palmer, 1926; Turi, 1931; and Paterson, 1956). Food supply, population density, weather, snow-conditions, insects, man, and a variety of other factors can alter the movement patterns seasonally or perhaps for several years.

Endogenous Factors.--Physiological rhythms exert a powerful, but often obscure effect on an animal's behavior. The interaction of the nervous and endocrine systems, often stimulated by cues from the external environment, provides the "drive" for the motor activity of the body. Perhaps the greatest of the internal "drives" are those related to reproduction and hunger, and these influence greatly the movements of caribou.

At the approach of the breeding season in the fall marked changes occur in the distribution of the animals in a caribou herd. As their testosterone levels rise, the mature bulls leave their summering areas (in Alaska these often are far removed from the main herd) and move toward the bands of cows and young animals. The shedding of velvet from the antlers may cause the animals to seek objects on which they can rub their antlers. During the rut, mature bulls move about constantly in the performance of their breeding functions. Their actions in turn influence the movements of the cows, and in fact keep the bands in almost continual turmoil and movement during late September and much of October.

During the spring, some stimulus causes the pregnant cows to move toward traditional calving grounds. In many herds this movement traverses great distances (100-500 kilometers), and invariably involves most of the other animals in the herd as well. During the calving period itself the cows remain mostly above timberline, and many tend to isolate themselves somewhat at the time of parturition. Those with young calves remain particularly alert, and move off at the first disturbance or sign of danger.

The need for food represents a potent force affecting the movements of all animals. In a gregarious animal such as the caribou, the search for food necessitates greater movement than that required in more solitary species. Obviously the total food requirement increases with increasing population densities, and therefore herd animals must shift feeding areas occasionally. In such shifting, the spatial distribution of the food plants necessarily plays an important role. Plant growth depends upon a variety of physical factors, of course; in addition, the availability of plant food changes with the seasons and with certain weather conditions. In the spring, caribou and reindeer avidly seek the new green shoots of various grasses, sedges, and willows. In a local sense the progressive increase in snow-free areas thus tends to direct the spring movements, for the new growth appears quickly once the snow leaves.

Undoubtedly the desire for certain plants exerts some influence on movements at other seasons as well. It is well known, for example, that caribou are particularly fond of mushrooms. Rumen analyses of Fortymile animals indicated that about 35 percent of the diet during late August and early September consisted of this plant food (Skoog, 1956). O. J. Murie (1935) and numerous other authors also have commented upon the caribou's predilection for mushrooms. To what extent caribou will move to find good stands of lichens during the winter is not known. Palmer's (1944b) feeding experiments with caribou and reindeer clearly demonstrated the animal's preference for certain species of fruticose lichens over a variety of other food plants offered. On the other hand, it is known that caribou will remain on lichen-poor ranges some years, even though lichens are available in other areas (see Part II, "Population Changes"). Thus, it would appear that the search for food affects primarily the local movements of caribou, for apparently the animal generally is able to find adequate amounts of palatable food.

Perhaps the most important endogenous factor affecting caribou movements is that which can be related to population densities--termed here, the social stimulus. It has been recognized for some time that the extent of the annual movements within a herd varies with the population size. Banfield (1951: 7) stated, "It has been the general experience during the past century that where herds of caribou have decreased drastically in numbers, the remaining

scattered groups cease to make definite regular movements and carry out local wanderings." Such can be said for the herds in Alaska as well. Those small in size are quite restricted in their movements and in the total area of range utilized. In the Nelchina herd of south central Alaska, I was able to demonstrate a direct relationship between density and the extent of movements. This aspect is discussed in more detail in a later section (see Part III, "Population Dynamics"). Such a relationship also seems to have been an important factor in the population shifts that have occurred in Alaska's caribou population during the past 100 years (see Part II, "Population Changes"). The various data examined suggest that there is a social limitation to the population density that can be attained by a free-ranging caribou population. As this limitation is approached (which I believe to be less than 10 animals/square mile), the movements of the herd become ever more extensive and erratic in nature until eventually an emigration occurs to new ranges. There has been no evidence to suggest that the areal shifts recorded in Alaska's herds during the past have been related to inadequate supplies of food. This behavior can be compared with the various social mechanisms discussed by Wynne-Edwards (1962) for the self-regulation of populations.

Exogenous Factors--Many factors in the external environment influence caribou movements, although none can be considered as being the prime cause of the major seasonal migrations or nomadic wanderings. Yet some exert considerable influence on the timing and direction of these movements. The most important can be classified under the headings of photoperiodism, terrain features, weather conditions, insect pests, and predators.

As with most organisms, photoperiodism plays an important role in the lives of caribou by the entrainment of circadian rhythms and by the timing of various physiological processes. Even though experimentation with caribou has been extremely limited, there can be little doubt that seasonal cycles in the production of some hormones are so triggered. In turn, many of these hormones are known to exert profound effects upon animal behavior, and, therefore, upon movements. The daily activity patterns are closely attuned to the changes in the light-dark schedule during the year, and, as discussed later, certain activities take place during certain periods of the day. For example, major movements of a herd tend to occur mostly during the early hours following sunrise and during late afternoon. Arctic schedules necessarily are at variance in summer and winter because of the extreme light:dark ratios. My field observations have suggested that dark nights inhibit extensive movement; thick fog seems to do likewise.

The influence of terrain features upon movements generally are rather obvious. Some represent barriers to varying degrees. For example, the open waters of seas, large lakes, and swift rivers; even though caribou are excellent swimmers and generally take readily to the water, frequently I have noted how a movement will change direction upon encountering a large lake or river and will parallel the waterway rather than cross it. Rivers filled with floating ice cakes represent barriers, and I have observed caribou migrations stopped temporarily during the spring breakup along the Susitna, Yukon, and Colville Rivers until the ice had disappeared. Kelsall and Loughrey (1957) reported an instance in northern Canada where an ice-choked river held up a migration until almost 100,000 caribou were piled up along one bank of the river. Lent (1966b) reported a similar example for the caribou of northwestern Alaska. Other terrain features that form barriers of sorts are those which represent forage "deserts"--the rock regions of high mountains, volcanic cinder areas (common on the Alaska Peninsula), glaciers, and burns. Banfield (1954, 10A: 32-33) has discussed in detail the effects of forest fires upon the movements of barren-ground caribou in northern Canada. He noted their avoidance of burned areas during migrations and attributed some of the major population shifts to extensive fires on winter ranges. In Alaska these effects are not so evident, because the principal burned

areas are restricted mostly to regions not normally frequented by caribou (i. e., the broad river valleys of the Tanana, Yukon, and Kuskokwim Rivers). In other sections the burns are quite discontinuous in distribution due to the interspersion of extensive alpine areas, tundra, meadows, and wet black-spruce (Picea mariana) muskeg. On the other hand, there are certain other terrain features that tend to facilitate movement. Those that might be mentioned include mountain ridge-tops, eskers, stream-beds, hard surfaced snow-drifts, and frozen lakes and rivers. Caribou frequently utilize such surfaces during their long seasonal migrations, and the last mentioned are particularly important avenues for travel.

Weather in itself does not seem to affect movements much. My field observations suggested that caribou tend to be less active on warm days (move less and travel more slowly) and to display a general restlessness during dark, stormy periods or during thick fog. Kelsall and Loughrey (1957: 9) noted in northern Canada that "On cold days, or during wind storms, they appear to be more restless and move at a greater rate of speed." During periods of intense cold (-50° C. or so) I have observed among Alaska caribou the tendency to remain rather sedentary.

The effects of temperature and other weather components are difficult to evaluate in the field, however, for a variety of other endogenous and exogenous factors are superimposed. Wind, for example, long has been described as an

important influence upon reindeer movements, the animals supposedly tending to head into the wind (Palmer, 1934: 11). Banfield (1954: 19) found no correlation of wind direction and the direction of caribou movements,nor have I. The only time that wind was noted to influence caribou movements during this study has been during the fly season in July and August. When the flies are numerous, the animals will congregate for long periods in windy areas, such as on hill tops and stream beds.

Perhaps the greatest influence of weather results indirectly from the changes occurring in snow conditions during the long winter. Formozov (1946) has discussed thoroughly the influence of snow upon the distribution and movements of Eurasian reindeer and caribou. As one might suppose, the animals tend to avoid those areas where the snow depth or snow hardness becomes so great that it becomes difficult to obtain food. Such areas occur in Alaska along the south slopes of the Alaska Range and of the Wrangell Mountains, and also throughout the Chugach Mountains and coast ranges. Many of these contain excellent stands of forage lichens, which remain unavailable during most of the winter because of the deep snows. Elsewhere, hard crusts on the snow surface can be a problem, caused by thawing and refreezing and/or freezing rains. Such conditions cause reindeer and caribou to move, but if the icing is widespread or if the animals are restricted in some way (i. e., barriers of some kind)

then extensive mortality can occur. In their travels caribou tend to avoid such snow and ice conditions and to feed mostly where the snow cover is relatively thin (generally less than 60 centimeters), especially along windswept ridges, and where the snow is reasonably soft, such as in wind protected spruce forests or shrub thickets. Paterson (1956: 15) stated as follows with regard to Lapland: "In the spring the crust of snow forces the reindeer westwards where the crust appears later. Sometimes this migration goes so rapidly that an entire herd of reindeer in only one night moves 60-70 km...."

The actual distribution of the animals, however, necessarily hinges upon the food supply. The presence of good forage can counteract the repelling effect of poor snow conditions, as evident in the following observation. On several occasions during the winter of 1959-60 I examined the wintering grounds of a large portion of the Nelchina herd (south central Alaska) located on the upper portion of the Talkeetna River. That winter approximately 20,000 animals arrived in early December; the snow depth was about 50 centimeters. The winter was a mild one and a thaw occurred in January and again in February. There was very little snowfall until March, and the snow-cover remained at 40 to 50 centimeters. After feeding in the area for about a month the caribou moved northward 25-30 kilometers for one or two weeks, and then returned to the same area; another

movement out and back occurred during February. By the time of the third visit to the wintering grounds, the surface of the snow had been disturbed throughout the area with feeding-craters, tracks and trails. The surface was quite hard, and the caribou literally had to chop their way through the snow to reach the lichens beneath, displacing chunks of hard snow as large as 30 centimeters in diameter. Yet the animals remained in the area for another three weeks before leaving. I presumed that in this instance, although the snow presented some barrier to the feeding caribou, the abundance of lush lichens (climax alpine stands of Cladonia alpestris) in that particular area probably offset any deterrent effect that the snow might have had. Lent (1961: 3) noted a similar occurrence in northwest Alaska where the caribou remained in an area in spite of having to chop through an ice layer to obtain food.

During their seasonal migrations caribou will traverse country through a variety of snow conditions. Although there is a tendency for the files of caribou to follow the windswept ridges or the ice of streams and lakes, they do not seem to hesitate to cross deep snow and crusted areas when necessary. Pruit (1959) presented an imaginative account of the influence of snow, based on his field observations with regard to the barren-ground caribou of northern Canada. He postulated the existence of "fences" and "corridors" of relative snow-hardness that "herded" the caribou along certain pathways during the

seasonal treks through a region. This interpretation seems a bit far-fetched, although certainly interesting. That snow conditions affect caribou there can be little doubt. To what extent, however, probably depends on a number of factors other than snow-hardness. The location of winter forage may exert much more of an influence than the snow in many instances.

Weather can affect the timing of the spring migration significantly. An early spring and loss of snow generally results in an early movement to the calving grounds; conversely, late lingering snows may delay the movements as much as a full month. Moisan (1959) reported this effect as occurring in the woodland caribou of the Gaspe Peninsula. Lent (1966b) made similar observations with respect to northwest Alaska. I recorded late migrations in the Arctic, Fortymile, and Nelchina herds during the springs of 1962, 1963, and 1964--all years in which deep snows remained in the alpine areas until late May. Why such conditions should delay the movement of pregnant cows to the calving grounds remains unknown. The stimulus for the start of this seasonal migration apparently resides in the external environment, apart from mere photoperiodism.

During the summer months the movements of caribou are influenced considerably by the harassment of certain blood-sucking and parasitic flies of the insect Order Diptera. These include, primarily, various species of mosquitoes (Culicidae), black flies (Simuliidae), and bot flies (Oestridae). Only a

relatively few species are involved in these attacks, but their numbers seem boundless during July and August. Anyone who has traveled in the north country is quite familiar with the swarms of mosquitoes and black flies that one is likely to encounter at times. They seem to attack most warm-blooded animals. Among the bot flies, the warble fly (Oedemagena tarandi) and the nose-bot fly (Cephenomyia trompe) are particularly serious pests and their larvae parasitize the caribou. These are discussed in more detail later (see Part III, "Mortality").

During the height of the fly season in July, many caribou herds are moving almost constantly as they seek to find relief in wind exposed areas. On the arctic tundra "plains" the animals may travel extensively. Hanson (1952) stated that Alaska reindeer will move 15-20 miles (24-32 km.) per day in summer. In most of Alaska, however, the caribou move into the high mountains, and extensive movements cease. At that time one commonly encounters large, compact, stationary groups of animals standing quietly on knolls, ridgetops, and other windswept terrain features. Remnant patches of snow and aufeis (extensive areas of ice formed on many stream beds due to "overflows" throughout the winter) are a special attraction to fly-harassed animals. Shaposhnikov (1955: 200) stated that the low air temperature immediately above the snow (seldom above 10° C. at 1 meter) inhibits the attack of flies. These various behavioral responses of caribou to flies are a wonder to behold. At times,

an entire group will stampede across a mountainside, eventually settling once again on another windswept knoll into the same "fly-harassment" posture--standing quietly, shoulder-to-shoulder, head down. It is readily apparent that Dipteran flies exert a powerful influence upon caribou movements during July (see also, Hadwen and Palmer, 1922; Shaposhnikov, 1955; Banfield, 1954).

Of final consideration is the effect of hunting upon the movements of caribou herds. Banfield (1954) suggested that such a disturbance, particularly with the use of firearms, was capable of turning a migration from its route, and cited one example at Baker Lake, Northwest Territories (Keewatin District). Lent (1966b) noted a similar interference along the Kobuk River in northwest Alaska. These effects probably were local in nature, however. During the course of my Alaska investigations (1952-1964), I have noted no change in the movement patterns of the Arctic, Fortymile, and Nelchina herds that can be attributed to the disturbance caused by hunting activity. In spite of annual depredations by humans along certain segments of the major migration paths of these herds, the animals have continued to move through as before. The differences observed in some years must reflect other factors.

Periodicity In Movements

Wide fluctuations occur in the movements of a caribou herd from day to day and year to year. These are influenced by a variety of factors, some of which have already been discussed. A band may feed peacefully in one area for several days and then travel 30 kilometers or so to another area, remaining there for a day or perhaps several weeks. Within a given locality the band constantly moves from place to place. Over a period of years wintering and summering grounds change, new migration routes may be established, and major population shifts may occur. Yet, in spite of such fluctuations a certain periodicity and pattern are evident in both daily and seasonal movements.

My own field observations have revealed that most of the resting and feeding occurs during the middle portions of the day and night. Caribou generally do their traveling during the early morning and late afternoon, mainly during the three to four hours following daybreak or preceding night. Flerov (1952: 215) indicated that the main resting periods for reindeer were approximately 0900-1200, 1700-2000, and 0100-0600. He also quoted (p. 216) another Russian as saying, "On the Kola Peninsula, the daily life of the deer is not governed by regular schedules. Several times during the day and night they go about grazing and then lie down to rest. In spring and fall, deer lying down can be observed in the first half of the day, from 9 a.m. to 3 p.m." Herre (1955), on the

other hand, stated that "....the reindeer live a quite rigid routine and ruminate at certain regular times. They lie down to ruminate around 0600, 1000, 1300, 2100, and 2400." Banfield (1954) indicated that "Caribou feed casually during the entire 24-hour period, but there are peaks in their feeding activity during the forenoon and evening....during mid-afternoon....long rest periods are taken....it seems that there may also be a period of relative inactivity at night....When migrating, movement is usually made at dawn and dusk." The seasonal changes in photoperiodism alter the behavior patterns somewhat, especially during the constant daylight of the summer. Individual and group variation is common, and some animals are traveling or feeding while others are resting. Turi (1931: 49) stated, "It is only where there is good pasture that reindeer have these fixed resting times...in hungry years the reindeer do not all find food at the same time, and so each animal rests when it has had its food...." As suggested earlier the attacks of flies can have profound effects upon the activity schedule during midsummer. Krebs and Cowan (1962) attributed the cessation of growth in one of the reindeer calves in their experiments to the excessive harassment by mosquitoes and other flies which disrupted the animal's nutritional regimen.

For the reindeer of Karelia ASSR in Russia, Segal (1962a) attempted to quantify their activity schedules. His data are

limited, having worked with only 11 animals in summer and 2 in winter, but nevertheless give an indication of the relative amount of time spent at certain activities. He found that in summer (June 24 to August 8) an average of about 43 percent of the animals' time was utilized for resting (standing or lying down), as opposed to 57 percent for activity (feeding or walking); for winter, these figures were 73 percent and 27 percent, respectively. Feeding activity (searching and ingestion) occupied 53 percent of the time during summer and 25 percent during winter. The decrease evident in feeding during the winter reflects the lowered expenditure of maintenance energy and reduced metabolic rate which have been found to be characteristic of these animals at that time of year (see Segal, 1962b; also, earlier section, "Boreal Adaptations").

The seasonal migrations of caribou are directional, long distance treks. Normally one occurs each spring and early summer as the cows and young stock move first to the calving grounds and then to the summering areas; the extent to which adult bulls participate in this movement varies considerably. Another occurs in the fall and early winter as the herd assembles for the rut and then moves to the wintering grounds. Other large scale movements are apt to occur at any time, however, and the animals may cover as much as 900 kilometers or more. In Alaska, herds of less than 10,000 animals are much more sedentary. Barriers to caribou are few, and mountains, rivers, or lakes offer little resistance to a

migrating herd. It is common for a migration seemingly to flow over the land as if there were not a hill, mountain, or river in sight. More likely than not, one is apt to find caribou at higher elevations than the Dall sheep, and frequently in more rugged terrain.

A principal characteristic of these seasonal movements is their uncertainty. One year the animals come through in great numbers, massed in good sized bands, moving swiftly and steadily in a given direction. Another year the movement may be almost unnoticed, as the animals move through in such small bands that one might think there were few caribou left in the country. In the past these irregularities often created hardships for the natives and miners who depended upon the caribou for food. Even today there are certain groups of natives in Alaska and Canada that suffer privation if the animals do not appear as "scheduled". Although the time, extent, and direction of the migrations cannot be predicted with certainty, definite seasonal movements occur in all populations.

In most herds the wintering grounds and the main calving areas are widely separated, and hence the first major movement generally occurs in the spring. As the days lengthen a stimulus of some kind causes the pregnant females to start moving toward the calving area. As noted earlier, snow conditions seem to influence greatly the timing of this movement. Since these females

usually constitute the largest segment of most wintering concentrations, their movement results in most of the other animals moving as well. Many of the adult bulls are segregated from the others, however, frequently wintering in widely separated areas. Some of these do not take part in this spring movement, and those that do usually lag far behind the others.

In mid-June, at the end of the calving period, most of the animals on the calving grounds assemble into large aggregations, sometimes numbering as high as 20,000 animals (Skoog, 1954), but usually less than 2,000. Olson (1957, 1958) and Lent (1966b) have noted huge concentrations in arctic Alaska at that time. Such aggregations mark the start of the post-calving movement that eventually reaches the summering grounds. The fly season begins during this movement and at its peak in July exerts considerable influence. During the summer a wide dispersal of the herd usually takes place; many of the adult bulls move off into small groups, but the cows and young stock tend to remain in much larger congregations. Extensive movements may occur. As the breeding season approaches in the fall, the bulls move to rejoin the cow segment of the herd.

By late September in Alaska both sexes and all age classes are fully represented in most of the large groups of caribou, and another major movement commences. At first the movement may be slow and leisurely with many stops; the breeding takes place

en route. After the main portion of the rut has ended in October, the movement increases in tempo and the migration toward the wintering ground is in full swing. Once again the large bulls begin to segregate themselves from the main groups of animals and lag slowly behind the others. Upon reaching the wintering grounds the animals again may disperse over a wide area, the bulls tending to be off by themselves. The main concentrations consist of the cows and calves, plus a variable number of young animals and adult bulls.

This general sequence of movements takes place in all the major caribou herds in Alaska, although it is not uncommon for other large scale movements to occur at certain times. A common characteristic of caribou movements and distribution is the segregation of the adult bulls, plus a few young ones, from the main groups of cows and young stock. Usually all age classes and both sexes are fully represented only during the breeding season in October.

The seasonal movement pattern described above encompasses definite areas in the major Alaska herds. Each herd tends to have a reasonably distinct calving area where most of the herd's pregnant cows drop their calves. This area may be rather extensive at times or perhaps quite restrictive, but usually the same general locality is used year after year. The fidelity of herds to a given calving area is discussed in detail later (see Part II, "Centers of Habitation"). Both the summering and the wintering grounds also tend to

be more or less specific for most herds, but a number of different areas are used and considerable variance occurs from year to year. Each year, however, major movements occur between these areas and the calving grounds. Thus, the latter can be considered to be more or less the focal point for the movements and range of an individual herd (Skoog, 1962).

The same routes to and from the calving area tend to be used year after year, and the same river crossings as well. Because caribou frequently move in long files during their travels, after several years deep trails are worn into the ground across the mountainsides. Such trails are evident in all the caribou regions of Alaska, and provide an index to the movement pattern that exists. Dixon (1938: 206) described these as follows:

> When undisturbed caribou often travel in single file....Trails thus formed are a conspicuous feature of the landscape. They average about 14 to 18 inches in width, and in some places the soil has been cut down to a depth of as much as 2 feet by the recurrent travel of generations of caribou. On the soft, springy tundra trails are usually mere depressions from 4 to 6 inches in depth.

The only modification that I would make to the above description would be that most trails measure 10-12 inches (25-30 cm.) in width, and few are wider than 15 inches. "Trailing" is a phenomenon known to all who have spent any time in caribou country, and

it has been commented upon by many authors (e. g., Bogoraz, 1904; A. Murie, 1944; Banfield, 1951; Harper, 1955; et al.). This behaviorism minimizes the total effect of large caribou movements upon the range vegetation by concentrating the destruction along narrow, parallel strips. In comparison, compact masses of reindeer herded across the ranges cause considerably greater damage to the vegetation, especially to stands of lichens.

The movement pattern for a given herd tends to remain rather consistent over a period of time, but certainly cannot be considered as permanent. The wintering grounds can vary considerably from year to year, although certain areas definitely are utilized more frequently than others. The summering grounds are somewhat more stable, and the calving grounds the most fixed of all. The migration routes tend to be of a semi-permanent nature, as evidenced by the deeply worn trails. Nevertheless, a considerable shifting of range use occurs through time, and this too can be considered as being extremely beneficial to the range vegetation.

Banfield (1954, 10A) has discussed distribution shifts with regard to the barren-ground caribou of northern Canada. MacFarlane (1905: 684) presented some pertinent data concerning a shift in the movement pattern of a herd in the vicinity of Reindeer Lake, Northwest Territories, Canada, as obtained from records of the Hudson Bay Company's Post there. In 1873, caribou were not

present in the area, nor had any been seen for several years previous to that time. In the spring of 1874 a large movement northward past the Post occurred, with a return southward in late fall. For the next 10 years large numbers of caribou migrated through each year--north in the spring and south in the fall. In 1884, the animals did not return in the fall, and for the next 5 years no migrations occurred. In the fall of 1889 the southward migration resumed, and in 1890 (last year of records) the north-south movement was again in evidence.

These observations illustrate the dynamic nature of caribou movements, and typify the changes in movement patterns that also have been observed elsewhere. Bogoraz (1904: 132) noted the shift of a migration route that occurred one year in eastern Siberia; the people in several villages starved as a result of the lack of caribou. In Alaska, shifts both in migration routes and in populations have occurred commonly during the past 100 years, and these have been documented in Part II. A discussion of the changing movement pattern in the Nelchina herd during recent times also is presented later (see Part III, "Movement Pattern"). The great vagility of caribou and the wide fluctuations in their movements are of particular importance to the population dynamics of this species.

FOOD HABITS

Caribou live in a wide variety of habitats. Their nomadic behavior takes them over an extensive area and brings them in contact with many different plant communities. In Alaska's mountainous terrain the animals extend their range use to nearly all elevations, from the permanent snow fields high on the slopes to the dense spruce forests of the river valleys, and to the sea itself in tundra areas. As one might expect, caribou are cursory feeders and eat an extraordinary variety of plant food. Their great vagility permits them to avoid "forage deserts" (e. g., burned areas or areas covered with deep and/or ice crusted snow) and to seek out food supplies adequate for maintenance. The only instances known by the writer of caribou starving to death have resulted from an extensive, ice crusted snow-cover, notably on the Alaska Peninsula and on certain islands in the Bering Sea and in the high arctic (see Part III, "Mortality"). The diet varies considerably during the year as seasonal changes in the vegetation occur. Lichens play an important role during the winter in many areas, yet certain other plant foods (e. g., sedges) can be substituted. In some cases the diet may contain lichens only in trace amounts, and thus the supposed need for these plants seems open to question. A discussion of food habits is essential to the understanding of this animal's population ecology.

Feeding Behavior

The restless feeding habits of caribou are well known. The animals continue to move as they graze, frequently remaining in one place no longer than it takes to ingest one or two mouthfuls of forage. Occasionally individuals are snatching vegetation practically while on the run. Such action is especially noticeable during the spring and fall migrations, and also when the animals are being harassed by flies during the summer. Olaus Murie (1935: 41) aptly compared the actions of one young bull to "....a commuter eating breakfast on the run." At certain periods, such as during calving or during mid-winter grazing, the animals feed more leisurely; yet even then they do not stay long in one area and may cover considerable ground in a day. Such cursory grazing and continual traveling tend to disperse the adverse effects of feeding activity and to reduce the possibility of over-grazed range.

These effects are lessened further because of the caribou's preference for only the finer parts of plants. Thus, among the main forage plants, the animals eat mostly the upper portions of lichens, the leaves and stem-tips of sedges and grasses, and the leaves, buds, and stem-tips of willows and dwarf birch. Such fastidious feeding habits were noted in the nutritional experiments of Palmer (1944b); the animals rejected all coarse material in the feed (e. g., grass stems). This behavior is readily apparent from the examination of the stomach contents, which characteristically (throughout the year) are quite fluid in consistency and

comprised of small particles of plant material. In 70 rumen samples examined by the author from animals killed during August 20-September 24, it was found that about 76 percent of the sample volume passed through a screen having a mesh of only 2 millimeters (Skoog, 1956: 127). Swift and Bishop (1963) analyzed 43 rumen samples distributed as follows: June-August, 10; September-October, 10; November-March, 16; and April-May, 7. They found that 88 percent of the samples passed through a mesh size of 5 millimeters, and 78 percent, through one of 2 millimeters. In addition, I have examined in excess of 500 rumens in the field, and the coarsest material found has been willow leaves and small stems (less than 5 mm. in diameter) of willow and dwarf birch. Other field observations by the writer also serve to point out the caribou's rather dainty feeding habits. These include the assiduous plucking of leaves and catkins from willow (*Salix alaxensis*), the stripping of leaves from the stems of dwarf birch (*Betula glandulosa*), and the picking of new sprouts from amidst the tussocks of sedge (*Eriophorum vaginatum*). In climax stands of *Cladonia alpestris* it is especially noticeable how grazing caribou have removed the globular tips of the plants; the exposed grey bases of these grazed plants contrast sharply with the yellow ungrazed plants nearby.

The caribou's habit of taking only a few mouthfuls at each feeding site greatly limits the amount of damage done to a plant. This habit, plus that of eating only the finer plant structures, results in a minimum of growth impairment. Contrast this type of feeding with the intensive browsing and grazing of most other ungulates. The latter commonly results in the death or stunted growth of individual plants; in some instances certain forage plants are eliminated, or severely reduced in abundance, and replaced by less palatable species.

Successional changes in plant composition due to feeding activity have been noted on most ranges utilized by large herbivores (Sampson, 1952: 71-74). With regard to Alaska caribou, however, there is little evidence to suggest that grazing itself has caused such changes. Most of the range damage noted can be assigned to the effects of trampling and trailing, which are especially obvious in those areas which are used seasonally, year after year, during the major movements. On the main wintering grounds the animals tend to disperse widely, and the effects of trampling are not so evident. Field work by the author during February and March, 1958, on the winter range of the Nelchina caribou herd revealed that only about 2 percent of the total feeding area had been utilized by the caribou in a section of heavy use (one feeding-crater in the snow for every 11 square meters of surface area). The caribou had been in that section for approximately one

week, at a density of about 1 animal/hectare. (This study is discussed in more detail in Part III.) Within the 138 feeding-craters examined closely, however, about 95 percent contained uprooted and/or broken portions of plants. Thus, the pawing action used by caribou in winter to penetrate the snow cover probably represents the principal destructuve factor due to feeding activity. Fortunately this destruction to the range vegetation is limited in extent because of the animal's habit of shifting winter ranges periodically.

Most Alaska caribou spend about seven months (October through April) on winter range, obtaining their food from beneath a snow cover of variable depth and hardness. Hanson (1952) has stated that reindeer can easily paw through as much as 60 centimeters of packed snow, and 90 to 120 centimeters of loose snow. I have observed caribou digging through 40 centimeters of packed snow, and on several occasions have recorded animals feeding in snow over 100 centimeters in depth. It should be noted, however, that it is relatively seldom that a free ranging herd must contend with such depths. The great mobility of this species usually permits it to find suitable forage where snow conditions are more favorable. Pruit (1959) has demonstrated to certain extent how snow hardness and depth can influence caribou distribution in the Canadian taiga. In some locales, a complete ice crust occurs occasionally, due to thawing-freezing conditions or to freezing

rains. At those times, in spite of having hooves well suited for pawing aside the snow, the animals may be unable to penetrate the ice layer and starvation can result (see Part III, "Mortality").

The manner of feeding during the winter has been described well by Flerov (1952: 212), quoting from another worker:

> Before starting to dig, the deer lowers its nose and snuffs in air, endeavoring to smell the moss through the snow. It then starts pawing through the snow with its forefoot, at times lowering its muzzle into the hole and sniffing. It then digs away the snow with alternate pawings of the forefeet, until the upper part of the moss is laid bare. The snow covering cements the moss tufts to each other and to the soil and prevents the moss from freezing. The deer tears off only the upper tips of the moss with his lips...and does not actually touch the food with his hooves.

The last statement is not completely accurate in my opinion, for my field observations (as noted previously) have indicated that considerable damage to the forage plants can result from the pawing action. Under certain snow conditions, however, and especially in vegetation stands containing a thick (10 centimeters or more) carpet of fructicose lichens, perhaps this damage is minimal. If the snow cover consists of no more than 8-10 centimeters of loose snow, the animals often push it aside using only their noses (the muzzle is entirely furred). Observations by Segal (1962) of the winter feeding of reindeer indicated that the animals spent about 25 percent of the total feeding time in pawing through the snow.

On the average, he found that each pawing bout lasted about 6 seconds and each ingestion bout, 15 seconds. This relationship would vary, of course, with changing snow conditions.

Use of the olfactory sensory mode to locate forage plants under the snow has been commented upon by a number of workers. O. J. Murie (1935: 40) described the feeding of a blind yearling reindeer on Unimak Island, Alaska; this animal was able to obtain a normal diet, as determined by direct field observations and by a later analysis of the rumen. Formozov (1946: 53) noted that "...lichens of the genus Cladonia give off a strong, fungous smell which is very easily distinguished at a short distance even by man. With the help of scent, deer find, without mistake, lichenous food that is hidden under a layer of snow 40 to 60 cm in depth." I have examined "hundreds" of feeding craters of Alaska caribou and never have found one that did not contain forage plants. Such ability to find food by smell certainly is not surprising, for it is well known that most ungulates have exceptional powers of olfaction.

The new-born calf develops rapidly, and when only a week old attempts to ingest plant material. I have examined digestive tracts of two calves estimated at two-weeks of age; both contained various amounts of the leaves of ground willow (Salix sp.) and labrador tea (Ledum groenlandicum), and of the leaves and stems of sedge (Carex sp.) and crowberry (Empetrum nigrum),

plus a smattering of fruticose lichens (Cladonia sp.). These plant materials comprised about 33 percent of the contents in one stomach, and about 20 percent of the other; the remaining food material present was curdled milk. In neither animal did the rumen appear to be functional yet. By the first of July, however, calves are grazing extensively, and presumably the animals are obtaining nourishment from the plants ingested. By September, at about 3 months of age, most calves suckle only occasionally. With the first major snowfalls in October, the animals seem adept at finding food and pawing aside the snow. Between September and December the calves are weaned--most probably before November, but information regarding this event is rather difficult to obtain. Of 7 cows autopsied in mid-December known to have been followed by calves-of-the-year, I found only 2 with milk in the mammary glands. No animals have been found in March or April with mammary milk among a sample in excess of 100 adult cows. On the other hand, the urge to suckle still remains among some of the yearlings, and it is not an uncommon sight to observe these animals attempting to nurse parturient cows during late May and early June. In all of my observations the cows chased the yearlings away. Lent (1966a), however, noted four instances of yearlings successfully suckling cows at that time of year. Presumably these cows had lost their new-born calves.

The diurnal feeding pattern already has been discussed somewhat. The main periods for feeding and resting seem to occur

during the hours surrounding noon and midnight, but many factors apparantly affect this schedule. As Turi (1931) noted among the Lapland reindeer, the feeding times are closely related to the availability of forage and the extent to which each feeding-bout supplies the animal's nutritional needs. On poor range, the animals will feed irregularly and often. In most caribou habitats in Alaska, from May to July there is abundant food, plus some daylight during all 24 hours, and the animals are active throughout. During the fly-season caribou tend to spend much of the daylight hours coping with these pests, and feed mostly during the twilight hours when the flies become less active. At that time the animals can be observed (in interior Alaska) dispersing from the tight groups on hilltops to graze the adjacent alpine meadows.

The rutting period in late September and October influences the feeding activity of adult bulls considerably. Flerov (1952: 214) stated that "During rutting the bulls almost refuse to take food." Field observations in Alaska have shown that most of the bulls continue to eat during the rut, but presumably at a much reduced rate, for all bulls lose most of their accumulated summer fat during a three-week period. I have examined 31 rutting bulls (all judged to be older than 4-years) from the Nelchina herd, Alaska. Only 5 of these (all 6-years+) had rumens which were essentially empty of food material; all contained varying amounts of urine, which frequently is ingested from cows

during the breeding activity. In addition, the livers of these 5 animals showed morphological changes typical of animals deprived of food for long periods: 1) a pale yellow coloration, indicative of excessive amounts of bile pigments and a buildup in ketones; and 2) a loose, rather spongy texture to the tissue, probably caused by the depletion of glycogen and fat reserves in the hepatic cells. The remaining 26 animals apparently were feeding often enough to keep their rumens at least half-filled, although 7 of these bulls also had livers in various stages of degeneration. The loss of body-weight associated with the rutting activity of bulls has been commented upon earlier (see MORPHOLOGY, "Body Size").

This restriction of food intake by rutting bulls, with the subsequent loss of fat reserves, poses a perplexing problem with regard to this species' population ecology. Why selection should have favored such behavior during the course of evolution is rather difficult to understand. Most bulls thus start the winter in their worst physical condition of the entire year--a rather paradoxical situation to say the least. The bulls in the 6-year+ age-class are the ones most affected, presumably because they are the most active during the rutting season. Those in the 3-5 year age-class lose less weight proportionately, and apparently all continue to eat during that period. The young bulls (yearlings and 2-year-olds), even though capable of breeding, mostly are excluded from doing so by the older males; their weight losses thus are minimal, and most individuals retain the rather meagre amounts

of fat that have been stored during the summer's feeding. It would seem, therefore, that selection operates against the full-grown males, at the same time favoring the survival of young, vigorous breeding stock.

Main Seasonal Diet

The wide variety of plant, animal, and mineral material known to be ingested by this species during the year seems extraordinary, especially when compared with the diets of other ungulates. Various factors influence the caribou's choice of food materials, of course, not the least of which are the available supply in the region occupied and the changing physiological needs of the animal itself. As with most herbivores, the plant component of the diet varies considerably with the seasons. Some plants, such as lichens, are available throughout the year; others, such as the club fungi (Basidiomycetes), become available only for a short while in late summer and early fall; and some, such as the sedges (especially species of Eriophorum and Carex), are most abundant in summer, but remain available in winter. Weather can modify plant availability; deep snow or icing conditions might restrict the animals to feeding on plants above the snow-surface, such as on various species of arboreal lichens or browse. The greatest diet changes take place in the spring and fall.

Studies concerning the food habits of Rangifer have been carried out by a number of workers in Alaska, Canada, and Russia. The main techniques used have included field observations and rumen-sample analyses; actual feeding experiments have been rather few. A comprehensive list of all the species of plant and animal food known to be ingested would be too voluminous for inclusion

here. For a partial listing the reader is referred to the following papers: Hadwen and Palmer, 1922; Palmer, 1926; Jacobi, 1931; O. Murie, 1935; Banfield, 1954; Herre, 1955; Shaposhnikov, 1955; Cringen, 1956; Segal, 1962c; plus numerous other papers by various Russian workers, notably Aleksandrova, Andreev, Avramchik, Glinka, Igoshina, Larin, Vasiliyev, and Zdobnikov.

Changes in the composition of the caribou's diet are best discussed on a seasonal basis. In most of that portion of Alaska inhabited by caribou the seasons can be designated as follows, relative to the available food supply: spring (2 months), mid-April to mid-June; summer (2 months), mid-June to mid-August; fall (2 months), mid-August to mid-October; and winter (6 months), mid-October to mid-April. Weather plays an important role in food availability, and in some years may cause the seasons to be shortened or lengthened by several weeks. The following discussion pertains mostly to Alaska caribou, with further comments upon other regions. It stresses the main dietary components for each season, relative to the nutritional needs of the animals and to the well-being of the populations, as determined from my field observations and rumen-sample analyses, and from various other sources.

Spring.--As the spring thaw advances the caribou are quick to change their diet to include the new sprouts that appear in the snow-free areas. The catkins of willow (especially *Salix alaxensis*, *S. pulchra*, and *S. glauca*) are among the first of the new growth to be eaten, often while an extensive snow-cover remains.

Other favored food at this time of year includes the dead vegetation and the new shoots of various grasses (mostly Festuca altaica, Calamagrostis canadensis, and Hierochloe alpina in interior Alaska) and sedges (notably Carex bigelowii, C. membranacea, C. podacarpa, and Eriophorum vaginatum);the latter group often begin their new growth while still covered with snow. Caribou frequently are observed grazing on "dead" tussocks of Festuca and Eriophorum, but actually their feeding is directed more at the small green shoots interspersed within the dried vegetation. These three plant groups (Salicaceae, Gramineae, and Cyperaceae) constitute the most important part of the diet during late April and May, although lichens continue to be eaten if available--especially so if the season is late and the snow lingers. In the mountainous habitat of the Nelchina herd in south central Alaska, however, extensive snow-free areas frequently appear as early as the first week in April along south-facing slopes and along wind-swept areas where the snow-cover remains thin during winter.

It should be noted also that at this time of the year the animals are moving into the calving areas. In Alaska these contain few lichens and are comprised mostly of grass-sedge communities, with willow and dwarf birch (Betula glandulosa) stands along the drainageways and sparse heath stands along the rocky ridgetops and knolls. The latter communities are comprised of varying proportions of Cassiope tetragona, Empetrum nigrum,

Arctostaphylos alpina, and Dryas octopetala, plus scattered plants of Poa, Hierochloe, other grasses, ground willows, dwarf birch and various forbs; a variable, usually thin, cover of lichens is present, those of most value for grazing being Cetraria nivalis and C. cucullata. In the arctic, the herds of northwest and northeast Alaska move onto the extensive Eriophorum vaginatum stands which dominate the foothill and coastal plain sections of the region north of the Brooks Range. This plant becomes almost an exclusive food item during much of May and early June. (Lent, 1966; Skoog, personal observations). On the Alaska Peninsula, the snow tends to leave quite early, and the caribou moving southward in late April and May traverse plant communities dominated mostly by sedges and grasses; forage lichens are extremely scarce in that region, and comprise but a small part of the diet at any time of the year. In late May and early June the buds, leaves, and sprouts of willow and dwarf birch (Betula glandulosa and B. nana) appear, and these become favored food items throughout Alaska. Adolph Murie (1944: 153) noted in Mt. McKinley Park that "...in May and early June willow and dwarf birch seem to make up the bulk of the food." This observation seems to hold for all caribou in interior Alaska. There can be no doubt that these animals exhibit a great fondness for the leaves of these plants, a liking that continues throughout the summer. Similar observations have been noted in Canada (Banfield, 1954, 10B; Kelsall and Loughrey, 1957), Russia

(Igoshina, 1937; Shaposhnikov, 1955), and Scandinavia (Herre, 1955; Paterson, 1956). A wide variety of forbs also become available as the season progresses, and many of these enter the diet as the summer begins. Small stands of horsetail (Equisetum arvense, E. pratense, E. palustre, E. scirpoides, and probably other species as well) are especially attractive. On several occasions in early June the writer has observed Fortymile caribou (east central Alaska) actually grazing plots of these plants down to the ground.

In other regions of the world it is apparent that the food habits of Rangifer during spring vary considerably. Work by Kelsall and Loughrey (1957: 12-13) has indicated that the caribou of northern Canada (R. tarandus groenlandicus) remain on their winter diet of lichens and "winter-killed" vegetation during most of the calving period, switching to the new growth of grasses and sedges as it becomes available in mid-June. It should be emphasized here that that portion of Canada (lying mostly between Hudson's Bay on the east and the Mackenzie River on the west) is considerably different than arctic Alaska, both in physiography and in vegetation structure: tundra merges gradually with the taiga; mountain ranges are absent and the terrain generally is rather flat and rocky; extensive stands of sedge meadows are relatively few; and the snow tends to remain late in the spring. The nutritional regimen can be considered as being much more restricted in these caribou at that time of year than in Alaska herds. The diet is even more restricted among caribou of the Canadian archipelago (R. t. pearyi).

Lichens continue to dominate the spring diet in some areas. Shaposhnikov (1955: 205) indicated that lichens still comprised about 70 percent of the diet in mid-May among caribou of the Altai region of Siberia. Paterson (1956) stated that reindeer in northern Sweden continued to graze on lichens until the snow left. He noted also (p. 15) that "Important spring nourishment is also offered by the Empetrum on bare spots, remains of the grass of the past year and the catkin of the willows." Of the last named plant he listed the species Salix lapponum and S. phyllicifolia. I would assume that those areas in which lichens and the previous year's vegetative growth dominate the diet during spring are those which contain relatively few palatable vascular plants or where snow and cold weather inhibit the new plant growth.

Such areas might be expected to maintain rather low caribou populations, or at least populations subject to wide fluctuations in numbers. Compared with the new, rapid growth of vascular plants in the spring, lichens and the winter-killed vegetation are rather low in total nutrients. They are adequate forage during the winter when the maintenance energy requirements are low (Kvitkin, 1950; Segal, 1962b), but not during the spring when a considerable increase in tissue growth occurs. Among adult bulls the antlers are growing rapidly and fat reserves are building for the fall rut. Rapid body-growth resumes in the juveniles (yearlings and 2-year-olds) after a winter dormancy characteristic of most northern ungulates (Magruder et al., 1957; French et al., 1960; and Wood

et al., 1962). Pregnant cows have particularly high energy demands during the last two months of pregnancy and the first few weeks of lactation. In domestic ruminants, approximately half of the total nutrients required by the products of conception are obtained during the last quarter of the gestation period (Maynard and Loosli, 1962: 432). Adequate nutrition also is needed for the proper development of the udder and the production of high quality milk. It is well known among domestic livestock that poor nutrition during this critical stage in reproduction can have dire effects: fetal mortality, difficult births and the retention of placental membranes, maternal mortality, weak and physiologically immature offspring, poor milk production (both in quantity and in nutritive quality), and high post-natal mortality among the neo-nates. There seems little reason not to suppose that similar effects occur among caribou exposed to adverse forage conditions during the spring. Gul'chak (1950) has reported that in well-fed reindeer herds parturition occured earlier and the calves were larger and more viable.

Evolution would favor the selection of a calving period most conducive to bringing forth healthy, viable young. The new, highly nutritious plant-growth in spring probably is required for a sustained reproductive success. Thus, one can understand readily the later dates for calving that are typical of caribou herds in the arctic regions, as compared with those of herds farther south. Phenologically, the north slopes and foothills of the Brooks Range are one to two weeks later than the south slopes in the development of the vegetation; the coastal plain, three to four weeks later (Spetz-

man, 1959). The Canadian arctic (referring here primarily to the tundra and forest-tundra of the mainland, between the Mackenzie River and Hudson's Bay) apparently approximates Alaska's arctic coastal plain in the phenology of vegetation growth. Kelsall and Loughrey (1957: 12-13) noted that green shoots of Eriophorum were not available until about June 15 in 1957; shoots of other sedges and grasses became available about June 20; the leaves of Betula glandulosa, about July 1; and the leaves of Salix, about July 10 (calving peak about June 12). Contrast this situation with interior Alaska (e. g., Fortymile and Nelchina ranges) where Eriophorum shoots become available in late April and the leaves of Salix and Betula as early as mid-May (calving peak about May 26). Nutritionally speaking, it is obvious that these interior herds have a much more favorable habitat at this time of year than do the arctic herds.

The variable weather during spring, however, can cause wide fluctuations in the timing of the new vegetative growth, and thus can be critical with respect to reproductive success for any one year. Such fluctuations in weather are not so important in interior Alaska, for the varied terrain features of this mountainous habitat act as a buffer, of sorts. Adequate spring forage seldom becomes a problem; willows, sedges, and grasses are readily accessible in patches of snow-free areas even during years of unusually late thaws. A different situation exists on the arctic

slope, however, for there the terrain is quite uniform over extensive areas. Such is true, also, of the Canadian arctic. A late spring inhibits plant growth over a vast area, and the pregnant caribou cows are forced to continue their winter diet at a time when their nutritional needs are critical. At such times one might expect rather low reproductive success.

There can be little doubt that spring forage is extremely important to the welfare of a caribou herd. It is at this time that the greatest potential for an inadequate diet occurs. The nutritional requirements of the animals are increasing rapidly, yet the supply of highly nutritious new-growth forage can be quite limited in quantity. It seems likely as well that the change from the winter diet requires an extensive modification of the micro-organism complex in the rumen, in order to properly digest the new types of plant tissues. Perhaps this changeover is facilitated by the caribou's continued utilization of lichens during the spring period.

Summer--By this season (mid-June to mid-August) forage is abundant throughout most caribou habitats. Nutritional needs remain high during this season, as lactation continues, the new antlers grow, the hair is shed and replaced, fat reserves are expanded, and body-growth occurs. Considerable storage of nutrients takes place at this time, which provides the animals with reserves for later periods of shortage (e. g., the rut; winter). Adult bulls in particular store great quantities of fat, mostly along the back and rump;

this fat carries them through the rutting period in October, when food intake is restricted.

In Alaska, caribou continue to utilize the leaves of willow and dwarf birch extensively during June and July. The latter (Betula glandulosa and B. nana) is especially important, because it is a major component of the vegetation throughout most of the North country, occurring in a wide range of habitats. Willows are abundant also, but the main ones utilized (Salix alaxensis and S. pulchra) tend to be restricted mostly to the drainageways. A. Murie (1944: 153) noted the fondness of caribou for these shrubs in Mt. McKinley Park region, stating "When the willows and the dwarf birch leaf out in May they are eaten in large quantities. For a period in May and early June willow and dwarf birch seem to make up the bulk of the food. The leaves are stripped from the twigs, and some of the fine twigs are also eaten at this time of year...." Olaus Murie (1935: 41) also had commented upon this feeding habit, as have numerous other authors with regard to reindeer and caribou throughout the northern hemisphere.

Browsing of these shrubs is accomplished not be "plucking" the leaves individually or by biting off the tips of the twigs to any extent, but rather by the stripping action implied above. The animals grasp the branches in their mouths, draw their heads backwards and upwards, and scrape off the leaves and small twigs between the incisors and horny palate of the premaxilla. The rhythmic extension and drawing back of the head during such feeding activity

produces a characteristic head-bobbing pattern that is a common sight among grazing caribou bands observed during early summer. Leaf stripping seems well adapted to the near constant movement of the animals at this time of year, as they move from the calving areas onto the summer ranges, continually harassed by hoards of flies. The rather hurried feeding behavior frequently observed in caribou is well known. As A. Murie (1944: 154) has stated, "Often, before a willow twig is stripped of leaves, the caribou has moved forward and is reaching far back to complete the action."

In the Fortymile and Nelchina herds of interior Alaska, field observations by the writer have indicated that willows and dwarf birch dominate the diet during early summer and remain important well into the fall period. These plants also comprise the mainstay of the diet in the Arctic herd (northwest Alaska) during the period late June through July (Lent, 1966b). Willows are widespread through the boreal zone, especially along the drainageways and on the wetter sites, and are utilized as food by a variety of birds and mammals. In addition to the main species already listed as being eaten by caribou (the larger, dominant species of the drainageways), these animals also utilize some of the prostrate, dwarf willows which are common on wind-exposed ridgetops, in tundra areas, and on other sites less favorable to the larger species. A. Murie (1944: 154) and Banfield (1954, 10B: 12) have mentioned *Salix arctophila* and *S. reticulata*. On the Nelchina range, caribou

have been observed to eat the leaves and catkins of the prostrate willow Salix arctica (personal observations).

Dwarf birch is a particularly abundant plant throughout most of Alaska, occurring on both wet and dry sites extending from near sea level in spruce (Picea spp.) and tundra communities to above timberline where it can be found in pure stands. On favorable sites the plants form a bush that may reach 7 or 8 feet in height, but in marginal habitat (e. g., high elevations, wind-exposed slopes) they become prostrate in form. In spite of the abundance of this potential food supply, however, the caribou seems to be the only mammal that utilizes it to any great extent. (The winter buds are a major food of the rock ptarmigan, Lagopus mutus.) There can be no doubt of the high palatability of the leaves and the new twig growth during the summer. As an illustration, the rumens of six Nelchina animals I examined in mid-June (1956, 1957, 1960) consisted almost entirely of these plant tissues from Betula glandulosa.

On the other hand, it must be stressed that many species of grasses and sedges are utilized heavily during the summer months, and, in fact, throughout the year. The main species known to be eaten in interior Alaska have been mentioned previously. Porsild (1954: 23) stated that nearly all grasses are eaten, and noted especially those of the genera Alopecurus, Arctagrostis, Dupontia, Festuca, Poa, and Puccinellia. In addition to these, Hadwen and

Palmer (1922: 26) mentioned Agropyron, and I would add Hierochloe and Calamagrostis. O. Murie (1935: 42) stated with regard to the Fortymile herd in the 1920's that large numbers invaded the Mosquito Flats area each June and July to graze upon a "luxuriant" stand of Calamagrostis canadensis. I have observed Nelchina caribou feeding upon this species during spring and summer, but the grass is not abundant in those areas utilized most by the animals. On the Alaska Peninsula and adjacent Unimak Island, however, this species of bluejoint grass is a dominant, and there it forms a major portion of the diet, along with various abundant sedges.

Throughout most of Alaska certain species of the sedge family, Cyperaceae, are particularly valuable forage plants. Most of these belong to the genera Eriophorum and Carex, the main species contributing to the diet having been listed earlier. In addition, Carex aquatilis and Eriophorum angustifolium are particularly important in some areas, and probably numerous other species as well. Sedges are widely distributed throughout the alpine and tundra areas of Alaska, and in total volume comprise a considerable proportion of the flora. These plants are utilized heavily during all seasons of the year. They assume considerable importance, however, as the summer advances and much of the early vegetative growth matures and becomes less nutritious; at this time caribou tend to concentrate their feeding activity in the moist, boggy areas, where sedges predominate and new plants continue to grow. In tundra and alpine areas the highly nutritious, early

vegetative growth remains available throughout the summer, because new areas for plant growth continually are being released from lingering snowdrifts and from earlier flooded conditions. The sedges are most important with respect to this continued "new-growth" period, but certain perennial grasses (e. g., Hierochloe alpina and Festuca altaica) and a number of forbs (e. g., Sedum roseum, Pedicularis spp., Saxifraga spp., and Equisetum spp.) also respond to the late "release" of certain areas from unfavorable environmental conditions.

In addition to the browse and grass-like plants utilized during the summer, caribou graze a wide variety of forb species (here limited to the non-woody dicots). Many of these belong to the families and genera listed as follows: 1) Family POLYGONACEAE--Oxyria, Polygonum, Rumex; 2) Family SAXIFRAGACEAE--Boykinia, Parnassia, Saxifraga; 3) Family LEGUMINOSAE--Astragalus, Hedysarum, Lupinus, Oxytropis; 4) Family GENTIANACEAE--Gentiana, Menyanthes, Swertia; and 5) Family COMPOSITAE--Achillea, Antennaria, Arnica, Artemisia, Aster, Petasites, Saussurea, Senecio, Solidago. To this list of genera should be added Caltha, Descampsia, Epilobium, Galium, Geranium, Hippuris, Pedicularis, Primula, Sedum, and Trollius, and perhaps a few others as well. For an extensive listing of the species eaten the reader should consult the authors noted in the introduction to this section (i. e., "Main Seasonal Diet").

Most of the forb species are quite discontinuous in distribution, and generally are available only a short time before fruiting and dying. Hence the proportion of these plants in the diet varies considerably, depending upon phenology, annual differences in weather, and the particular areas being utilized by the caribou. Nevertheless some species are widespread throughout the alpine areas of Alaska and are highly palatable, and therefore contribute significantly to the caribou's nutritional regimen during the summer months. Legumes are especially important and, as is well known, are especially nutritious (e. g., about 19% protein in early growth stages--Larin, 1956: 68); in the Nelchina area, species of particular note include *Astragalus umbellatus*, *Lupinus arcticus*, *Hedysarum alpinum*, and *Oxytropis nigrescens*. The succulent herbs *Gentiana glauca*, *Swertia perennis*, and *Sedum roseum* are common in the alpine meadows and of high palatability. In addition, the following species deserve mention as important food plants: *Antennaria monocephala*, *Artemisa arctica*, *Epilobium latifolia*, *Pedicularis* spp., *Petasites frigidus*, *Polygonum bistorta*, *Rumex arctica*, and *Saxifraga* spp. These are species known to be grazed, as determined by field observations by the author; all are quite common throughout the near timberline and alpine areas of interior Alaska.

Summerhayes and Elton (1928) noted the extensive use of the forb Oxyria digyna by reindeer on Spitzbergen, stating (p. 216), "...and for some distance every plant of Oxyria was found to have its leaves, and sometimes its flowers, nibbled. About August the Reindeer mostly desert the fjaeldmark for the summer grasses (Arctophila fulva, etc.) which have then grown up in the swamps around tarns; but they still continue to eat the Oxyria on the dry regions." This plant is rather common in the alpine areas of interior Alaska also, but generally of such scattered distribution as to be relatively unimportant in the diet. The remarks of these authors illustrate, however, what might be considered the usual role of most forbs in the summer feeding activity. In short, many kinds of forbs are eaten as they become available; when abundant, they can comprise a major portion of the diet for short periods of time. The primary foods, however, remain the browse and grass-like plant species mentioned earlier, plus certain lichens to greater or less degree, depending upon the area involved.

Shaposhnikov (1955: 205) listed lichens as comprising 45.8 percent of the total weight of the rumen contents among caribou examined in the Altai Mountains of USSR during mid-July. This percentage is quite high for that time of year, and he noted that this figure was at variance with data obtained from reindeer in other parts of USSR, where herbaceous vegetation comprised the

bulk of the diet. Palmer (1926: 10) stated that reindeer along the Bering Sea coast of Alaska ingested lichens "...in summer to the extent of about 15 percent of their food." My examination of rumens from Nelchina animals during the summer suggested that this estimate by Palmer would be more nearly a maximum figure for Interior caribou.

It seems likely that the amount of lichens eaten at this time of year will vary considerably between different populations, regions, and years, influenced by a number of environmental factors. Basically, it is a well known fact that these plants are a highly palatable food throughout the year, in spite of their relatively low nutritive qualities (e. g., a protein content of less than 5 percent for most forage species). Feeding experiments (Palmer, 1944b) have shown caribou to be rather fastidious feeders, eating mainly the finer, more succulent plant tissues. When lichens are soft and moist they are preferred over many other, more nutritious forage plants; when dry (a common occurrence during certain periods of the summer), they become coarse, brittle, and practically unpalatable. In addition, the accessibility to good lichen forage during July and August often becomes restricted due to the attacks of flies, which tend to drive the caribou into the generally lichen-poor, windswept areas. Finally, much of the terrain utilized in summer by Alaska caribou tends to be rather poor in lichen cover. The

Interior herds frequent the alpine meadows, often located far from the main wintering grounds and often in regions characterized by a minimum of lichen forage. In the Arctic, the herds move onto the extensive coastal plain, where lichens are quite scarce in the Eriophorum-dominated landscape. Weather, of course, at either end of the summer period, also would be an important factor affecting the use of lichens because of its effects upon herbaceous growth. The inhibition of such growth due to cold temperatures might force the animals to utilize more lichen forage than normal.

A number of other plants occasionally enter the summer diet in quantity. Some authors have recorded the utilization of the leaves from certain woody plants commonly found on caribou ranges: Arctostaphylos alpina (alpine bearberry), A. uva-ursi (common bearberry), Empetrum nigrum (crowberry), Ledum decumbens and L. groenlandicum (Labrador tea), Vaccinium uliginosum (bilberry), and V. vitis-idaea (lingenberry). Kelsall and Loughrey (1957) have suggested that Ledum may be important in northern Canada. Segal (1962c) reported these plants being eaten regularly by the reindeer in Karelia ASSR, excepting Ledum spp. and Vaccinium vitis-idaea which were eaten rarely, but included additionally as palatable forage the leaves of Alnus incana (alder) and Populus tremula (aspen). Cringan (1956) noted that woodland caribou in Ontario, Canada, browsed the leaves of numerous shrubs other than Salix and Betula. Palmer (1926) listed

Alnus alnobetula (alder), Empetrum nigrum, and both Vacciniums as being of medium importance in the summer diet of Alaskan reindeer along the Bering Sea Coast. My studies among the Fortymile and Nelchina herds of interior Alaska, however, revealed no evidence for other than incidental feeding upon the woody plants mentioned above. Presumably more palatable food is readily available.

In some locales Equisetum spp. (horsetail) is eaten in considerable quantities. There can be little doubt that some species are highly palatable, and this fact has been noted by many authors. In Alaska, these plants (main species listed earlier in "Spring" section) are utilized mostly during spring, early and late summer, and fall. It is then that caribou frequently seek out the succulent herbage growing on wet sites. Equisetum often is found in dense stands in the bogs of such areas and along the shores of ponds and lakes, and such stands are grazed intensively on occasion.

A plant food particularly sought when available during late summer and fall are various species of Basidiomycetes (the mushrooms). The apparently strong craving of caribou for this food is exemplified by the following quotes. With regard to eastern USSR, Bogoraz (1904: 76) wrote, "In the fall the reindeer has a great relish for mushrooms, and seeks for them so obstinately as to neglect its ordinary fodder...." Paterson (1956) noted that fungi were a favorite delicacy to the forest reindeer of northern

Sweden, and remarked (p. 16) that the plants were "...looked for and eaten with great eagerness...." Herre (1955: 3) commented further regarding the reindeer of northern Europe and Russia: "In the fall, mushrooms are extremely popular; the search for this delicacy often causes the animals to roam over long stretches of terrain." Porsild (1954: 22) stated, "In addition, all kinds of fleshy fungi are devoured greedily by the reindeer....", referring to the Mackenzie River Delta area of northwest Canada. In reference to interior Alaska Olaus Murie (1935: 41) wrote, "In July and August, when mushrooms become plentiful, these are promptly placed on the caribou menu....the stomach (of one young buck) was filled with mushrooms, almost to the exclusion of other food. On this occasion numerous fungi were found to have been bitten into by caribou."

My own field observations with regard to the Fortymile and Nelchina herds are consistent with the comments expressed above. After the fly-season ends in early August, caribou frequently venture below timberline, particularly after the frosts have started in the alpine areas and the herbaceous vegetation begins to deteriorate. This downward movement brings the animals into the upper sections of the spruce forest, where various types of fleshy fungi abound in certain years. My analysis of 19 rumen samples from caribou killed in late August, 1954, showed that fungi comprised approximately 45 percent of the total food volume,

with a high of 84 percent in one animal (Skoog, 1956: 124). Species of especial importance are those of the genus Boletus, because of their wide distribution and frequent abundance. Other species known by the author to be eaten are representatives of the genera Coprinus, Lycoperdon, and Morchella. Undoubtedly there are other genera represented in the diet as well. Banfield (1954, 10B: 12), for example, also listed Hygrophorus, Lactorius, and Russula.

The abundance of mushrooms can vary greatly from year to year, however, and their period of availability can be restricted by cold weather. These plants seem to be especially sensitive to freezing temperatures. Also, it must be remembered that caribou movements and distribution exert an important influence on the composition of the diet. Animals which remain on the alpine areas or on the arctic tundra during late summer and early fall therefore do not have ready access to this type of forage.

The nutritional qualities of mushrooms generally seem to be quite high, but also quite variable as to species. Mendel (1898) found the crude-protein content among several genera of edible species to vary from 15 to 37 percent; the fat content, 2 to 8 percent; ash, 6 to 20 percent; and crude fiber, 3 to 12 percent; with carbohydrates comprising the remainder. The water content ranged from 75 to 90 percent. Thus, it would appear that these plants would be of considerable nutritional value to caribou if available in quantity. Reindeer herders in Swedish Lapland have found mushroom forage to be a desirable addition to the

diet in order to fatten the animals before slaughter (Paterson, 1956). The availability of such forage extends the high-plane of summer nutrition into the fall period at a time when most food plants have reached maturity and have lost much of their nutritive value.

Porsild (1954: 240) has said that "The summer range is expendable and will renew itself each summer." Such a statement probably holds true for most of Alaska as well. Food is indeed abundant and varied, and the main forage (i.e. willows, dwarfbirch, grasses, and sedges) consists of plants well able to withstand the rather minimal damage resulting from caribou grazing. Yet the importance of summer range often is not fully appreciated. One should remember that the physiological demands for energy are high during this season and that at this time must occur the replenishment of depleted nutrient stores, the growth of new tissue, and the storage of food materials for the lean months ahead. Thus, the nutritional qualities of the summer range are quite important to the welfare of a caribou herd. In Alaska, there is no indication that these nutrients are in restricted supply on any of the major caribou ranges I have examined. It seems likely that the most critical seasons for caribou nutrition must occur during the spring and fall, when fluctuations in weather are most apt to affect the availability of food.

Fall.--During this season (mid-August to mid-October) the forage gradually becomes restricted both in quantity and quality. Frosts commence in the high country during early August, and continue with ever increasing intensity. The foliage of most of the vascular food plants begins to die soon afterwards. Fungi and forbs are the first affected, followed by the leaves of willow, then those of dwarf birch, and finally the grasses and sedges. The "foliage" of lichens, mosses, and a number of evergreen shrubs (e. g., *Ledum groenlandicum*, *L. decumbens*, and *Vaccinium vitis-idaea*) is affected little by the cold. The changes evident in early fall were described vividly by Olaus Murie (1953: 37) for the 1922 season in Mt. McKinley National Park:

> Early in August the vegetation began to turn yellow. A willow limb here and there, a few clumps of *Arctous alpina*, or blueberry bushes, showed yellow and red. Later in the month, and early in September, pure green vegetation was apparent only in swampy plots, recesses of the hillsides where seepage was working out toward the main stream. Such green "oases" are utilized to the last by the caribou that linger in the higher valleys.

As the herbaceous vegetation withers, the number of plant species utilized decreases considerably. A relatively small number of the summer forage plants retain their palatability, but these remain important food items throughout the fall and early winter.

Concurrently, the quality of the forage plants also changes substantially. Larin (1956) has presented a thorough discussion of the growth patterns and nutritive qualities of the

principal forage plants of livestock (including reindeer) in the USSR. He listed (Table 2, p.68) numerous data regarding their chemical composition at various growth-stages. In all six plant families examined, the content of both protein and fat was highest during the tillering stage (budding, shoot formation), and then fell progressively through the flowering and fruiting stages to reach a low in the withering or dry-plant stage. Larin's data showed that in the Gramineae and the Cyperaceae the average plant-composition (in percent dry-weight) for protein and fat during the four stages was as follows: Gramineae--14.9 and 3.5, 10.4 and 2.9, 8.8 and 2.8, 5.8 and 2.6, respectively; Cyperaceae--17.1 and 3.7, 14.5 and 3.1, 12.1 and 2.3, 7.1 and 2.6, respectively. Thus, between the tillering and withering stages the drop in nutritive value for grasses was about 75 percent in protein and 36 percent in fat and for sedges, 59 percent and 30 percent. In the comparison of these two families, the sedges contained more protein and albumen, more fat, and less cellulose at all growth-stages, and more ash in the withering stage (Larin, 1956: 68). Individual species vary, however, and the short, alpine-meadow sedges (important forage for Alaska caribou), for example, have a higher protein content and a lower proportion of cellulose (Larin, 1956: 161). Other data presented by Larin (p. 79) permit further comparisons of caribou food-plants: 1) the leaves of willow contain an average of 17.6 percent protein, 5.3 percent fat, 15.4 percent cellulose, and 5.1 percent ash; 2) the leaves

of birch--17.2, 6.5, 17.2, and 5.1, respectively; 3) horsetail (Equisetum spp.)--12.4, 3.6, 19.8, and 14.3, respectively; 4) fungi--25.5, 5.3, 32.1, and 8.0, respectively; and 5) lichens--4.0, 3.6, 34.7, and 2.4, respectively.

The rather low nutritive value of lichens is quite striking, even when compared with the dried grasses and sedges. Considerable variation occurs, however, and some species have significantly higher values than the average noted above. For example, Larin (1937: 93-94) indicated that Stereocaulon spp. had protein values ranging from 7.5 to 10.9 percent; Parmelia encausta and P. saxtilis, from 6.3 to 7.3 percent; and that the fat content reached 10 percent in Alectoria ochroleuca and over 17 percent in Parmelia saxtalis. Scotter (1965: 248) listed the protein content for Stereocaulon spp. as averaging 7.3 percent, and that for Peltigera aphthosa and P. canina as ranging from 17.8 to 21.9 percent. Of these, however, only certain species of Stereocaulon are utilized to any great extent, and only in some areas. The most important forage species relative to palatability, abundance, and utilization include the following: Cladonia alpestris, C. rangiferina, C. sylvatica, C. mitis, C. uncialis, C. amaurocraea, Cetraria cucullata, Cet. islandica, and Cet. nivalis, plus various species of arboreal lichens from the genera Alectoria, Evernia, and Usnea. The average composition of these species excluding the arboreal lichens, is as follows, based upon data presented by Courtright (1959: 140-141) from various sources and upon work by Scotter (1965: 248): protein, 2.7 percent of the dry weight; fat, 2.3; N-free extract, 57.5; and ash, 1.7. The same components measured

by Scotter for three species of arboreal lichens (Alectoria jubata, Evernia mesomorpha, and Usnea hirta) averaged 4.9, 2.8, 82.7, and 1.4, respectively.

It is generally accepted that the forage lichens tend to maintain approximately the same nutritive quality throughout the year (Florovskaya, 1939: 311; Porsild, 1954: 240). Scotter (1965: 248) found, however, that the three species of arboreal lichens he examined decreased in protein content by about 25 percent between summer and late winter. This finding is difficult to evaluate at present without further data, because it is well known that rather wide differences in chemical composition can occur within the same plant species relative to differences in the substrate. On the other hand, reindeer herders in Lapland recognize three groups of lichen forage, according to Llano (1944: 31): 1) the main forage species (including many of those listed above) "on which they fatten"; those of low palatability (e. g., the foliose types, Nephroma, Parmelia, Peltigera, etc.), eaten mainly when other food is scarce; and 3) the arboreal species of "...Allectoreae and Usneae for which the animals have great fondness, and though these will support life, the reindeer do not fatten on them." One wonders at the significance of this statement. It suggests that the tree lichens may lack some nutritive quality which is present in the forage Cladonia's and Cetraria's. Chemical analyses available (see above) for the various lichen species examined thus far,

however, indicate little difference in the nutritive components measured, i. e., protein, fat, etc. Seasonal changes in nutritive quality may indeed be implicated; or perhaps differences in digestibility. Certainly more research is needed in this regard, for the arboreal lichens constitute a major food item in the winter diet of some caribou populations, particularly in Canada. It seems unlikely that the Lapp herders would err in their evaluation of different lichens as nourishment for their reindeer.

In the fall, then, as the quantity, quality, and palatability of the summer forage decreases, the caribou's diet gradually shifts toward the more restricted winter forage. Weather plays an important role in this shift. In interior Alaska mild temperatures can extend the fall period well into late October or even November, thus prolonging the period of high nutrition. Such a phenomenon seldom occurs in the arctic regions lying to the north of the Brooks Range. Caribou distribution is affected by the palatability changes. In the Interior, the animals tend to move to lower elevations. On the arctic slope, caribou move to wetter sites on the tundra, where the vegetation remains green longer. O. Murie (1935) believed that seasonal changes in food availability were a prime factor influencing the movements and distribution of caribou. Certainly this belief seems to hold true for local movements at any rate.

The leaves of willow continue to be utilized heavily as

long as they are available--generally till mid-September in interior Alaska. Dwarfbirch leaves are available till late September, but seem to be less palatable than the willow. Both are much less important in the diet than during early summer when these shrubs are leafing. The fondness of caribou for fleshy fungi has been discussed earlier; these plants can be a major food item in some areas during some years for a month or so in late summer and fall. Few mushrooms remain by mid-September generally, but they are utilized as long as any is available. The grasses and sedges are eaten throughout the fall period, and become increasingly important as the winter approaches. In arctic Alaska the sedges tend to dominate the fall diet, with lichens increasing in importance as the animals move onto the south slope of the Brooks Range in October or November (sometimes the animals stay to the north, however). In the Interior, fungi and woody plants are the main food items, with lichens becoming more dominant in late fall and early winter.

Data obtained from 91 rumen samples of Nelchina caribou during September indicated an average volumetric composition as follows (Lensink, 1954: 3): lichens, 31 percent; grass-sedge, 23 percent; and woody plants (primarily willow leaves), 41 percent. In that region, alpine meadows are relatively abundant, and the caribou tend to remain above timberline until late September or early October. In the Fortymile region, however, the alpine areas

are much more discontinuous in distribution, and the animals frequently drop into and cross the timbered valleys. This difference in terrain probably accounts for the fact that Fortymile caribou ingest proportionately more mushrooms than do the Nelchina animals. In 1954, the author (Skoog, 1956: 124) analyzed 70 rumen samples obtained from Fortymile animals during the period August 20-September 24. The results provided some insight into the shift in diet occurring at that time and are briefly summarized here. During the period August 20-31, 19 samples showed an average volumetric composition of 15 percent lichens, 1 percent grass-sedge, 36 percent woody plants, and 45 percent fungi; during September 1-7 these percentages for 29 samples were 18, 4, 43, and 30, respectively; during September 12-24, for 22 samples, 48, 10, 12, and 19, respectively. The actual percentages are subject to question, of course, for it is well recognized that considerable error and variability are inherent features of most analyses of rumen contents (Bergerud and Russell, 1964). Nevertheless, for comparative purposes the results are of value, and they illustrate well the shift toward a heavier utilization of lichens and grass sedge as the fall progresses.

By the time of freeze-up and the first permanent snows (mid-October for much of interior Alaska) the summer forage is mostly gone, but the caribou continue to search out

the green vegetation where available. The fall migration to the wintering grounds usually is in full swing, and large numbers of animals are moving through the lowland areas. Once the ice is firm on lakes, ponds, and sloughs the ubiquitous water sedge (Carex aquatilis), which lines the shores of these waters, becomes a favored food item. The animals eat the green foliage protruding above the ice. When the snow is not too deep (less than 30 centimeters) I have observed that Nelchina caribou will spend a considerable amount of time feeding on this plant during October and November. Larin (1956: 158-160) has stated that this palnt is a valuable hay species for livestock in the northern regions of the USSR, and is especially important for reindeer, which utilize it "...in the spring and also in winter as feed under the snow." Florovskaya (1939) also commented upon its value as reindeer forage. His chemical analysis data for C. aquatilis (p. 306) showed that the plant still retained about 6 percent crude protein even in the dried,brown winter state; in summer the protein content reached 17 percent. Presumably while the plant remains green during early winter the protein remains high as well, and hence caribou can obtain a highly nutritious food even at that late period. Lent (1960: 37) has commented upon the similar feeding habits of the Arctic caribou during October and November.

At the same time of year, muskrat pushups furnish green plant food also. These structures, located over shallow portions of lakes, consist of a variety of aquatic vegetation and organic material deposited on the ice by the muskrats to enclose their air holes. Apparently this vegetative matter is highly palatable, for caribou are strongly attracted to these structures during early winter. In 1960 the muskrat population was high in the Lake Louise Flat section of the Nelchina caribou range, and the snow cover, light. In mid-November the muskrat pushups were numerous on nearly all of the many lakes covering the Flat. During a two-week period a large concentration of caribou (10,000 + animals) roamed across the area feeding upon the sedges and muskrat pushups along the lake shores. In an hour's flight across this lake strewn region, I did not find a single pushup within the area of caribou distribution (about 500 square miles) that had not been disturbed by caribou. One might well wonder at the effect of such feeding activity upon the muskrat population itself.

Other green vegetation utilized during October and November includes species of Equisetum. I have not observed the utilization of horsetail at that time, but Lent (1960: 37) recorded such with regard to the Arctic herd. On October 6, 1960, he watched caribou chopping through hard crusted snow along a slough to reach a "thick Equisetum cover." Florovskaya

(1939) has indicated that this plant tends to remain green for some time under the snow (into the January-March period), and retains a protein content of 6-7 percent.

A variety of other plants also retain green foliage through the fall period and well into the winter, including some species of Festuca, many of Carex, and other species as well. Green vegetation is considered by Russian reindeer specialists to be a necessary component of the reindeer's winter diet. A further discussion of this aspect appears in the next section. Weather probably is an important factor in the relative abundance of green plants present on a caribou range from one year to the next. Early hard freezes probably exert much the same effect upon some vegetation as the commercial freezing process upon vegetables. Such a phenomenon was evident in the Nelchina region during 1962. Freezing temperatures in late August and early September of that year inhibited the fall color change, and a large portion of the foliage of many species remained green (strikingly noticeable--the leaves of willow). The greenness was especially evident among plants on moist or wet sites. I did not investigate this circumstance further after September, but I assume that many plants (especially the sedges) retained this greenness after the snows arrived.

On the two caribou ranges examined closely by the author during his studies--the Fortymile of east central and the Nelchina of south central Alaska--it would appear that these

caribou are able to maintain a highly nutritious diet throughout September and October. Those in arctic Alaska are faced with winter conditions much earlier, and hence it seems likely that the diet would be on a lower nutritional plane during this period. On the other hand, the severe energy demands of summer (lactation; fly harassment; antler, hair, and body growth) have been reduced considerably. The primary "extra" energy drain remaining is that attending the rut (October). This concerns mostly the adult bulls, however, and the energy needed is obtained from the heavy fat stores accumulated during the summer. These bulls lose most of their fat during the rut, and thus enter the winter season in relatively poor condition. The adult cows continue to build fat stores throughout the fall and early winter. Most of the energy ingested by immature animals has gone into growth, and hence these too are quite lean as the winter commences. Thus, both the adult bulls and the immatures would seem to be vulnerable if the winter were unusually severe and/or if adequate forage were not readily available.

Winter.--This season extends for approximately six months, mid-October to mid-April, depending upon weather conditions. It has been considered to be the most critical period for many large herbivores in the northern latitudes as regards food supply, physiological stress, and, ultimately, survival.

The caribou, however, is well adapted for arctic living. Except in areas subject periodically to freezing rains and crusting snows (e. g., Greenland, the Bering Sea coast, and other maritime regions), winter survival tends to be high; the principal mortality results from predation and disease rather than from the effects of winter adversity. The caribou is able to maintain a broad zone of thermoneutrality (Scholander et al., 1950), because of the high insulating quality of the hair, the low melting point of the leg fat, and the vascular counter-current mechanism in the legs. Thus, even in extremely cold temperatures (-40° C.) there is little need for increased metabolism. Furthermore, the Russians (Kvitkin, 1950; Segal, 1962b) have found that the basal metabolism of reindeer is reduced during the winter by 40 percent or more. Both of these factors obviously have great survival value, and they permit the caribou to subsist on the much lower quality forage characteristic of this season. This aspect was discussed more fully in an earlier section, "Boreal Adaptations."

The number of plant species available as forage becomes much reduced in winter as compared with summer. Palatability further limits the number utilized. Yet the main summer forage groups--lichens, grasses, sedges, and browse--continue to furnish abundant food on the winter ranges in Alaska. In most areas, lichens gradually increase in importance as the winter approaches, and continue to increase as the winter progresses. The proportion

present in the diet, however, varies considerably depending on where the animals are spending the winter, the type of winter (amount of snowfall, primarily), the extent of herd movements, and the relative abundance of lichens in the region as a whole. For example, that portion of the Alaska Peninsula herd occupying the southwest end of the Peninsula (including Unimak Island) subsist almost entirely on grasses and sedges throughout the winter, plus a few dwarf shrubs (e. g., Empetrum nigrum); fruticose lichens are quite rare. Those animals at the northeast end of the Peninsula ingest less than 25 percent lichens when wintering to the northwest of Becharof Lake (the usual pattern) where fruticose lichens (mainly Cladonia sylvatica and Stereocaulon spp.) occur in rather small, discontinuous patches; when wintering farther south, the diet contains only trace amounts of lichens. In northwest Alaska, caribou wintering in the Brooks Range, the arctic slope, or the coastal plain subsist on a primarily sedge diet (see also Lent, 1960: 9-11); those wintering in the taiga of the Kobuk River drainage feed mostly upon lichens.

On the Nelchina range of south central Alaska, both lichen and sedge forage are abundant. Interestingly enough, each seems to occupy about the same relative importance in the winter diet. Chatelain (1951) reported the heavy utilization of lakeshore sedges (presumably Carex aquatilis) by Nelchina caribou during December, 1950, and also in March, 1951. Two rumens

examined by him from December-killed animals contained an estimated 99 percent sedges. His field observations for March indicated that in addition to the sedges the animals also were feeding on Sparganium sp. (Bur-reed) foliage protruding above the ice and on Calamagrostis canadensis (Bluejoint grass) along the lake-banks. He noted that the caribou were eating mostly dried foliage of the sedge, but also the few green stalks that seemed to be present in every clump.

During the course of this study, I have had the opportunity to examine in excess of 500 rumens of Nelchina animals killed by hunters during October and November, and not less than 100 from December kills (exact number not recorded). During this period the sedge-grass component of the diet averaged about 50 percent and lichens, about 30 percent. All were from animals associated more or less with the Lake Louise Flat, a spruce-covered plateau of some 3,000 square miles where sedge-lined lakeshores abound. A sample of 46 animals during December, 1962, however, from the northwest portion of the range (where fruticose lichens are numerous), revealed about an equal proportion of the two plant groups. During the period January-April, 1956-1964, another 128 animals were examined in connection with reproduction and pathology studies. This sample also showed the two plant groups about equally represented. The figures were obtained from visual estimates in the field at the time of examination, based simply upon the relative amounts of the two plant groups present. No attempt was made to use more

precise methods of rumen analysis; thusfar a dependable technique has yet to be developed. The extensive use of grasses and sedges by Alaska caribou in winter had been noted also by O. Murie (1935) and by A. Murie (1944).

In many other areas of the world, however, lichens assume a much greater importance as winter forage than seems to be the case in Alaska. Such is particularly evident wherever the caribou herds move into the extensive spruce stands which characterize the taiga biome in northern Canada and the USSR. For the most part, the caribou and reindeer are more or less confined to the spruce once they enter this zone, for alpine areas are relatively uncommon. Therefore, unless the animals remain on the arctic tundra or in the forest-tundra ecotone along its southern edge, by necessity their forage must be predominantly lichens. Banfield (1954), Kelsall (1957a; 1960; 1968), and Scotter (1964) have commented upon the dominance of lichens in the winter diet of Canada's mainland herds. However, other plants are of importance also. Scotter (1964: 46) stated, "Various grass and grass-like species appeared to be moderately important winter forage. One of these, horsetail (Equisetum spp.), appeared to be a highly preferred plant...." Later analyses of winter rumen-samples showed the following average composition (Scotter, 1967: 35): lichens, 58 percent; woody plants, 20 percent; grass and grass-like plants, 3 percent; with other plants totaling about 3 percent and with an unidentifiable portion of about 16 percent. Strangely enough, in this particular sample (n=20) he found only trace amounts of arboreal lichens.

These plants have been considered to be important forage for taiga-wintering animals (Hustich, 1951; Banfield, 1954; Shapashnikov, 1955; Cringan, 1957; Edwards and Ricey, 1960; Scotter, 1962; and others). Other authors have commented upon the fact that arboreal lichens are utilized by caribou particularly at times when the ground lichens are not readily available--not present or covered with a deep or crusted snow (Dugmore, 1913; Formozov, 1946; and Ahti, 1959). In Lapland, reindeer herders cut down lichen-laden trees to augment the diet of their herds during adverse periods of the winter (Llano,1944). The apparent low nutritive quality of these lichens has been discussed earlier. In addition, a further comment by Paterson (1956: 18) concerning Lapp reindeer is of interest: "On grazing too much hanging lichen during the winter, the reindeer contract what is called throat-creak, probably some kind of inflammation of the throat." The significance of this "ailment" is not readily apparent from the text. In Alaska, although the arboreal lichens are eaten from time to time, they do not comprise a significant portion of winter diet. In fact, their greatest value in most of the taiga areas would seem to be as supplementary feed when the supply of other forage is restricted.

The winter forage of reindeer in the USSR has been discussed in detail by a number of Russian authors during the past 30 years or more (e. g., see Sdobnikov, 1935; Igoshina, 1937; Avramchik, 1939; Florovskaya, 1939; Glinka, 1939; Formozov, 1946; Shaposhnikov, 1955; Larin, 1956; Karev, 1961; and Segal, 1962a). The consensus with regard to the mainland populations has been that terrestrial

lichens comprise the bulk of the diet during winter. In a wild population of the Altai Mountains the lichen component of the diet remained dominant throughout the year--70 percent in early May; 46 percent in mid-July; and 75 percent in mid-August (Shaposhnikov, 1955: 205). To what extent these figures may have been biased due to small sample-size is not known; the lichen percentages are quite high in comparison with results obtained elsewhere. In contrast, Karev (1961: 207) stated that in areas where the tussock-tundra predominated, such as in eastern Yakutia and Kamchatka, the cottonsedge (Eriophorum) constituted up to 90 percent of the reindeer's winter diet. Alaska caribou which winter along the northern foothills of the Brooks Range and the coastal plain have a comparable diet; except for different sedge species, the same can be said for the Alaska Peninsula caribou. Such might be expected in any region where the lichens were scarce, as is the case on most of the tundras throughout the arctic.

Sdobnikov (1935) noted for the January-February period that the reindeer's diet in the Malozemelsk region contained about equal proportions of lichens and flowering plants. Mosses reached 10-15 percent in some rumen samples examined. On Novaya Zemlya in the mid-1930's, Aleksandrova (1937) found the winter diet to consist of 20 percent lichens, 39 percent mosses, and 41 percent "green" forage (analysis of 14 rumen samples). Mosses reached 61 percent in one sample. Shaposhnikov (1955) also found mosses to be utilized by

the Altai caribou. Most other authors, however, have considered these plants to be eaten only incidentally (Palmer, 1926; O. Murie, 1935; Banfield, 1954; Skoog, 1956; and Scotter, 1967). Mosses might well be an emergency-type food, eaten primarily when other food plants are not readily available.

As noted earlier, the Russian workers have stressed the importance of green forage in the winter diet. Karev (1961: 204-210) summarized much of the current ideas relating to this aspect of reindeer nutrition, and discussed the relative value of the main plants contributing green foliage. These plants included several species of Equisetum; many species of Carex; Eriophorum vaginatum; certain grasses of the genera Arctophila, Deschampsia, and Festuca; plus a variety of forbs and woody plants. The relatively poor nutritive quality of the forage lichens is well recognized, and has been discussed. In Russia, green forage is considered necessary for maintaining the weight and fatness of reindeer during the winter, and is especially desirable for pregnant cows. Animals living exclusively on lichens begin to suffer from nitrogen and ash starvation toward the end of the winter. Such deficiencies can be quite severe in the pregnant female, whose fetus is demanding more and more nutrients as parturition approaches.

Nevertheless, the caribou generally seems well adapted to a low-plane of nutrition during the winter, for starvation is not a common cause of mortality among these animals (except where snow-crusting is a factor). This adaptation in part results from the

lowered basal metabolism. It is possible too that the caribou is able to recycle much of its nitrogen supply via the rumen, blood, and saliva. The caribou is known to secrete great quantities of saliva (Aksenova, 1937; Nikolaevski, 1961), as is the case with most ruminants. The high alkalinity of the saliva functions in maintaining a suitable environment in the rumen for digestion of food and for the populations of micro-organisms associated with that digestion; in addition, nitrogen is carried back into the rumen via the urea in the saliva (Annison and Lewis, 1959; Dougherty, 1965). During the winter I have noticed that the rumens of caribou are extremely liquid, as compared with those examined during the summer. Perhaps an increased saliva flow accounts for this more-liquid state. In part, this increase could be the result of the greater utilization of lichens in winter; the acidity of these plants would necessitate larger amounts of saliva in order to maintain a given pH in the rumen. Regardless, the increased saliva flow would result in a greater amount of urea (i. e., nitrogen) entering the rumen as well. Thus, low demands for protein in the body (as a result of growth retardation), plus a high recycling of nitrogen (with presumably a low nitrogen excretion via the urine), might well be the principal factors permitting the minimal nitrogen-intake associated with feeding on lichens. Such a physiological mechanism probably would not suffice for cows during late pregnancy. It would be desirable to

test this hypothesis with appropriate feeding experiments. This mechanism also might be operative in other large herbivores that seem able to withstand severe "droughts" in the nitrogen-content of the forage (e. g., the zebra).

Karev (1961: 210) also commented upon various browse species, including Empetrum nigrum, Ledum palustris, Rubus arcticus, Vaccinium vitis-idaea, and others. He stated that these were utilized as forage primarily during "famine" years, when other foods were not readily available. Most authors seem to agree with this statement, yet the evidence tends to be rather conflicting. O. Murie (1935: 40) found that E. nigrum and Arctostaphylos uva-ursi formed an important segment of the caribou's diet on Unimak Island, Alaska. As mentioned earlier, Scotter (1967: 35) noted that the browse species comprised about 20 percent of the winter diet in the Canadian caribou he examined. Woodland caribou are known to ingest considerable browse (Cringan, 1956: 211). Sheldon (1930: 144) observed caribou in McKinley Park, Alaska, browsing extensively on willow during late November, 1907, when there was a hard crust on the snow. R. Brown (1868: 355) speculated that the caribou present in Greenland in the mid-1800's subsisted primarily on "various species of Empetrum, Vaccinium, Betula, etc." Tener's (1963) account of the caribou on the Queen Elizabeth Islands of the Canadian arctic archipelago suggested that there too these dwarf woody plants were important components of the winter diet. The

caribou on St. Mathew Island in the Bering Sea were eating considerable Empetrum nigrum during the winter before the population crash; Klein (1967) considered this usage the consequence of range deterioration and severe competition for the limited, more choice forage.

From the literature reviewed, and from my own field observations in Alaska, I have concluded that browse species generally do not comprise a major component of the winter diet, especially when food other than lichens is readily available. Of course, as has been noted previously, the willows and dwarfbirches are important during late fall-early winter and late winter-early spring. Scotter (1964: 47) also has pointed out that lichen digestibility can be enhanced if small quantities of other vegetation are ingested as well. Perhaps this is an important function of the minor utilization of certain plants in winter. Most caribou-ranges contain an abundant supply of the evergreen shrubs Empetrum nigrum (crowberry), Ledum palustre (Labrador tea), and Vaccinium vitis-idaea (lingonberry). All three are fed upon to certain extent, but in spite of their abundance and widespread distribution remain rather insignificant in the diet except under special circumstances. Tener's (1965: 32-36) chemical analyses of these species in northern Canada revealed them to be more nutritious on the average than the forage lichens (vegetation samples from early April and early August): crude protein, 4.2-7.3 percent; fat, 2.6-10.4 percent; N-free extract, 57.0-69.0 percent; and ash, 1.8-6.1 percent. The limited utilization of these ubiquitous plants probably reflects a low palatability.

In summary, one can say that the winter feeding behavior of caribou tends to be opportunistic. On most ranges, even at this time of year a rather wide assortment of palatable plant-species are available, and many of these enter the diet. The proportions of different types of plants actually ingested result more from relative abundance and/or availability than from merely palatability alone. Once again the great mobility of caribou should be stressed, as well as the differential movements occurring from one year to the next. In Alaska, extensive shifts in winter-range use have occurred over a period of years; also, during any one year an individual herd might move continually throughout the winter, and thus traverse and utilize a variety of vegetation types. A statement of O. J. Murie (1935: 39) aptly described the winter feeding of caribou in interior Alaska: "And there is a certain amount of wandering from one mountain to another, across a valley, or along the ridges, some indulgence in the wanderlust so characteristic of this animal." Such behavior obviously could affect considerably the composition of the diet at any particular point in time.

The forage lichens, because of their high palatability, widespread distribution, and general abundance, tend to comprise the major portion of the diet in most regions. Whenever available, these plants can be considered a preferred food, in spite of their poor nutritive qualities. Even where abundant, however, lichens seldom constitute more than 75 percent of the diet at any

one time, and more commonly reach 50 percent or less. Certain grasses and sedges seem to be almost equally important, and in some areas (as noted) actually become dominant. On ranges where both lichens and sedges are abundant, the two are about equal in the diet. The importance of browse plants, green vegetation, and diet variability (as related to digestibility) needs to be explored in greater depth. It is evident from the work thus far that a diet consisting entirely or primarily of lichens does not provide adequate nutrition.

The ability to utilize a wide variety of plant food, the lowered basal metabolism, and the lowered energy requirements during winter provide the caribou with considerable capacity for surviving the nutritional adversities of this season. Alaskan caribou reach mid-April with little evidence of poor health. All animals examined (in excess of 200 from the Alaskan Peninsula, Arctic, and Nelchina herds) by me during March and April have been in good to excellent condition (excepting diseased or crippled animals), based upon the quantities of visceral fat present and the condition of the bone marrow. It is mostly after this point in time (i. e., about mid-April) that nutrition can become a serious problem, as a result of increased energy demands and depleted body-stores of certain nutrients. Tissue growth resumes during late April for many animals other than pregnant cows--antler growth, shedding of hair, body growth in the immatures.

The need for nutrients is especially great in pregnant cows, because during April and May (the last two months of gestation) most of the fetal growth occurs. The spring migration to the calving grounds adds a further energy drain. There is a need for a forage of greater nutritive value than that upon which most animals have been subsisting during the winter. This need is filled by the new plant-growth which becomes available as the snow melts.

The vicissitudes of spring weather obviously play an important role in the welfare of a caribou herd. At a time when the need for nutrients is great, a late thaw due to cold temperatures and snow-storms can prolong winter conditions and force the caribou to continue their winter feeding. Snow-crusting conditions can become a serious problem when the snow-cover remains unbroken over extensive areas. The effect of a late winter was particularly in evidence during 1964 in the Arctic herd of northwest Alaska. Most animals examined during mid-April of that year at Anaktuvuk Pass in the Brooks Range were in good health, as regards fat reserves; there was no evidence of poor nutrition. The main movement northward to the calving grounds was delayed about three weeks, and most pregnant cows did not reach there until early June; many stayed farther south than usual. The snow-cover remained over considerable areas until the last of May. Animals autopsied near the main calving grounds were in extremely poor condition--almost complete absence of visceral fat and red,

watery bone-marrow. One pregnant cow in such condition was bearing a normal sized, full-term fetus, but its udder had not developed to the extent found in most cows at that stage of pregnancy. Its bone tissue showed evidence of regression, the ramus of the mandible being quite fragile and easily broken--about one-half its normal thickness. Presumably this condition reflected the severe drain of nutrients from the cow's body in response to high energy-demands and the continued use of low-quality winter forage. In addition, the bodies of adult cows floating down the upper Colville River were sighted regularly, a further indication of the weakened condition of many of the animals. That stream does not present any difficulties for traverse to a healthy caribou. The loss of body fat after the winter season was observed to occur each year in the reindeer on Spitzbergen by Lydekker (1893). He noted (p. 329) that the animals returned to the coast each spring in "very fat" condition; but some weeks later, after facing snow-crusting conditions, they became "so poor as to be scarcely eatable."

In conclusion, it is my belief that the winter season itself presents no serious problems for caribou survival during most years. The critical period seems to come at the transition to spring and summer. This period of the caribou's annual cycle needs considerable study, for it well may be the key to population regulation in this species.

Other Dietary Components.

The tremendous variety of plant and animal food utilized by the caribou attests to the opportunistic nature of its feeding habits. In no other ruminant for which the food habits are well known have so many kinds of food been identified in the diet. Such a feeding adaptation has obvious survival value for an animal living in the difficult environment of the Arctic. The main seasonal diets have been discussed. It seems pertinent also to point out a few of the other foods utilized. Some might well be ingested as much for their mineral content as for their other qualities. To maintain normal metabolic activity the caribou must obtain certain chemical elements and compounds, and like most animals must ingest a certain amount of water.

Food.--There seem to be relatively few plants occurring in the Boreal zone that are not eaten at least occasionally by caribou. Many are not prevalent enough to be of much value even if highly palatable, but some could provide abundant forage. Of the latter, mosses are of particular interest, for they abound throughout the north country. Most workers have considered these to be of only incidental value as food, but in some areas, as noted earlier, they comprise a considerable part of the diet (see Aleksandrova, 1937; Shaposhnikov, 1955). Segal (1962c: 75) stated that various mosses of the genera Sphagnum, Polytrichum, Dicranum, Pleurozium, and Hylocomium were eaten "not infrequently" by reindeer in Karelia ASSR. The inclusion of Sphagnum is of

particular interest, for the biomass of this moss is quite large in most bogs and other moist areas; the reference is one of the few which has indicated Sphagnum as a food plant. In addition, Shaposhnikov (1955: 204) listed edible mosses from the genera Calliergon, Hipnum, Mnium, and Ptilium. No significant use of mosses has been reported in Alaska and Canada, although Hadwen and Palmer (1922: 27) listed various mosses (including Sphagnum fimbriatum) as being grazed by Alaska reindeer in winter, and Scotter (1967: 35) found Bryophytes comprising 3 percent of the winter diet in Canadian caribou. The role of mosses as caribou forage remains unclear, however, and it would be desirable to determine the extent of its utilization, its relative palatability, and its value as a supplementary and/or major food-item. If caribou can maintain their health when feeding on these plants, the carrying capacity of the ranges would be much higher than presently presumed.

Another group of ubiquitous plants in the boreal zone whose forage value remains unclear are the conifers (Order Coniferales). Most authors have believed these to be utilized but rarely, or not at all. The presence of conifer needles (mostly pine or spruce) in the rumens has been considered the result of accidental ingestion while feeding on other forage. Larin (1937) implied that needles falling on lichen pastures decreased the value of those pastures considerably, and often were the source

of serious infections (presumably from punctures in the rumen). Yet, on occasion, caribou do in fact feed upon these plants. In Ontario, Cringan (1956: 256) reported the occasional use by woodland caribou of ground hemlock (Taxus canadensis) and of spruce (Picea spp.), and rarely of balsam fir (Abies balsamea); plant parts of Picea eaten included roots, bark, twigs, and needles. Shaposhnikov (1955: 204) found plant tissue from pines (Pinus sibirica and P. pumula) in the rumens of Altai caribou. The needles of both white and black spruce (Picea glauca and P. mariana, respectively) occur commonly in the rumens of caribou feeding within the taiga. I have observed many instances where both caribou and moose (Alces alces) in Alaska have stripped and eaten the needles and branches of small spruce (1-2 meters tall) during the winter. Frequently, all that remained was the central trunk, plus various debris on top of the snow. The significance of such feeding is not clear, but spruce needles do contain large amounts of Vitamin A (Guther, 1962). Deficiencies in this vitamin can occur whenever there is a lack of green vegetation in the diet for a long period of time. The body stores tend to be quite large in ruminants, however, and J. Riggs (1940) found that range cattle could store enough for about 178 days. If such held true for caribou as well, then Vitamin A generally would not be a nutritional problem in most years. Nevertheless, a long winter might deplete the reserves and a deficiency of Vitamin A at the

end of the winter period could have adverse effects upon reproduction--fetal mortality, difficulties at parturition (such as retained placentae), still births, and weak offspring. This aspect of nutrition in northern ruminants should be investigated.

A number of other plants and plant tissues not normally considered as caribou forage can become an important segment of the diet at times. Various authors have noted the ingestion of the berries from certain shrubs, including Arctostaphylos alpina, A. uva-ursi, Empetrum nigrum, Rubus spp., Vaccinium uliginosum, and V. vitis-idaea (Segal, 1962c: 75; see also Flerov, 1952: 212; Herre, 1955: 3). The leaves of alder (Alnus spp.) also are eaten on occasion (Cringan, 1956: 258; Segal, 1962c: 71). Lent (1960: 25) implied only an occasional utilization of alder leaves by the caribou of northwestern Alaska during June and July. I have found no evidence of alder grazing or browsing during the summer among animals of the Fortymile and Nelchina animals. On one occasion, however, I observed a band of Nelchina animals feeding extensively in an alder stand during early February, pawing through the light snow-cover to obtain the fallen leaves. Aspen (Populus tremuloides) twigs were reported by Banfield (1954, 10B: 13) as being browsed during the winter by the tundra caribou of Canada. Various aquatic plants are utilized. Cringan (1956: 219) observed woodland caribou in Ontario feeding in the water on a few occasions, and also eating the roots of the yellow water-lily (Nymphaea variegetum) which were lying along the lake-shore.

Dugmore (1913: 31-32) observed that Newfoundland caribou fed extensively during the autumn period on water-lilies (Nuphar spp. and Nymphaea spp.). He described one feeding incident as follows:

> ...a herd of several caribou swam across the river near where I was hidden, and coming to the lily pads, immediately began eating the large leaves. The water was over four feet in depth so the animals could not touch bottom. They bit off the leaves as they swam about, frequently putting their heads entirely under water in their efforts to get possession of a submerged leaf. For over half-an-hour they continued their feast....They reminded me strongly of...moose, except that they did not go completely under water, and, of course, they swam much higher and with less effort.

The ingestion of sea-weed (presumably species of the brown algae, Phylum Phaeophyta) has been well documented in areas where the caribou or reindeer reach the sea-coast (R. Brown, 1868: 355; Kumlien, 1879: 54; Lydekker, 1893: 329; Jacobi, 1931: 223; Porsild, 1954: 22; Herre, 1955: 5; and Paterson, 1956: 16). Jacobi (op. cit.) listed the following species as being eaten: Ascophyllum nodosum, Fucus serratus, and F. vesiculosus. Herre (op. cit.) however, stated the belief that it was not so much the plant which attracted the animals, as the salt layer covering the tissue. The need for salt will be discussed in the next section.

Perhaps the most unusual aspect of the caribou's diet relates to the ingestion of animal food. Palmer (1926: 9)

stated that reindeer "...are known at times also to eat mice, dried fish, and ptarmigans and their eggs, a habit that probably may be attributed to a craving for certain mineral substances." Other authors have commented upon this feeding behavior, also: Gates (1928: 158), with regard to Lapland; Flerov (1952: 213), the USSR; and Porsild (1954: 22), Canada. Stuck (1920: 142), referring to reindeer along the northwest coast of arctic Alaska stated "...I was amused to hear that they sometimes kill and eat the ptarmigan out of snares set by the herders, and constantly rob the ptarmigan nests, eating the eggs greedily." Bogoraz (1904: 76-77) described some of the feeding habits of Siberian reindeer as follows:

> The Yukaghin on the middle Omolon...feed them all this time [animals penned and fed during fly-season] with willow sprouts and fresh fish. Two small grayling...is the daily allowance of a grown reindeer.... Occasionally it catches mice in the moss, and unfledged birds...and picks up around the house scraps of fish and meat. Some even steal frozen reindeer-meat from the stores....

A somewhat amusing account of the reindeer's predilection for fish appeared in one of Jackson's reports (Jackson, 1906: 89, 92, 101, 128), taken from the diary of a man driving a herd of reindeer from the Seward Peninsula to Bettles, Alaska, during November, 1904:

> Hardly had we retired before, eagerly searching for dry fish, quite a number of deer came around our tent....The fresh grayling...prove to be a source of great temptation to some of the reindeer...Even now some of the most eager fish-eaters are gathering outside, scratching and smelling where once the fish lay....some fresh fish had been in the sleds...they were scratching away all night to get it....many of the deer we have are just as fond of fish--dry or fresh, either--as any Eskimo ever can be.

In his monograph concerning the reindeer, Herre (1955) related the ingestion of animal food to a need for certain minerals. He stated that the reindeer in Lapland ate large numbers of lemmings only when the forage was inadequate and a mineral shortage occurred. No evidence for this statement was presented, however, so it well may be only an assumption. The ingestion of live animals, or animal food comprised mostly of muscle tissue, suggests a need somewhat greater than for minerals alone. Perhaps such feeding behavior can be related merely to taste, similar to some people's craving for sweets. On the other hand, there are some animal products eaten (e. g., urine, antlers) for which there seems little purpose except the need for minerals. These are discussed in the next section.

Minerals.--Little is known about mineral metabolism in reindeer or caribou, but this lack of information extends as well to most of the ungulates. My observations in interior Alaska suggested that these caribou can maintain an adequate mineral balance via their "usual" vegetable diet. I base this assumption upon the fact that the hundreds of carcasses examined have revealed no evidence of metabolic disorders and that the food habits studies have revealed no "unusual" feeding behavior of any apparent significance. Admittedly, the evidence is subjective and considerably more information is needed.

Of the various minerals required by caribou for normal metabolic function, calcium and phosphorous probably are the ones most likely to be in short supply at certain times. (Lichens are particularly lacking in both Ca and P--Scotter, 1965.) Significant losses of these elements undoubtedly occur during late pregnancy in the cows; the antlers of adult bulls require substantial amounts as well. Both of these needs become accentuated during late winter and spring when the fetus and the antlers are growing rapidly. It is perhaps significant that Nelchina caribou (both bulls and cows) during late May and early June are observed to frequent a number of "mud-licks" in various parts of the range. None of these licks have been analyzed for mineral content; both water and mud were ingested. Similar behavior at that time of year has not been observed

in Fortymile caribou, which also have been under extensive observation by the author, nor is there evidence for such in the animals of northwest Alaska.

On the other hand, various kinds of "licks" are known to be used at other times. I observed Fortymile caribou to frequent a mineral spring during fall and winter along Walker's Fork near Lassen, Alaska, and during mid-winter to dig into the stream banks of Jack Wade Creek in the same area and eat the silt (Skoog, 1956: 114). Animals in other parts of the range, however, and during other years, did not evidence such behavior. Dixon (1938: 207) stated that caribou in McKinley Park were

> ...prone to visit mineral springs or 'licks' during the summer. On the trail between Double Mountain and Igloo Creek there is a well-developed mineral spring which is visited by large numbers of caribou during the summer. Here we found a muddy area nearly 100 feet square that had been trampled bare of all vegetation....

He noted also that both caribou and mountain sheep (Ovis dalli) used the same licks. Cringan (1956: 219) stated that woodland caribou in Ontario often were observed eating mud. Shaposhnikov (1955: 205) observed that liquid salt-licks were visited by caribou throughout the year in the Altai Mountains of USSR.

Many authors have commented upon the utilization of salt by reindeer. Hadwen and Palmer (1922: 37) stated that "Reindeer are very fond of salt, and when held along the coast

they get it during the summer season by drinking the sea water or licking up the deposits on the beach." A similar statement was made by Porsild (1954: 22). Herre (1955: 9) implied that the addition of salt to the reindeer's diet was a necessity for the animals' maintenance, especially in those herds located inland; he used Alaska as an example. On the contrary, reindeer herding in Alaska has been carried out without the use of salt supplements in the diet. In Jackson's annual report on the reindeer industry (1894: 63), Supervisor Bruce stated, "In my experiments in trying to get the deer to eat salt but indifferent success was met with....and I discontinued it." Twenty-five years later the experiment was still continuing, and it was found that "...the reindeer are very fond of crushed salt, but that they scarcely touch the block salt," (Hadwen and Palmer, 1922). Ultimately the experiment ended, and "salting" never became an established management procedure in Alaska. Nevertheless, the reindeer prospered; the <u>need</u> thus seems doubtful. Apparently the animals can obtain adequate amounts of Na and Cl in their normal diet.

There is no question, however, that reindeer have a craving for certain forms of salt, as has been implied already. Reindeer herders in the Old World long have used urine as a means for attracting animals used for harness. The Siberian herders in Alaska during the first years of the reindeer importation (Jackson, 1894: 63)

> ...carried a little vessel with them, made of seal skin....The herders made a practice to urinate in this vessel, and when held toward the deer a half dozen would start for it and drink greedily....and eat the snow saturated with it eagerly. They would eat snow where dogs had urinated, but not with so much relish.

Similar comments were made by Bogoraz (1904: 85) and by Hatt (1919: 93). The latter author also noted that caribou and sheep in Asia frequented the same salt-licks, and that salt was used by the Tungusian hunters to induce caribou to frequent certain localities.

Other examples of mineral ingestion are evident as well. Bogoraz (1904: 76) observed that Siberian reindeer consumed "...bird-dung with relish, quantities of which are heaped around the moulting-places of ducks." The utilization of shed antlers is well known (Hadwen and Palmer, 1922: 57; Flerov, 1952: 213; Banfield, 1954, 10B: 13; Herre, 1955: 9). O. J. Murie (1935: 42) made a pertinent observation of a reindeer herd in the Beaver Mountains, west of McGrath, Alaska, during early March, 1922:

> Many of the animals had shed their antlers and were seen eating them. The antler was worked back between the molars on one side and bits gnawed off. Frequently another animal would rush up and appropriate the piece of antler, until it, in turn, might be driven away. Evidently there was a shortage of shed horns, for the reindeer were gnawing at those of their companions,

> still unshed....Most of the fawns had antlers much reduced....Human control may have developed to the extreme a practice that existed in the wild herds. Probably, however, lacking the freedom to wander where minerals might be had, the domestic herds were deficient in this respect and took to antler chewing....

Murie (op. cit.) also noted that the velvet shed from antlers was ingested commonly by both reindeer and caribou. Hadwen and Palmer (1922: 57) had discussed this eating of both shed and unshed antlers by Alaska reindeer, and had stated that this behavior was particularly evident toward the end of winter. It is significant that during the winter reindeer herds are comprised mostly of adult, pregnant cows, plus young of the year, and that late winter is the time when calcium and phosphorous shortages would be most apt to occur, as discussed earlier.

There seems little doubt that mineral shortages do occur in reindeer, judging from the feeding behavior which has been discussed. As Hadwen and Palmer (1922: 57) have stated " ...the fact that reindeer crave lime salts at certain times of the year indicates that their systems lack some essential requirement in mineral matter." This aspect of nutrition also needs considerable study.

In the caribou, however, mineral shortages seem to be of rare occurrence, as implied by O. J. Murie (1935: 42). The wide dispersal and continual movements of this animal tend to

assure a more nutritious, well balanced diet in most areas. The only evidence for a mineral shortage I have encountered was described earlier. In northwest Alaska, a pregnant cow in early June, 1964, was autopsied, and its jaw-bone was found to be reduced to half its normal thickness; I attributed this condition to the late spring thaw, and the fact that most animals in this herd were forced to subsist on winter forage (mostly lichens) for a much longer period than was customary for that area. The high calcium demands by the fetus in late pregnancy probably resulted in the degradation of the maternal bone-tissue. Such a late spring as in 1964 is a rather uncommon phenomenon for the western Brooks Range, however, as well as for most of the other caribou regions of Alaska. Mineral deficiencies cannot be considered a problem to Alaska's caribou population.

Water.--In one form or another, water is abundant and available throughout the year on probably all caribou ranges. During the winter the animals ingest snow along with their food, but I have observed also numerous animals eating snow from the ice covered surface of lakes, where snow was the only ingredient evident. The animals also drink water from overflows on streams and lakes, sometimes having to break through an upper crust with their forefeet (Skoog, 1956: 114). Edwards and Ritcey (1960: 6) observed caribou in British Columbia eating both snow and slush on lakes in that area.

In summer, however, in spite of many field observations over a period of 10 years, I have yet to witness caribou drinking water. Harper (1955: 99) commented upon the fact that none of the caribou he observed in northern Canada paused at the river crossings to drink. I have not found any other references to the drinking of water by reindeer or caribou during this season--excepting sea- water and water from mineral springs, which presumably are ingested for other reasons. Perhaps these animals obtain most of their water from the succulent vegetation eaten at that time. I have recorded bands of caribou remaining on dry ridge tops for over 24 hours during late June and early July, without any free water supply; in these instances the animals were seeking relief from the flies. Nevertheless, the fact remains that water generally is in plentiful supply, and it is hardly conceivable that shortages ever occur.

Summary.

The basic food habits of this species in Alaska can be summarized as follows:

1. Caribou are cursory feeders, frequently remaining in one place no longer than it takes to ingest one or two mouthfuls of forage. At the same time these animals are rather fastidious in their feeding habits, eating predominately the finer portions of the forage plants (e. g., leaves, buds, stem-tips). Such behavior, coupled with the continual shifting of grazing areas--both from day to day, as well as from one year to the next--disperses the effects of feeding activity widely and reduces considerably the possibility of overgrazed range. A wide range of habitats and vegetation types are utilized by caribou throughout the year, and the number of palatable plant species is enormous. The main diet varies with the seasons and the available plant forage.

2. In the spring (mid-April to mid-June) the new growth of various grasses (*Festuca*, *Hierochloe*, *et al.*) and sedges (mainly *Eriophorum* and *Carex*) are important, and especially the leaves and buds of certain willows (*Salix*) and dwarf birch (*Betula*). A large number of forbs are eaten as they become available. Lichens are incidental food items among Alaska caribou at this time of year, except during late thaws when winter conditions inhibit the spring plant growth. This season

probably is the most crucial with regard to nutrition in caribou. The high energy demands (antler growth, resumed body growth, late pregnancy, etc.) require nutritious food to prevent a net energy loss and the further depletion of stored nutrients, already reduced after a winter of low quality forage (e. g., lichens). Poor nutrition at this time of year could affect the production of calves adversely.

3. During the summer (mid-June to mid-August) a wide variety of highly nutritious plant food becomes available, and the caribou diet reflects well this variability. The basic forage during this period, however, consists of the succulent portions (leaves, buds, stem-tips) of willow, dwarf birch, grasses, and sedges. A large number of forbs supplement this diet, and in late summer mushrooms are especially sought when available.

4. The fall grazing season (mid-August to mid-October) is characterized by a gradual shift to the winter forage plants as the succulent vegetation withers. The animals continue to utilize the green vegetation that lingers in the moist sites, and move to the lower elevations as the season progresses. Lichens assume ever increasing importance, but preference still is shown toward mushrooms (as long as available) and toward the green sedges bordering the lakes, ponds, and bogs. The browse plants (willow and dwarf birch) steadily decrease in importance.

5. Alaska caribou continue to utilize much sedge (particularly the Carex aquatilis on bogs and lake shores) during early winter. The Interior herds tend to spend much of the October-December period at the lower elevations amidst open stands of spruce, and particularly in flat, "muskeg" terrain where lakes, ponds, and bogs abound. Lichens become increasingly important in the diet as the winter progresses. Characteristically the animals return to the alpine areas after November, and there the diet consists mostly of sedges and lichens in about equal proportions. In some areas (e. g., the Alaska Peninsula) and during some winters (e. g., the Arctic herd when wintering on the arctic slope) the diet may consist almost entirely of sedge during most of the winter.

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PART II. THE POPULATION

It is apparent that during the Wisconsin glacial stage of the Pleistocene epoch caribou occurred throughout much of the region now designated as Alaska and the Yukon (Banfield, 1961; Guthrie, 1968). At the height of the last major glacial advance, dated variously from about 18,000 (Flint, 1957; 341) to 20,000 (Frye, Willman and Black, 1965: 551) years ago, the animals necessarily were confined to the unglaciated refugium encompassing central and northern Alaska and the "land-bridge" now submerged beneath the Bering Sea. Presumably the caribou ranged freely across much of the ice-free region into Asia, until the Bering "land-bridge" disappeared about 12,000 years ago. As the ice retreated and sea levels rose, it can be assumed that the animals dispersed into new areas as the habitat became favorable. Some of the first areas on the east to become free of ice provided dispersal corridors (e. g., along the arctic coast and along the upper Yukon and Mackenzie Rivers), which permitted the interchange of caribou

between populations previously isolated in the three major refugia of North America--Beringia, Pearyland, and the periglacial continental region to the south (Banfield, 1963).

Frye et al. (1965: 58) have indicated that the sea level reached its present level about 5,000 years ago, although minor fluctuations have occurred since then. Thus, one can assume that the caribou population of Alaska and the Yukon had approximately the same range available to it then as during the early 1800's, before the intrusion of modern civilization. During the past 5,000 years then, one can assume further that the caribou would have been able to occupy fully the habitat available. No doubt a considerable interchange of animals has occurred within certain regions, as seems to have been the case during the past 100 years in Alaska. These population shifts are discussed later. I believe it necessary to present in some detail an historical account of the caribou in Alaska and the Yukon (i. e., the region lying west of the MacKenzie River). Such information provides a needed background for understanding the fluid nature of this caribou population, of which the Nelchina herd is a part.

CENTERS OF HABITATION

On the basis of the historical material examined I have postulated that Alaska has but one caribou population, encompassing six main "caribou regions" and consisting of various sub-populations or herds. Since the early 1800's caribou have been present continuously in these six regions in varying numbers. Interchanges and shifts of animals have occurred at various times. Within each region I hypothesize a "center of habitation", which acts as a focal point for population dispersion. This center presumably encompasses the most favorable portion of the region, and supports the main sub-population during periods of low numbers. As the density increases, the caribou extend their movements, utilizing more and more marginal areas and traveling greater and greater distances, but the center of habitation remains the focal point.

During periods of high numbers within any one region, the movement pattern may change and/or become quite erratic. Major segments of the main herd may branch off and eventually emigrate into another region to become part of that sub-population. At some point during the high, the various "controls" become active and the population curve levels and turns downward. The decline in numbers, excluding the human element, could result from low reproduction and high mortality as the result of poor range, from starvation due to severe winter conditions, from excessive mortality due to disease, from emigration to new ranges, or, more likely, a combination of these factors.

After the decline, remnant herds may be found in various portions of the region, but the principal regional sub-population remains at the center of habitation. The remnant herds tend to remain static in size, possibly due to marginal range, whereas the "main population" increases steadily. Insofar as possible the dynamics of the six sub-populations are independent of one another, but an egress or ingress of animals between regions can occur at any time due to shifts of animals.

The centers of habitation encompass much of the best caribou range in each region. Such range includes extensive areas beyond treeline, especially for spring, summer, and fall use, where calving and breeding take place, where relief from flies can be obtained on wind-swept ridges or meadows, and where high-quality tundra or alpine forage is available. Such areas I consider to be of prime importance for a successful caribou population. Also important to the caribou are wintering areas where the snow conditions are suitable--a low to moderate snow-cover with a minimum of crusting conditions. Of course, an adequate supply of winter forage is necessary as well, and if not present, the caribou probably will move elsewhere. I believe that the wintering grounds are less of a problem, because adequate areas are common to all of the regions designated. Winter provides the caribou with a choice of a variety of habitats and a certain freedom of movement as well, for the restrictive physiological and psychological "drives" associated with calving,

breeding, and the fly-season are absent. In addition, energy demands are reduced considerably during most of the winter months. Growth ceases and movements tend to be more restricted; pregnancy energy demands remain rather low until late winter; and other maintenance energy demands are reduced due to various morphological and physiological adaptations.

Caribou Regions of Alaska.

The availability of suitable alpine or tundra areas to great extent determine the centers of habitation for the six major sub-populations of caribou in Alaska. These six "caribou regions" are depicted in Figure 1 and described in more detail below. The artificial limits shown tend to pass through areas that are mostly devoid of resident caribou (e. g., forested river-valleys). Some of these boundaries, however, such as between Regions III and IV and between IV and V, encompass "good" caribou habitat, but past observations have shown these areas to be used mostly in transit. None of the boundaries indicated are intended to be actual barriers to caribou movement, but simply designate regions in which the sub-populations of caribou have been more or less discrete entities over the past 100 years and somewhat isolated as well. As will be shown later, there have been interchanges of animals between these regions on various o occasions.

Region I. Southwest Alaska.--This region encompasses the Alaska Peninsula, extending from Lake Illiamna and the Kvichak River on the north to Unimak Island on the southwest, plus various other offshore islands adjacent to the southwest end which have supported caribou occasionally. The extensive black-spruce forest and bog along the Kvichak and Nushagak Rivers presents a generally undesirable habitat for caribou, and

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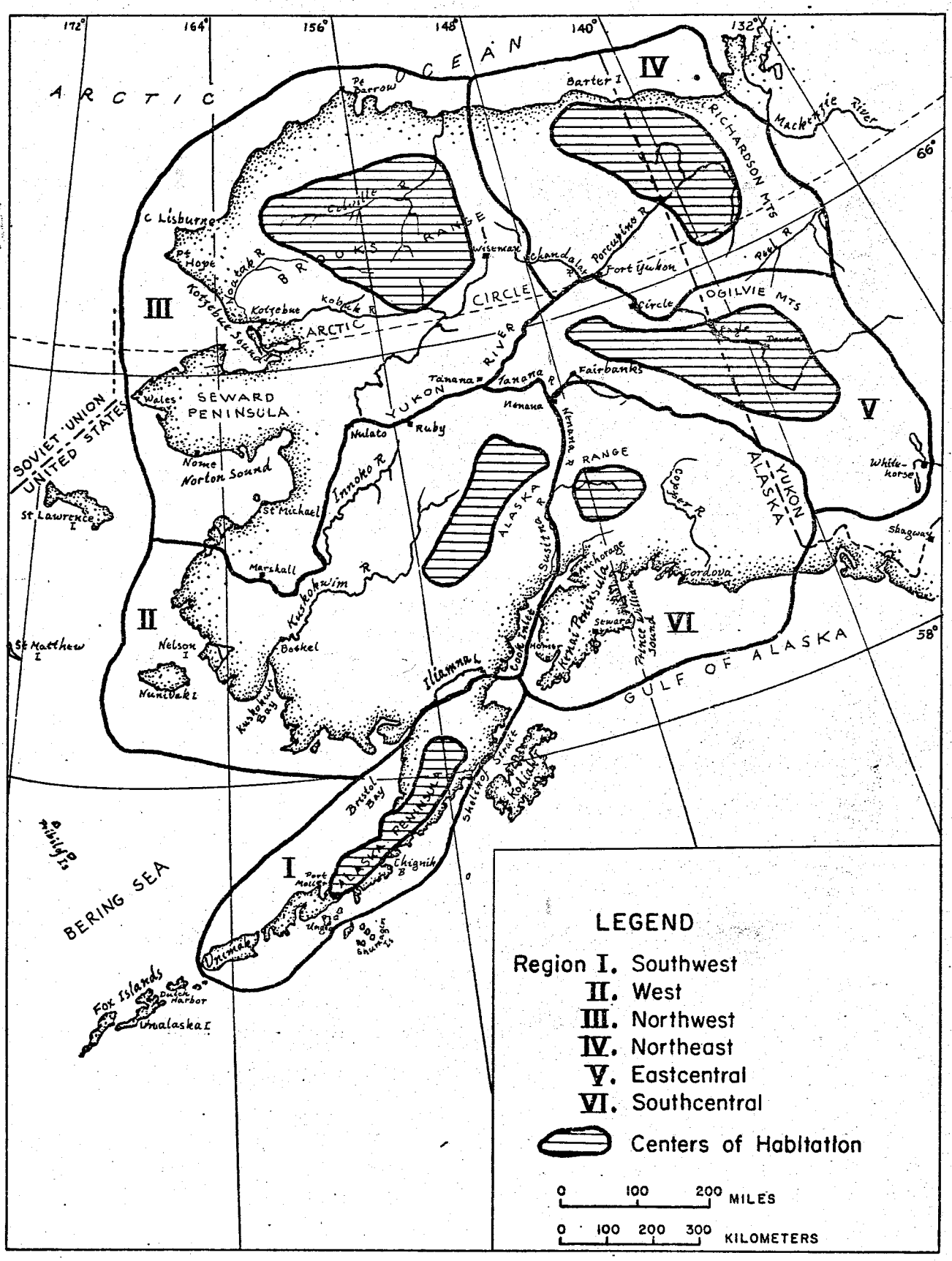

Figure 1. Six caribou regions of Alaska and adjacent Canada, and their "centers of habitation".

therefore represents a barrier of sorts. Extensive fires in that area since 1900, especially during the summer of 1935 (Heintzleman, 1936), have rendered the northern border even less acceptable to caribou. No movement across this border has been recorded since prior to 1900. The only portion of the entire region which contains forage lichens for winter use is that lying north of Becharof Lake. Much of the area to the south of Becharof is excellent for spring, summer, and fall use, consisting primarily of various types of tundra vegetation. Several volcanoes south of Port Moller continue to be active, and have spewed volcanic ash over the terrain on numerous occasions during the past 200 years (Powers, 1958). I consider the northern half of this region to be the best caribou habitat, and have designated as the center of habitation that area lying between the Naknek River system and Port Moller. Forage lichens are scarce throughout the region, and most of the winter diet consists of various sedges. This is the only portion of Alaska in which the caribou cannot obtain "normal" quantities of lichens during the winter. No adverse effect due to this diet lack has been noted. Reindeer on various of the Aleutian Islands and on other islands in the Bering Sea (e. g., Umnak, Atka, Kodiak, Nunivak, and St. Mathew) apparently have continued to do well after the original lichen cover had been destroyed or reduced to a minimum.

Region II. West Alaska.--This region extends northward from Lake Iliamna and the Kvichak River to the Yukon River, and eastward from the Bering Sea to Cook Inlet and the Susitna, Chulitna, and Nenana Rivers. It encompasses the drainages of the Nushagak, Mulchatna, and Kuskokwim Rivers, plus those of the southern tributaries to the Yukon River below the Nenana River and those of the western tributaries to those rivers forming the eastern boundary. Included within this region is the western segment of the Alaska Range. Most of the terrain along the Yukon River supports a rather dense, continuous spruce forest, burned in many locales, boggy in some. This vegetation extends over much of the Kuskokwim River drainage to the south, interrupted here and there by some of the low, mostly rounded hills of the Kuskokwim Mountains that manage to extend above timberline. In the southwest, the Kilbuck Mountains and adjacent segments of the Kuskokwim Mountains support a tundra vegetation; this area extends eastward across the low, sparsely wooded Taylor Mountains to the Alaska Range. The western slopes of the Alaska Range from Lake Iliamna northward contain excellent caribou habitat, with extensive alpine tundra vegetation. The river valleys of the Kvichak, Nushagak, Yukon, Nenana, and Susitna Rivers are considered to be impediments to caribou movements. The main gap in the boundaries of this region occurs in the Broad Pass area, lying between the Susitna and Nenana River

drainages. Here, an intermingling of caribou commonly occurs between animals of Regions II and VI. On the basis of terrain features, extensive alpine areas, and past caribou utilization, I consider the center of habitation to lie along the west slopes of the Alaska Range between Mt. McKinley Park on the northeast and the upper reaches of Big and Swift Rivers on the southwest.

Region III. Northwest Alaska.--This is the largest of the caribou regions, and currently it supports the bulk of Alaska'a population. It extends northward from the Yukon River to the Arctic Ocean, and eastward from the Bering and Chukchi Seas to the Kuparuk River north of the Brooks Range and to the North Fork of the Chandalar River south of the Range. The eastern boundary is indefinite, and merely approximates the extremes of movement east and west of the caribou in Regions III and IV. The border encompasses "good" caribou habitat, and no impediments to movements are evident. Crossings from both directions have occurred periodically in the past. Most of the region north of the Kobuk and Koyukuk River drainages are timberless, and hence support various vegetation types of alpine-tundra flora. On the west, the Seward Peninsula and the highlands adjacent to Norton Sound also support extensive stands of alpine-tundra vegetation. The remaining area, i. e., the Kobuk and Koyukuk River drainages, is comprised mostly of spruce forest, with the exception of the Ray Mountains on the southeast. This caribou

population unit seems to have maintained a continuous residence during historical times in the area encompassing the Endicott Mountains and that portion of the Brooks Range containing the middle and upper drainages of the Noatak, Utukok, and Colville Rivers. This area is considered to be the center of habitation.

It might be desirable to discuss briefly the general lack of "long-time" resident caribou populations in the western portions of Regions II and III. To be sure, these areas have been utilized during periods of high populations, but it would appear that at other times these areas are not well suited for resident herds. In particular, I am referring to the Kilbuck Mountains, the delta areas of the lower Kuskokwim and Yukon Rivers, the Seward Peninsula, and the highlands adjacent to Norton Sound. These areas were utilized prior to 1875 by major segments of the apparently huge caribou population occupying western Alaska at that time. Sometime before 1880, however, and before the introduction of reindeer to the Seward Peninsula, the population shifted its range and/or was reduced drastically in size, and these areas essentially were abandoned. At the time of abandonment these ranges still contained vast lichen stands. A more detailed discussion of this aspect is presented later. I postulate that these western areas are undesirable for continuous caribou habitation, because of periodic severe winters of heavy snow and icing conditions which greatly limit the availability of food. In this respect then, most of the Alaska Peninsula is marginal habitat, and perhaps this factor is the main reason for the generally low caribou numbers there since before 1900. Thus, the centers of habitation in these three regions also encompass, perhaps, areas which are somewhat immune to this type of adverse weather, e. g., a disrupted and varied mountain terrain, where windswept areas are present and/or where low temperatures inhibit icing conditions. I have considered this factor in my designation of the centers of habitation in these regions.

Region IV. Northeast Alaska.--This portion of Alaska and northern Yukon adjoins Region III to the east. The Beaufort Sea forms the northern boundary; the lower Mackenzie and Peel

Rivers, the eastern; and the Yukon River and upper drainages of the Peel River, the southern boundary. The region encompasses the eastern Brooks Range, the British and Richardson Mountains, the large drainage basin of the Porcupine River, the northern portion of the Mackenzie Mountains, and most of the drainage of the Chandalar River. The western boundary has been described in the discussion of Region III. On the east, the wet, boggy tundra and spruce forest along the lower Mackenzie and Peel River valleys act as a barrier to restrict (but not to prohibit) east-west movements or interchanges of animals. Much of the southern boundary traverses caribou habitat, and, like the western boundary, can be considered as merely demarcating the usual extremes of movements in the adjacent regions, in this case Regions IV and V. There is a definite overlap here between the two regions, because animals from both periodically winter along the upper drainages of the Peel River. The center of habitation encompasses the Shublik, Franklin, Romanzof, Davidson, and British Mountains, the western slopes of the Richardson Mountains, and the Old Crow Flats, including the adjacent highlands.

Region V. Eastcentral Alaska.—This region is bounded on the north by the Yukon River and the southern limits of Region IV (as previously described); on the west and south by the Tanana River and St. Elias Mountains; and on the east by a rather vague

line of demarcation, which crosses various mountain ranges and river valleys and outlines merely the known eastern limits of movements by this sub-population. Included within the region are the Yukon-Tanana upland, the Ogilivie Mountains, the Dawson Range, and the northern slopes of the St. Elias Mountains. The center of habitation essentially encompasses the Yukon-Tanana upland, plus the southern portions of the Ogilvie Mountains and the western portions of the Dawson Range.

Region VI. Southcentral Alaska.--The sixth caribou region of Alaska lies between Regions II and V, encompassing the eastern portion of the Alaska Range; the Wrangell, Chugach, and Talkeetna Mountains; the entire drainage of the Copper River; the upper and eastern drainages of the Susitna River; and the Kenai Peninsula. The lowland along the Tanana River boundary on the north and east tends to discourage movement of caribou between Regions V and VI. Similar terrain along the western boundary (i. e., along the lower Susitna and Nenana Rivers) tends to inhibit movement between II and VI, with the notable exception of the Broad Pass area, as discussed under Region II earlier. The center of habitation is considered to encompass the Talkeetna Mountains, the drainages of the upper half of the Susitna River, and a portion of the western drainages of the Copper River.

Caribou Herds as Sub-populations.

Within the regions outlined various "herds" of caribou are evident. It seems desirable to define what I mean when referring to these units, e. g., the Nelchina, Delta, Mentasta, and Chisana herds comprising the sub-population in Region VI. It has long been known that reindeer tend to acquire an attachment, of sorts, for certain portions of their range (especially the calving grounds) and that they express a "homing instinct" in their movement behavior which brings them back again and again to familiar areas (Jackson, 1892-1908, various reports; Lomen, 1920: 250; Palmer, 1926: 4, 1929: 1-2; Turi, 1931: 92; and Paterson, 1956). Palmer (1926: 4) stated as follows:

> Reindeer become attached to their accustomed haunts, and once well located on a range will unerringly return to it if moved away. In one case, several adult animals were transferred from one herd to another over a distance of 200 miles, and the next year were found back in the original herd, in spite of the fact that there were five other herds between the two places. Unless restrained the reindeer instinctively seek successively their favorite fall, winter, or summer pastures.

Similar behavior seems apparent in caribou. Indeed, the deep trails etched in mountain-sides and the presence of drive fences constructed by the aborigines attest to the "regularity" and "fidelity" of caribou movements over variable periods of time.

The "homing instinct" seems especially strong in the females, which have a tendency to return each spring to the

same calving area. Perhaps one of the most consistent behavioral characteristics of an Alaskan caribou herd is that sometime during the period mid-April to late May the calving segment of the herd will move toward a definite calving area where most of the herd's pregnant cows will drop their calves (Skoog, 1962: 1-2). This area may be rather extensive at times or perhaps quite restrictive, but usually the same general locality is used year after year. In some years the calving area is displaced due to one reason or another, frequently to heavy snows remaining late in the spring, which appear to delay the calving movement. In general, however, the calving area is relatively fixed, as compared with the wintering or summering areas, and it becomes a focal point for movements of the herd during the year. I have discussed previously this behavior for the Fortymile herd of east central Alaska (1956: 41, 68) and for the Nelchina herd of south central (1959: 2). Lent (1966a: 739-741; 1966b: 484) has documented the historical use of a specific calving area by the Arctic herd in northwest Alaska.

As stated by the writer several years ago (Skoog, 1962: 1-2), "The calving grounds, then, can be considered to be more or less a focal point for the movements and range of an individual caribou herd." Thus, a herd becomes an entity (sub-population) when it establishes a calving area distinct from that of any other herd and uses this area repeatedly over a period of years. Mixing

between herds at other seasons (primarily winter) occurs from time to time, and has been reported by wildlife biologists in both Alaska and Canada. Such intermingling is not considered contradictory to my definition, for invariably the herds separate and return to the ancestral calving grounds each spring, even though substantial gains or losses in animal numbers may have occurred. Such interchanges will be discussed later. All of the herds referred to in this paper have been identified according to their geographic location, relative to a specific calving area for each.

DISTRIBUTION

A review of the historical distribution and abundance of any wild animal generally is not an easy task. Too often the observations and data available are meager and incomplete for proper evaluation. The history of Alaska's caribou is no exception. First, not many of the travelers and explorers in Alaska took the trouble to record detailed observations regarding caribou, or other animals. Much of the information available is found in general comments interspersed through the narrative portion of reports. Second, these early travels mostly occurred during the summer months and were confined to the usual routes along the coast or along rivers. Thus the observers were exposed to a relatively small portion of the caribou range, frequently at a time when the animals probably were in the high country seeking relief from flies. Third, the tendency of caribou to assemble sometimes in a large, compact herd within a relatively small area makes it easy for one to be completely unaware of the animal's presence. Thus, the fact that an observer has seen few or no caribou is not necessarily significant. Fourth, caribou populations are known to shift their ranges and change their movement patterns, gradually over a period of time or sometimes rather suddenly. A population decline in any region does not mean necessarily that the animals have died off.

Observations of carcasses and skins of animals killed by humans are concrete indicators of the availability of caribou.

Information from natives and long-time residents can supply good information provided one is able to properly judge the reliability of the observer. Estimates of numbers are always difficult to evaluate, what is "many" or "large" to one person may be "few" or "small" to another. Generally, however, if a number of observations from various sources all indicate a low or a high population, one likely can conclude such is the case.

Each reviewer, however, must decide for himself what appears to be true and what false, and yet try to avoid bias--a difficult chore at best. The task requires a certain amount of insight and a good knowledge regarding the life-history of the animal species involved. By knowing the species well, one can definitely dismiss certain statements as untrue and accept others as being quite plausible. Having worked with caribou for 12 years, I am well aware of the problems involved in interpreting caribou distribution and numbers, even when one has a seemingly large array of current facts. The evaluation of observations made in the past can be quite exasperating.

Historical Resume.

The information obtained from historical accounts and reports spans about 150 years. I have divided this time-span into five periods, as follows: 1) Prior to 1875, 2) 1870-1895, 3) 1895-1925, 4) 1925-1945, and 5) 1945-Present. These seem to outline best the principal changes that have occurred in caribou distribution and numbers. Each region will be discussed separately, relative to the time-periods designated. This brief resume and discussion provide a desirable background for a better understanding of the population dynamics of this species and, in particular, of the Nelchina herd, whose ecology constitutes the central topic of this paper.

Region I. Southwest Alaska.--Caribou have ranged the Alaska Peninsula continuously during the past 200 years or so, sometimes occupying the entire length, but at other times mainly one end or the other. The records prior to 1875 are scanty, but include observations from some of the early Russian explorations. In the spring of 1773, Soloviev found caribou numerous at the southwest end of the Peninsula, presumably around Cold Bay, and plentiful on Deer Island, just off the coast (Masterson and Brower, 1947: 140). These same authors (p. 149) referred to Zaikov's finding caribou abundant on Unga Island of the Shumagin group in 1775; oddly enough, in his account of Unimak Island (p. 148), Zaikov failed to mention the presence of caribou there.

Elliott (1875: 257) noted from Veniaminov's writings in 1840 that caribou ranged all along the Peninsula and traveled to several islands of the Shumagin group and to Unimak. O. J. Murie (1959: 329) stated that caribou were present on Unga Island in considerable numbers at one time, and had been reported on Deer Island; in 1925 he found an old caribou skeleton on Amak Island, which lies in the Bering Sea some 15 miles north of the Peninsula's tip. The presence of caribou on these outlying islands is significant, because it implies a large population on the Peninsula itself. It seems doubtful that caribou would swim the 5-15 miles necessary to reach these islands unless population pressures were fairly high on the mainland; of course, the animals might have crossed via the ice-pack during an exceptionally cold winter. Elliott (1875: 49) noted during 1872-74 in trading posts at Nushagak and Ugashik (northeast end) "...quite a fair number of reindeer skins, the country being fairly alive with these animals." Later (1897: 397) he wrote,

> Reindeer cross and recross the Kvichak River in large herds during the month of September, as they range over to and from the Peninsula of Alaska....At the mouth of this stream is one of the broadest deer-roads in the country.

Apparently during the early 1870's, and before, the caribou were numerous and utilized the entire Peninsula.

During the next period, however, 1875-1895, a shift occurred in the caribou distribution. Petrov (1881: 23) noted

in 1880 the recent scarcity of caribou at the southwest end of the Alaska Peninsula, stating

> ...and until quite recently they used to have an opportunity of getting an abundance of reindeer here; these animals coming down at regular intervals from the great land to the northeast in droves, extending as far as the westernmost point of the peninsula, and running over...to...Oonimak Island. Latterly, or within the last year or two, the reindeer, from some cause or other, have ceased to make their appearance.

It would appear from this observation that the main population was centered at the northeast end of the Peninsula and major segments had extended seasonally to the southwest. O. J. Murie (1935: 58) implied that caribou were numerous on Unimak Island in the 1870's, but stated they had decreased to only a few hundred animals by 1894.

The reports of Petrov (1884) and the U. S. Census Office (1893) noted the abundance of caribou at the northeast end of the Peninsula, with relatively few remaining to the southwest. Nelson stated in 1887 (Nelson and True, 1887: 285) that "Reindeer are still very numerous on the peninsula of Aliaska and the adjacent district, but a few winters since many of them died from some contagious disease, and I am told they are becoming scarcer every year there." (No further explanation of this "contagious disease" was given.) In 1890 Fort Alexander, located at the mouth of the Nushagak River, was still doing "a fine business" in reindeer

skins (U. S. Census Office, 1893: 96). All of these observations point to a decrease in the numbers of animals utilizing the Alaska Peninsula, with most of the population located at the northeast end. It seems likely that the large migrations across the Kvichak River had stopped sometime prior to 1890; otherwise they probably would have been mentioned in the U. S. Census Office report. On the other hand, it would appear that large numbers of animals remained in the region north of the Kvichak River and to certain extent to the south as well.

After 1890 the center of caribou abundance shifted to the southwest. By 1902 Osgood (1904: 28) could state that "The large herds which occur farther west on the peninsula do not, as a rule, come as far east of Becharof Lake, although small herds are scattered all along." He lamented the extensive killing of caribou on the Alaska Peninsula for meat and hides, and noted (p. 28) that a trading post had been established near Port Moller in September, 1902, "...for the express purpose of trading for caribou skins....about 1,000 caribou skins was confidently expected during the following year...." Radclyffe (1904: 65) made similar comments regarding the caribou distribution in 1903 and the large trade in caribou skins; natives from Unga Island crossed to the mainland to participate in this market (p. 157). By 1905 caribou numbers on Unimak Island had expanded to "full carrying capacity" (O. J. Murie, 1935: 59), being augmented considerably by influx from the mainland. The animals were still numerous at the southwest end in 1913 (Scull, 1913: 172-184), and Madsen (1916: 5) noted that annual movements occurred

to and from Unimak Island. It is interesting to speculate on the possible influence of the Katmai eruption in early June, 1912, upon the distribution of caribou at the northeast end. At Kodiak, some 80 miles to the east, the blanket of ash lay 18-24 inches thick and the ground vegetation essentially was wiped out (Dailey, 1912; Griggs, 1915, 1918a, 1918b). Such a catastrophe probably occurred on the adjacent portions of the Alaska Peninsula as well, and I would suppose that one effect would have been to drive the caribou there to the southwest. The continued scarcity of caribou in the northeast section was noted by U. S. Geological Survey parties in 1921, 1922, and 1923 (Capps, 1923; Smith, 1925). By 1925 animals were ranging northward to Port Heiden (Knappen, 1929: 168), but the bulk of the population remained farther south, with an estimated 7,000 on Unimak Island and 5,000 on the mainland (O. J. Murie, 1959: 330). The general consensus seemed to be that caribou numbers had dwindled considerably since the late 1800's (Alaska Game Commission, 1926c; O. J. Murie, 1935: 59).

In the late 1920's, however, all reports of the Alaska Game Commission (a and c) called attention to the rapidly expanding caribou population on the Alaska Peninsula. Most of the animals remained south of Port Moller, but regular movements northward occurred as far as Ugashik and also took place between Unimak Island and the mainland (Alaska Game Commission, 1929c; 1930c).

During the early 1930's a shift in the population took place toward the north. Heavy kills due to deep snows and icing conditions were reported in the area south of Moller during the winters of 1930-31 and 1933-34 (Alaska Game Commission, 1931; 1934c). According to Rood (1942), a drive of 1,500 reindeer was made in 1932 from the Kuskokwim River area with the intent of establishing a herd south of Port Moller; this drive was halted at Naknek, however, "...because....a volcanic ash had descended on the range southwest of Port Moller." Powers (1958: 64-65) listed the volcanoes Aniakchak, Veniaminof, Pavlof, and Shishaldin (Unimak Island) as being active about that time, and especially Pavlof during the period 1929-31. The total effect of volcanic ash is not known, but one can assume it would affect adversely the food supply and/or availability, at least for a short while, and thereby cause caribou to move. The 12th Annual Report of the Alaska Game Commission (1937c), however, noted that the animals were "quite numerous" along the entire Peninsula below Becharof Lake. Reindeer herders at Pilot Point reported seasonal movements north-south past Ugashik (Rood, 1942). The winter of 1938-39 was particularly severe, in terms of deep snows and icing conditions, along the entire Bering Sea coast. Many reindeer starved to death as a result, and Burdick (1940: 11) stated that "Estimates of losses ranged higher than 50 percent." In areas where caribou were exposed to similar

conditions, such as the Alaska Peninsula, one probably can assume similar losses. Yet, in 1940 and 1941 the Alaska Game Commission reported the Alaska Peninsula caribou population to be "in good condition", at the same time remarking pessimistically about the decreases elsewhere (1940c; 1941 b,c). Caribou were still present on Unimak Island. In 1942 the Alaska Native Service reported reindeer herds at Naknek and Egegik numbering 3,500 and 3,000, respectively (Alaska Game Commission, 1949d, V.3, No.3).

At some time during the 1940's the caribou population reached a low-point, and a definite shift to the northeast occurred. The reindeer herds were abandoned, and most of the remaining animals probably joined the caribou population, although some of those at Naknek may have moved northward into the Mulchatna River country. A survey by the U. S. Fish and Wildlife Service during November, 1949, resulted in an estimate of 2,000 caribou to the northeast of Port Moller and 500 to the southwest, with none occurring on Unimak Island. The extent of intergradation between reindeer and caribou is not known. In addition to having received animals from the reindeer herds at Naknek and Egegik, the caribou population also had been augmented earlier by strays from herds at Pilot Point, Port Moller, and Unimak Island, all of which were abandoned prior to 1940. It would appear that the caribou population contained considerable reindeer "blood", especially in those animals north of Port Moller.

Nevertheless, the population has increased slowly, but steadily, since 1949. A survey in July, 1953, indicated a population of about 3,500 north of Port Moller and about 500 to the south, with none reported on Unimak (Alaska Game Commission, 1953d, V.8, No.1). In June, 1960, I made a census of the area and estimated 7,000 animals north of Moller and 1,000 south, most of the latter being on Unimak Island (Skoog, 1961: 11). As far as known, this split in the population has continued and each segment has continued to increase in size. Calving occurs in three separate areas--Unimak Island, the Black Hills (near Cape Leontovitch), and the Sandy Lake region (north of Port Moller)--and thus one can postulate the Alaska Peninsula caribou population as being comprised of three herds, with little interchange at present between them.

In summary, the caribou population of Region I has fluctuated considerably during the past 100 years, both in distribution and in numbers. It would appear that prior to 1875 the population was large and was centered in the northeastern half of the Alaska Peninsula. The entire region was utilized, and seasonal movements extended both southward to Unimak Island and other coastal islands and northward into the Nushagak and Mulchatna River drainages of the mainland itself. It would seem logical that many animals wintered north of the Kvichak River, where lichens were most abundant. These plants are scarce south of the Naknek River drainage, possibly as a result of the relatively frequent volcanic eruptions in the south which periodically have blanketed the terrain with ash (see Powers, 1958: 64-65). By the 1880's the southward movement essentially had stopped, and in 1895 few animals remained to the southwest of Port Moller. The north-south movement across the Kvichak River also stopped about this time, and it seems likely that the bulk of the once large population had remained to the north of the Alaska Peninsula. This shift might have been influenced in part by the extensive

hunting of caribou during the period 1880-1910, occasioned by the high demand for meat and hides by the whalers and miners of that era and accentuated by the scarcity of sea otter, which caused the natives to look elsewhere for revenue. By 1905 the remaining population had shifted its center of abundance to the southwest of Port Moller, where it remained until the early 1940's. In 1925, O. J. Murie (1959: 330) estimated the population at 12,000 animals. Three severe winters (1930-31; 1933-34; and 1938-39) resulted in heavy mortality, and a low point in the population probably was reached during the 1940's. On the other hand, an unknown number of reindeer were absorbed into the population during 1930-1945. By 1949 the population was estimated at 2,500 and once again had shifted to the north; Unimak Island had been abandoned. Since then, Unimak has been repopulated, but most of the animals remain to the northeast of Moller. In numbers, it seems doubtful that the total population has exceeded 20,000 animals since the 1890's. The fluctuations in distribution and numbers that have occurred since then can be attributed probably to weather and perhaps, in part, to volcanic activity, both as influences upon food supply and/or availability and therefore upon movements and survival. From a population estimated at 8,000 animals (calves excluded) in June, 1960, I estimate the current population (June, 1967, calves excluded) at 16,000, assuming a 10 percent annual increase. I consider most of the Alaska Peninsula to be rather marginal habitat for a sustained large caribou population, because of the severe icing conditions that occur periodically.

Region II. West Alaska--Most of the Kuskokwim River drainage has not supported a particularly large caribou population during historical times. This lack probably can be attributed to the fact that much of the terrain consists of low, rather densely forested hills and stream valleys. As noted earlier, the main tundra/alpine areas suitable for sustaining a caribou population lie to the southwest (the Kilbuck Mountains and adjacent highlands) and to the east (the western portion of the Alaska Range). Periodic severe winters (i. e., heavy snows and icing conditions) may be a limiting factor in the former area.

The latter area, however, has contained a caribou population throughout the past 100 years or so.

The earliest notations regarding caribou distribution in this region come from the accounts of Russian explorations in the mid-nineteenth century. Vanstone (1959) indicated that the Russian Glazunov found caribou to be common in the highlands between Norton Sound and the Yukon River during the fall of 1833. Although this area is considered to be part of Region III, the observation is of importance because of later records concerning caribou movements across the Yukon, into and out of the western portion of Region II. The same Russian found no caribou along the middle portion of the Kuskokwim River nor along the lower half of Stony River, as far as the Lime Hills, during the period January-March, 1834. Lutz (1960: 15) stated that the Russian Zagoskin in his travels along the Yukon and Kuskokwim Rivers in 1843-44, reported "...large herds of caribou and moose on the Innoko River and observed that the native tribes... made their summer clothes of both caribou and moose." Zagoskin observed that the whole region of the lower Kuskokwim River was "...well supplied with feeding areas for caribou...." and that the natives living on the upper Kuskokwim River killed caribou. Neither of these two Russians reported the occurrence of such huge migrations across the lower Yukon and Kuskokwim Rivers as whose which seemed to occur commonly during the 1860's, and perhaps earlier.

E. W. Nelson, who spent the years 1877-81 exploring the region surrounding St. Michael on the coast of Norton Sound, stated (Nelson and True, 1887: 285) that "When the American Telegraph explorers visited Alaska in 1866 - '67, Reindeer were found everywhere, and herds containing thousands of individuals were no uncommon sight. They were very abundant on the hills and valleys bordering Norton Sound...." Seasonally, large numbers of caribou crossed the Yukon River at various places below Nulato. When William Dall came down the Yukon River in June, 1867, he saw "...over four thousand skins of reindeer fawns hanging up in a village near Anvik...." (Nelson and True, 1887: 286). The previous winter (1866-67) "...an enormous herd of reindeer passed so near Saint Michaels that a 6-pounder loaded with buckshot was fired at them....Hundreds were killed for their skins alone...." (Nelson and True, 1887: 285). Raymond (1900: 26, 32, 33) noted the abundance of caribou in that area during the summer of 1869, but stated further (p. 32) that "They are said to have diminished greatly since the introduction of firearms." O. J. Murie (1935: 61) indicated that a common migration path about that time extended southward from this region, across the Yukon River near Andreafski, across the Kuskokwim River between the present locations of Aniak and Bethel, and into the Kilbuck Mountains; a northward movement occurred each fall past St. Michael. Large numbers of caribou were present on Nunivak Island

as late as 1878 (Nelson and True, 1887: 285) and occurred earlier on Nelson Island in the Kuskokwim Delta area (U. S. Census Office, 1893: 110). The presence of deep trails along the slopes of the Taylor Mountains in 1890 indicated the former abundance of caribou in the region separating the drainages of the Kuskokwim and Nushagak Rivers (U. S. Census Office, 1893: 97). As mentioned earlier, in the discussion of Region I, a regular migration occurred seasonally across the Kvichak River between the Alaska Peninsula and the Nushagak River drainage (Elliott, 1897: 397). Many of these animals probably continued north and/or northwest through the lowland spruce forests into the Kilbuck and Taylor Mountains. It is possible that some of these caribou were part of the north-south seasonal movement across the lower Kuskokwim and Yukon Rivers that eventually passed St. Michael.

Nothing is known concerning the eastern portion of this region during this early period, other than the fact that natives on the upper Kuskokwim River killed caribou (Lutz, 1960: 15). Caribou probably were present along the Alaska Range from Lake Iliamna to the Mt. McKinley park area, especially in view of the apparent abundance of animals in the Taylor Mountains. To the west, there are indications that the population along the lower Yukon and Kuskokwim Rivers had begun to decline by the early 1870's, for Elliott (1875: 46-50) mentioned no trade in reindeer skins during 1872-74 at trading posts on Kotzebue and Norton Sounds, Nunivak, and the lower Kuskokwim River and Delta, while pointing out the heavy trade in such skins at Nushagak and Ugashik.

In summarizing the above historical records for this region during the 40 years prior to 1875, I postulate the following:

1) Caribou were present in the east along the Alaska Range in unknown densities.

2) The presence of remnant heavy trails in the Taylor Mountains in 1890 indicated a former high population in the Mulchatna-Holitna river drainages, probably coinciding in time with the high farther to the west and to the south (Alaska Peninsula) and probably resulting in movements into and along the Alaska Range to the east, and onto the Alaska Peninsula.

3) A large caribou population occurred along the Bering Sea coast from Bristol Bay to Norton Sound. It probably was on the increase during the 1830's (based on the Russians' lack of mention of large migrations, yet the presence of caribou on the Innoko River, which is rather poor caribou habitat); reached a peak by the 1860's, or perhaps earlier; and was starting to decline in numbers by the early 1870's. During the peak, this apparently huge population ranged over a wide area, including the Kuskokwim-Yukon lowlands and even Nunivak Island (reached, no doubt, via the ice-pack). The main movement pattern was north-south across the Yukon and Kuskokwim Rivers: extending probably north to the Seward Peninsula, definitely south to the Kilbuck Mountains, possibly southeast to the Alaska Peninsula, and probably east to the Alaska Range. Quite likely the animals ranged into the upper Kuskokwim River area as well.

During the next 20 years, 1875-1895, the caribou distribution within this region changed considerably. Sometime during the 1870's the migrations across the lower Yukon and Kuskokwim Rivers ceased. During Nelson's stay at St. Michael, 1877-81, he failed " ...to see a single living Reindeer." (Nelson and True, 1887: 285). He stated further (p. 285-286) that "Only a few stragglers now remain...." in the country between Norton Sound and the lower Yukon and Kuskokwim Rivers, and that " ...near Anvik....scarcely half a dozen deer, old and young, are taken yearly...." Petrov (1884: 60) in 1880 commented upon "the almost total disappearance of this animal"

from the immediately adjacent areas along the lower Yukon and Kuskokwim Rivers. Nelson stated that caribou were " ...very abundant on Nunivak Island in 1877 and 1878, but are nearly exterminated there now." (Nelson and True, 1887: 285). The lack of caribou on the mainland caused the Eskimoes to journey to Nunivak to obtain skins and meat for their needs and for the trade with whaling ships (O. J. Murie, 1935: 60). By 1890, the animals on Nunivak had been exterminated (U. S. Census Office, 1893: 114). The same report noted (p. 110) the disappearance of caribou from Nelson Island and stated (p. 103), with regard to the lower Kuskokwim River, "Not many years ago large droves of reindeer grazed over the lowlands and hills on both sides of the river...." The disappearance by 1890 was attributed to the large scale slaughter of animals by the natives, " ...the result being an almost total extermination of the animal."

In the Kilbuck Mountains, however, as far as Aniak, large numbers of caribou were still present during the 1880's, judging from the census reports of 1880 and 1890 (Petrov, 1881: 50; 1884: 72; U. S. Census Office, 1893: 99, 106). On the other hand, in 1890 no caribou were present in the Taylor Mountains, a short distance to the east, the report stating (U. S. Census Office, 1893: 97) as follows:

> The hills are bare of timber, only being covered with the usual coat of moss. It has been at one time a great range for caribou, and though there are none to be found there now, tracks and well-defined paths can be seen running for miles around on the hilltops....

As mentioned previously, caribou apparently were still numerous at the base of the Alaska Peninsula in 1890, including, no doubt, the Mulchatna River drainage, judging from the large trade in reindeer skins at Fort Alexander at the mouth of the Nushagak River (U. S. Census Office, 1893: 96). Elliott (1897: 397) commented upon the seasonal migrations across the Kvichak River, a movement of animals between Regions I and II, but these probably had ceased during the 1880's. Deep trails in the ground--some two feet below ground level and partly grown in with shrubs--were noted by Smith (1917) during the summer of 1914 in the area lying west and northwest of Lake Clark; these trails attested to the former abundance of caribou in that section of the Alaska Range. Similar trails were observed along the Kuskokwim Mountains by Dice (1921: 28) in 1912, notably in the highlands just west of McGrath and also in the Sischu Mountains to the northeast. Eakin (1918) noted "well-worn trails" (and a scarcity of caribou) during the summer of 1915 in the area encompassing the North Fork of the Kuskokwim River, mostly to the east of the Sischu Mountains mentioned by Dice. Eakin also commented upon the presence of an Indian "drive-fence" for caribou in the valley of the North Fork,

west of Lake Minchumina, the "fence" then being old and in disuse; such fences clearly indicated past caribou abundance.

In summarizing the period 1875-1895, I concluded that the two large seasonal migrations that occurred previously in the west and south (between Regions II and III and between II and I) ceased during this period--the first in the mid-1870's and the second in the 1880's. A remnant herd remained in the Kilbuck Mountains, but the Taylor Mountains were abandoned; large numbers of animals were present in the northeastern portion of the Kuskokwim Mountains and in the western Alaska Range (mainly the Mount McKinley and Mulchatna River regions). This distribution indicated a shift in the population to the east and northeast. Concurrently the Alaska Peninsula population was reduced in size when the north-south migrations across the Kvichak River stopped. It seems likely that the cessation of seasonal movements across the lower Yukon River was responsible in part for the abundance of caribou then remaining in the Kuskokwim Mountains. Further remarks concerning the Norton Sound-Seward Peninsula caribou are presented in the discussion of Region III. No major movements of caribou across the lower Yukon River (i. e., below the Koyukuk River) are known since the 1870's, and across the Kvichak River, since the 1880's.

At the end of the 19th century caribou were still abundant in the Kilbuck Mountains and were noted as present in the Rainy Pass area (Spurr, 1900). Loring (1902: 145) stated that caribou were " ...common in the country some seventy-five miles north of Tyonek," which would approximate the upper Yetna River and Rainy Pass areas. In the summer of 1902, Brooks and Prindle (1911: 19, 204) had observed abundant caribou sign on the northwest slopes of the Alaska Range, between Rainy Pass and Mt. McKinley, and Osgood (1904: 27-28) found caribou common in the region north of Iliamna Lake and west of Lake Clark. Numerous caribou were sighted by Sheldon (1930) along the drainages of the upper Toklat River in 1906-07, both summer and winter, and also by Browne (1913) in the same area during 1912.

Caribou were common, but not abundant, west and northwest of Lake Clark in the summer of 1914 (Smith, 1917), although well worn trails indicated former large numbers there, extending to the upper Hoholitna River and to the Lime Hills. Farther to the north and northeast, Eakin (1914: 17) encountered a few caribou in the Beaver Mountains area during 1913, and in the region of the Sischu Mountains and the North Fork of the Kuskokwim River during 1915 (Eakin, 1918)--more numerous in latter region, but actually not plentiful anywhere in the areas covered during the two years. The heavy trails in the Sischu Mountains noted by Dice (1921: 28) indicated a former abundance. It is possible that this apparent decrease of animals in the Kuskokwim Mountains could have resulted from a movement northward across the Yukon River, between Kokrines and Tanana. Osgood (1909: 13) reported that "immense numbers" crossed the Yukon River near the mouth of the Tanana River in the winter of 1907-08. Such movements also were known to have occurred in later years.

Meanwhile, the sub-population ranging the Mount McKinley region (part of which is now the national park) appeared to be increasing steadily. Capps (1917; 1919) noted that caribou were quite abundant in 1915 and 1916. Riggs (1920: 6) stated that the McKinley herd numbered about 25,000 animals in 1919. In 1922, Bone (1923: 3) estimated the herd in excess of

30,000 animals and increasing, with large numbers being sighted near Nenana and also in the hills between McGrath and Rainy Pass. In 1925 Capps (1927b: 80) stated, "The northern slope of the Alaska Range from Nenana River westward....is a summer feeding ground for great herds of caribou." By then caribou were rarely seen in the Kilbuck Mountains, and they continued to be absent from the lower Yukon and Kuskokwim Rivers. Large numbers of reindeer, however, were being herded along the entire Bering Sea coast, in a strip some 50 miles or more wide; some of these had escaped and were known to be ranging portions of the Kilbuck and Taylor Mountains.

During the next time period, 1925-1945, the caribou population of Region II was in a state of flux, relative to both numbers and distribution. In the fall of 1924 a movement of animals from the north brought caribou into the Ray Mountains and Kokrine Hills, just north of the Yukon River, and some crossed the river southward into the Nowitna River area of Region II (Murie, 1935: 64). It is not known whether any of these animals remained; presumably most of them returned northward. On various field trips of the U. S. Geological Survey during 1926-29, Capps (1929; 1935) reported caribou as being numerous in the Rainy Pass area and in the Kuskokwim River drainage to the westward; he also noted them to be present, but less numerous, in the upper Stony River basin and southward to Lake Clark.

The McKinley herd had become large enough by 1926 so that it no longer remained intact during the seasonal movements, even though the same calving grounds were used each year; in winter, the herd split and utilized several distinct areas (A. Murie, 1944: 146). A major portion of the herd wintered to the eastward during the period 1925-1930, passing through Broad Pass in the spring and fall (p. 146-147). Frank Glaser (1950) noted that the fall movement in 1926 extended eastward well into Region VI, and that many caribou wintered in the area encompassing Monahan Flat, Valdez Creek, and the Maclaren River. Large numbers also wintered to the west during that period--near Lake Minchumina, the North and South Forks of the Kuskokwim River, and along the Kantishna River (Alaska Game Commission, 1929c; A. Murie, 1944). Glaser (1950) stated that a large segment of the herd moved northward through Nenana in the fall of 1927, and that miners from the upper Koyukuk River said caribou by the thousands had moved in during the winter and continued north in the spring (see also O. J. Murie, 1935: 64, 67). The same winter A. Murie (1944: 146) noted that large numbers of McKinley caribou were reported along both sides of the lower Tanana River. Presumably a substantial number of the McKinley caribou moved into the arctic that year, for subsequent reports all note the decrease of animals in this herd. The movements into Broad Pass ceased after the spring of 1931; since then the main wintering grounds have been to the west,

notably near Lake Minchumina and along the foothills of the Alaska Range (A. Murie, 1944; observations of long time residents; personal observations, 1956-64).

In the late 1920's and early 1930's a shift occurred to the south and southwest. Alaska Game Commission reports (1929-1935, a and c) noted increasing numbers of caribou in the Rainy Pass area (particularly) and along the Alaska Range to Lake Clark. Seasonal movements occurred from Rainy and Merrill Passes to the drainages of the upper Stony and Mulchatna Rivers. Scattered small herds were present throughout the McGrath area, i. e., the Kuskokwim Mountains. In 1931, a large segment of the McKinley herd was reported to have moved westward from the Lake Minchumina area across the Sischu Mountains to the head of the Innoko River (Alaska Game Commission, 1931c).

The Rainy Pass area became more or less the center of abundance for caribou in this region (O. J. Murie, 1935: 61); at the same time the density of animals in McKinley Park decreased, while that in the Stony River-Mulchatna River area increased. In 1935, the McKinley herd was estimated at 20,000 animals (O. J. Murie, 1935: 62), and in 1941, 20,000-30,000 animals (A. Murie, 1944: 145), indicating a more or less stable population, providing the estimates are comparable. Beach (1938) noted the general lack of caribou in McKinley Park

and to the west in 1937, as compared with his observations in 1922 and 1925. Yet, in June, 1936, and July, 1937, an estimated 25,000 animals were reported moving through the Park (A. Murie, 1944: 147). Also, in June, 1936, the Alaska Game Commission (1936c: 55) reported the hills southwest of Broad Pass " ...black with thousands of caribou"; the animals had departed to the west by the first of July. Various other reports (Alaska Game Commission, 1937c: 106; A. Murie, 1944: 147-148; Chatelain, 1949) revealed the periodic influx of McKinley caribou to the Broad Pass area during the 1930's and early 1940's. Obviously there was considerable variance in the movement pattern during this period among the caribou of the Rainy Pass-Mount McKinley section.

In other sections of Region II the caribou numbers remainedlow. Alaska Game Commission reports during the late 1930's (1935-1939, a and c) suggested a stable or declining population in the Stony River-Mulchatna River area, with no caribou along the lower Yukon and Kuskokwim Rivers, a few scattered herds in the Kuskokwim Mountains, and feral reindeer in the Kilbuck and Taylor Mountains (Mertie, 1938: 38). Of interest during this time were the rather large numbers of caribou wintering along both sides of the Yukon River between Tanana and Ruby; these animals apparently came from the north.

By 1945, there were no reports of any large numbers of caribou in Region II, and there seems to have been little change since then. It is possible that another northward emigration into the arctic might have occurred in the early 1940's, but there is no evidence of such. Suffice it to say that the McKinley herd decreased from an estimated 30,000 animals in 1941 (A. Murie, 1944: 145) to an estimated 12,000 in 1963 (Skoog, 1963: 29); the wintering grounds along the Yukon River were abandoned by the arctic caribou sometime during the early 1940's, or before. At present I recognize three sub-populations in Region II, each with its own separate calving area: 1) the McKinley herd, ranging the center of habitation, from the Rainy Pass area northward to McKinley Park; 2) the Mulchatna herd, encompassing the Mulchatna River drainage, the Stony River basin, and the Taylor Mountains; and 3) the Beaver herd, centered in the Beaver Mountains west of McGrath. Other groups sighted at various locations within the region are thought to belong to one of these three.

In summary, it is evident that the caribou population of Region II also has fluctuated considerably in numbers and distribution. Historical records have shown that large numbers of caribou formerly moved north-south across the lower Kuskokwim and Yukon Rivers (between Regions II and III) until the early 1870's and across the Kvichak River (between Regions II and I) until the early 1880's. Both movements ceased prior to 1890, and neither has resumed since then. The main population shifted from the west and south to the east in the 1870's and 1880's.

By 1895, however, it became evident that a major segment of the population had moved elsewhere, probably across the Yukon River into the arctic (Region III), judging from remnant heavy trails in the northeast portion of the Kuskokwim Mountains. At the turn of the century the center of abundance lay in the northeast. This herd (McKinley) increased steadily and by the late 1920's had peaked, judging from the numbers reported and from the extensive, erratic movements recorded. An emigration of substantial numbers of caribou northward into the arctic occurred in the winter of 1927-28. In the 1930's the main population remained at the center of habitation, but shifted in local abundance from McKinley Park to the Rainy Pass area. At present the center of habitation continues to support the main sub-population (McKinley herd) of the region, shifted back once again to McKinley Park. To the west and south, and in the Kuskokwim Mountains, caribou have not been abundant since before 1900. Possibly these other areas--including now the Mulchatna and Beaver herds--are of marginal habitat for a sustained, large population, and originally were primarily utilized by caribou in transit from adjacent regions.

Region III. Northwest Alaska.--The abundance of caribou in the mid-1800's along the lower Yukon River, the hills between that river and Norton Sound, and the Seward Peninsula itself has been mentioned already in the discussion of Region II. Judging from Russian accounts, the animals were numerous there as early as 1833 (Vanstone, 1959) and were still abundant in 1843 (Lutz, 1960). By the 1860's huge migrations were reported moving north-south along highlands east of Norton Sound and across the lower Yukon and Kuskokwim Rivers--north in the fall and south in early summer (Nelson and True, 1887). Based on Dall's observation in June, 1867, of some 4,000 skins of recently killed caribou calves in a village near Anvik (Nelson and True, 1887), I would presume that the calving grounds of this herd lay to the north. How far north the herd ranged is not known, but it was apparent that the

Seward Peninsula was utilized. In 1899 Moffit (1905: 77) observed that caribou must have been abundant there at one time because of "...the great number of antlers scattered over the tundra and the heaps of bones near old, deserted native igloos....they followed permanent well-beaten trails along the crests of the ridges...." The abundance of shed antlers indicated that the area was used during the winter. Quite likely this large herd would have ranged northward to the Kobuk River as well, and possibly into the upper Koyukuk River drainages, but little evidence exists to support this idea. The U. S. Census Office report for 1890, however, noted (1893: 146) that formerly in "...the Kozebue Sound district numbers of deer made yearly visits...."

The relative numbers of caribou along the drainages of the Kobuk, Noatak, and upper Koyukuk Rivers prior to 1875 are not known. To the north of the Brooks Range, however, the animals seemed to be abundant. In late July, 1837, Dease and Simpson (1838: 217-218) sighted "numerous herds" along the Arctic Ocean coast between the Colville River and Point Barrow and "The tracks of reindeer were everywhere numerous." Just east of Smith Bay and north of Teshekpuk Lake they sighted "an immense reindeer pound." The presence of such a structure (built by the Eskimoes to drive, trap, and kill caribou) indicated that the population probably had been high for some time and that the animals appeared along the coast at regular intervals. Ray (1885: 27) stated in 1883, with

regard to the lower and middle portions of the Meade River, that "...the natives say that three generations ago all this region was inhabited by a people that lived by fishing and hunting reindeer, and did not come to the coast, but that the deer and fish grew scarce....now this whole region is not inhabited...." This observation implied that the caribou had abandoned that portion of the arctic slope region sometime after the explorations of Dease and Simpson. If the animals had remained numerous from 1837 until 1883 (when they were abundant once again), then one might suppose the area would have remained populated by "inland" Eskimoes as well. Such movements of Eskimoes, to and from the coast, are known to have occurred periodically, depending upon the supply of food available in the inland areas (Larsen and Rainey, 1948). Furthermore, this lack of inland Eskimoes on the Meade River at a time (1883) when caribou were numerous on the arctic slope year-round, and had been for a few years at least (Murdoch, 1885), suggests that the animals had "arrived" rather recently.

During the next time-period, 1875-1895, major changes occurred in the distribution of caribou. As noted earlier, the migrations across the lower Yukon River ceased during the early 1870's. By 1877 caribou were extremely scarce in the St. Michael area, eastward to the Yukon River, and Nelson remarked (Nelson and True, 1887: 285), that "...their former abundance is indicated only by the number of antlers scattered over the country and the well-marked trails...." It is probable that this decrease resulted primarily from a shift in the migration pattern. Large numbers of caribou remained in the Kilbuck Mountains to the south and in the Kuskokwim Mountains to the southeast, with substantial numbers still present, apparently, on the Seward

Peninsula. Regarding the last named area, Petrov (1881: 58) noted in 1880 that the natives at Wales and Port Clarence (the western end of the Seward Peninsula) "...are fishers and reindeer hunters," and Schwatka (1885 a, b) in 1883 observed that the natives in all the villages along the Yukon River from about Kaltag upstream to Ruby hunted caribou "...on the tundra north of the river...." It has been suggested already that the animals present on the arctic slope along the lower Meade River in the early 1880's were "recent arrivals"; such an influx could have resulted from a number of causes. One possibility, however, is that the arctic population had been augmented by an immigration of animals from the Seward Peninsula - lower Yukon River area. The distance involved is not much greater than some of the seasonal north-south movements occurring in this region today (Lent, 1966b; Skoog, personal observations).

During the 1880's caribou were rather scarce along the northwest arctic coast from the Seward Peninsula to Cape Lisburne, but numerous eastward to Point Barrow and beyond. Nelson stated (Nelson and True, 1887: 285) that "In the summer of 1880 one man from Point Barrow took about five hundred skins...." Petrov (1884: 56, 58) commented upon the abundance of caribou along the arctic coast eastward from Point Hope, but that "...they often change their habitation, at times migrating in immense numbers to regions hundreds of miles away...." Hooper (1884: 50) noted that the Point Hope Eskimoes each year traveled north in July to the Cape Beaufort area to hunt caribou, returning in September. In the Point Barrow area, 1881-83, caribou were reported to be very abundant during the fall and winter, but scarce in summer;

the center of abundance during the winter seemed to be the foothill area lying north of the upper Colville River (Murdoch, 1885, 1898; Ray, 1885). Explorations by various expeditions up the Noatak and Kobuk Rivers during the 1880's (Cantwell, 1887, 1889; McLenegan, 1887, 1889; and Stoney, 1899) reported an abundance of caribou north of the Kobuk, in the Baird and Delong Mountains, especially at the heads of the two rivers and of the Colville River. Most of the Kobuk Eskimoes traveled to the head of the Noatak River to get caribou. Stoney (1899: 837-838) reported the presence of several village of Eskimoes in the mountains adjoining the upper Noatak and upper Colville Rivers; drive fences were being used in several passes, and he reported a large one at Chandler Lake. The presence of these island Eskimoes and drive fences suggests the caribou had been numerous in this section of the Schwatka and western Endicott Mountains for some years prior to the late-1880's.

By 1890, caribou were extremely rare along the entire western coast from Bristol Bay to Point Hope, on the Seward Peninsula, in the hills east of Norton Sound, and in the region drained by that section of the Koyukuk River lying below the John River (U. S. Census Office, 1893). That year, also, Sheldon Jackson noted the starving condition of the people in all the villages along the Bering Sea, an observation which resulted two years later in the first introduction of reindeer from Siberia to the Seward Peninsula (Jackson, 1892). He reported that there were no caribou for the natives to hunt and caribou clothing had become uncommon; nearly all skins came from reindeer in Siberia. In addition, caribou were no longer abundant, apparently, in the Baird Mountains and along the entire Kobuk River, because Joseph Grinnell commented to O. J. Murie (1935: 65)

that he had not seen a live caribou in any of the Kobuk country, where he spent considerable time in 1898. During the same time, miners moving into the upper Kobuk and upper Koyukuk River drainages (especially the Wiseman area) found the region devoid of caribou (O. Murie, 1935: 67). These observations suggest that the caribou had shifted to the north, because they remained numerous, apparently, throughout the area north and east of Bering Strait. The report of the U. S. Census Office (1893: 146) concerning the latter area stated "...8,000 to be a fair estimate of the number of deer killed annually by the natives...." The same report indicated that the caribou were abundant on the arctic slope year-round. O. J. Murie (1935: 45) quoted Herendeen as saying, with regard to Point Barrow about 1890, "The great mid-winter hunt begins soon after the sun returns; or about the last of January."

Various reasons have been given for the loss of caribou from the Bering Sea coast. Some have suggested the excessive slaughter of animals by the natives during the period 1860-1900, stimulated by the great demand for skins and meat by whaling ships and facilitated by the introduction of the rifle (Nelson and True, 1887; Lent, 1966; Leopold and Darling, 1953; and Sonnenfeld, 1960). It is important to realize, however, that as late as the mid-1880's relatively few Eskimoes had rifles and those that did could not obtain adequate supplies of ammunition (Healy, 1887, 1889); the whalers themselves rarely hunted. Also, the demand for skins and meat in this area apparently did not reach large proportions until about 1880 and later, <u>after</u> the main decline in caribou in the coastal regions already had taken place. For example, Elliott (1875: 46-50), in discussing the various trading districts in Alaska during 1872-74, made no mention of caribou skins being among the trade items in the Kotzebue and Norton Sound areas, but noted such in the Nushagak and Ugashik areas at the base of the Alaska Peninsula. Petrov (1881: 68), however, recorded a "considerable trade" in caribou skins in 1880, and a year later Nelson (O. J. Murie, 1935: 64-65) observed Eskimoes from the upper Noatak and Kobuk Rivers at Hotham Inlet of Kotzebue Sound with "numerous flat skins" of caribou. During the same period, however, the caribou remaining on Nunivak Island were exterminated, but then such a restricted population was extremely vulnerable and provided the main source of caribou for Eskimoes in that area (O. J. Murie, 1935: 60). Another reason advanced for the decline of caribou along the coast has been the introduction and buildup of reindeer (Bee and Hall, 1956). As pointed out by Lent (1966a: 705), however,

such reasoning is erroneous, because the caribou had abandoned the region long before the reindeer were first introduced in 1892. Later, reindeer herds were established north and south along the coast from the Seward Peninsula, but in all cases only in areas already devoid of caribou.

Caribou remained scarce in the southern portions of Region III throughout the early 1900's (Schrader and Brooks, 1900; Mendenhall, 1902; Jackson, 1903, 1906; and Moffit, 1905). The animals reported at the base of the Seward Peninsula in 1909 by Smith and Eakin (1911: 33) probably were feral reindeer. O. J. Murie (1935: 65) stated, "The Kobuk and Noatak Basins, apparently, have not been good caribou range since the eighties, and only a few stragglers occur." Cantwell (1902: 222) noted during 1899-1901, however that the Indians in villages along the Yukon River, between Nulato and Rampart, spent considerable time during the winter hunting caribou in the "hills" to the north--presumably the Kokrine Hills and the Ray Mountains--although caribou were absent along the lower Koyukuk River. These animals might well have come from the northeast (Region IV), because caribou remained scarce throughout the year in the Wiseman area (lying directly to the north) through which the animals would have traveled if they were part of the population of Region III. Mendenhall (1902: 56) stated the Kobuk natives had to travel to the upper Noatak River for caribou, yet Schrader (1904: 33) said that caribou were the chief source of food in 1901 for the natives at Bettles, only 100 miles to the east. Presumably these natives obtained their caribou from the mountains farther east (Region IV), as did the miners at Wiseman (O. J. Murie, 1935: 67). It will be recalled also, as noted in the discussion of Region II, that Osgood (1909: 13) stated a

large number of caribou crossed the Yukon River near the mouth of the Tanana River during the winter of 1907-08. These animals presumably moved into or came from the Ray Mountains, the direction of travel not being noted. Schrader (1904: 21-23) also found an abundance of caribou in the Anaktuvuk Pass area and along the drainages of the Colville River all the way to the Arctic Ocean.

During the same period the caribou had shifted eastward from the Meade River-Point Barrow area. Jackson's report (1898: 29) for 1897 commented upon a large kill of caribou by the Eskimoes at Barrow during November of that year, from several herds that had wandered close to the village. Later, however, O. J. Murie (1935: 65) pointed out that"...in the years 1901 to 1905 natives from west of the Colville travelled east of that river for caribou, showing that they had already become scarce...." Stefansson (1913), speaking of the arctic coast west of the Colville River in 1908-09, said (p. 48) "...where ten years before there had been vast herds of caribou...there now is practically no game at all.", and further (p. 502) "...the numbers have been enormously decreased nearly everywhere within the last twenty years.... as a consequence most of the Eskimoes have been compelled by starvation to move out, notably from the Colville River region." On the other hand, he found large numbers of caribou in 1908 on the southern slopes of the Endicott Mountains, east of the John River. In 1910 and 1911 Smith (1912, 1913) reported caribou numerous along the upper Noatak River, but still scarce in the Kobuk River basin, while Eakin (1916) found caribou abundant throughout the Ray Mountains and Kokrine Hills in 1913.

In the 1920's the caribou remained numerous along all the drainages of the upper Colville River, in the Delong Mountains, and especially in the Endicott Mountains from Chandler Lake eastward (Smith, 1927; Smith and Mertie, 1930; and O. J. Murie, 1935), but did not range northward very far onto the arctic plain nor southward into the Baird and Schwatka Mountains. Murie (1935: 64) stated, "Westward from John River, upper Koyukuk district, caribou do not normally occur." Throughout the 1920's the animals were abundant in the Wiseman area of the upper Koyukuk River, and miners no longer had to travel to the Chandalar River for meat. These caribou, however, came from the northeast (Region IV) according to Murie (p. 67-68), repeatedly moving southwestward in the winter, sometimes as far as the Yukon River, and in 1924 actually crossed the Yukon into Region II. These movements continued well into the mid-1930's. In the fall of 1927 a large immigration of McKinley caribou (Region II) was received into the Ray Mountains (Alaska Game Commission, 1928c; Glaser, 1950), and many of these apparently remained in the arctic, moving northeastward in the spring into Region IV. O. J. Murie (1935: 63) considered the highland separating the Koyukuk and Chandalar River drainages, from the Ray Mountains on the southwest to the Philip Smith Mountains on the northeast, as being a center of caribou abundance.

In December, 1936, a huge herd of caribou (estimated at 90,000 animals) was sighted on the Cutler River, which drains into the upper Noatak (U. S. Congress, Senate, 1939: 20323). During the

same winter of 1936-37 Collins (1937) reported that a large herd wintered on the arctic slope between the Kuparuk and Colville Rivers. He also stated that the animals were "coming back into their former range", with animals seen regularly in the Meade River area once again. Alaska Game Commission reports (a, b, and c) during the late 1930's and throughout the 1940's continued to remark upon the ever increasing herds of caribou in the arctic regions. In 1943 it was stated (1943c: 3), "There are many indications that the caribou herds are moving into the Arctic ranges in a northwesterly drift from the interior." The animals were extremely numerous in both Regions III and IV at that time, and it is difficult to determine how the animals were distributed and to what extent interchanges of animals may have occurred. Apparently separate calving grounds were evident then, as now--notably along the upper Utukok and Colville Rivers to the west and, on the east, the foothills south of Barter Island eastward to the Alaska-Yukon boundary. In 1947 a huge herd, estimated at over 250,000 animals, was sighted in an extensive migration north of the Baird Mountains (Alaska Game Commission, 1948c: 1). A similar migration was noted in August, 1949, directed across the Noatak River into the DeLong Mountains (Scott _et al._, 1950: 623). By 1950 the largest concentration of arctic caribou was considered to be in the western Brooks Range (Scott _et al._, 1950), while to

the east (Region IV) only some 20,000 animals remained. The implication is that the caribou had shifted westward, and also, possibly, eastward into Canada, as will be discussed later under Region IV.

At present, there is but one herd in northwestern Alaska, based upon the utilization of but one main calving area. The herd numbers some 300,000 animals, as estimated in 1964 by the writer based upon the magnitude of the native kill (Skoog, unpublished data), and its movements have become erratic and widespread. All records prior to 1945 showed that this herd wintered north of the Baird Mountains, and frequently on the arctic slopes and coastal plain. According to Harry Brown, a long-time resident on the Kobuk River (personal communication), caribou were not abundant along that river until the late-1940's. Since then the herd has wintered each year mostly to the south, extending from the Waring Mountains, Baird Mountains, and lower Koyukuk River, eastward to the Wiseman area (Lent, 1966b; Skoog, personal observations). In the winter of 1963-64, a large segment of this herd wintered to the east and southeast of Bettles, between the Koyukuk River drainage and the Yukon River, extending as far as Venetie on the Chandalar River (Region IV). Aerial reconnaissance the following spring by the author revealed that these animals had returned to the northwest. It is evident, however, that this population has reached a level where such erratic and widespread movements are apt to result in an emigration. At the present time, also,

small bands of caribou or feral reindeer are known to occur at the base of the Seward Peninsula, but their status is unknown.

In examining the historical records concerning caribou in Region III, one notes that here too, as in all the caribou regions of Alaska, periodic major changes have occurred in distribution, movement patterns, and numbers. In 1837 it was apparent that large numbers of caribou frequented the arctic coastal plain east of Point Barrow (Dease and Simpson, 1838). It has been suggested that these animals may have moved elsewhere sometime later (eastward or southward), based upon Ray's (1885) comments regarding the absence of inland Eskimoes along the Meade River in 1883 at a time when caribou were numerous there; this observation suggested a "recent" return of animals to the area. Concurrently to the south, the animals were abundant in the area embracing the Seward Peninsula and the hills east of Norton Sound to the Yukon River until the early 1870's. By then it appeared that the main population had shifted northward and eastward, with remnants remaining to the south (Kilbuck Mountains) as well. This Norton Sound group probably was a separate herd from that farther north, wintering over the Seward Peninsula, calving somewhere north and west of Anvik and the Yukon River, and ranging southward in summer and fall across the Yukon and Kuskokwim Rivers as far as the Kilbuck Mountains, and perhaps farther. Although hunting often has been advanced as a major cause of the loss of caribou from the Bering Sea coast, it is important to realize the decline actually occurred prior to the period of maximum demand for caribou meat and skins as trade items. This trade was just beginning in the late 1860's and had not reached major proportions until the 1880's. By then more and more whaling ships began to ply the arctic waters, concurrent with the decline in the sea-otter to the south.

During the late 1800's caribou continued to be numerous on the arctic slope east of Cape Lisburne, but scarce throughout the Bering Sea coast, and along the Kobuk and upper Koyukuk Rivers. The Chandler Lake area was particularly well populated. By the turn of the century the animals had retreated inland from the arctic coast and perhaps eastward; the center of abundance for Region III lay along the upper Colville River and in the DeLong and Endicott mountains. This center had shifted farther to the east by the 1920's (into Region IV), mainly east of Chandler Lake, and regular movements of caribou occurred in the fall and winter from the north and northeast into the Wiseman area of the upper Koyukuk River and southwestward to the Ray Mountains. The main population of Region III,

considerably reduced because of the eastward shift, remained in the DeLong and western Endicott Mountains throughout the year, extending into the foothills north of the upper Colville River, but not onto the coastal plain. The Baird Mountains and the Kobuk River drainage were not frequented.

During the late 1920's and later, the population in Region III continued to grow, being augmented by shifts of animals from the east and by a general movement northward from the south (Regions II and V). In the mid-1930's caribou once again were being sighted along the Bering sea coast north of the Seward Peninsula, and the reindeer herders for the first time began to have serious losses of reindeer due to wandering bands of caribou (Rood, 1942). By the late 1940's Region III contained the bulk of the arctic caribou population in Alaska, and major portions of the herd began to winter along the Kobuk River drainages. Prior to that time the animals had wintered north of the Baird and Schwatka Mountains, frequently on the arctic foothills and coastal plains. The large population size caused the herd to split into numerous groups seasonally, with the utilization of several wintering areas. Even today, however, only one major calving ground is being used, although the calving seems to be spread over an ever-increasing area.

Region IV. Northeast Alaska.--Early explorations along the arctic coast west of the Mackenzie River all noted an abundance of caribou in the region. Franklin (1828: 128, 153) found them numerous west to the Cannin River in 1826, with large numbers sighted on Herschel Island and a few animals on the Mackenzie Delta. Eleven years later Dease and Simpson (1838) recorded similar observations, and remarked (p. 223) with respect to the Demarcation Point area that "The pasture in the deep valleys among the mountains was luxuriant; herds of reindeer were browsing there, and we procured some venison." In a later publication, Simpson (1843: 105-106) noted that caribou were sighted commonly on the Mackenzie Delta in early July, 1837. While exploring the Rat River in November-December, 1840, Isbister

(1845: 341) found large herds of caribou common in the area lying west of the Mackenzie River from the mouth of the Peel River. Pullen still found caribou numerous on the Mackenzie Delta in late August, 1850 (Russell, 1898: 139).

In the mid-1890's, caribou appeared to be numerous year-round near Herschel Island, because the whaling ships were able to secure great quantities of meat there (Russell, 1898: 227; Jackson, 1894: 42). Stone (1900: 57) remarked how one winter fifteen whaling ships were reported to have used some 300,000 pounds of caribou meat, consisting of primarily of the hindquarters. During the same period caribou were numerous from the Mackenzie Delta eastward to Cape Bathurst (Russell, 1898: 227). Commenting upon this latter area, Porsild (1945: 20) stated "In many places on the Caribou hills and in the Eskimo Lake basin deep-worn trails were still clearly visible in 1927 and 1928, and testified to the former presence of numerous caribou." Sometime during the period, however, the caribou apparently deserted the Mackenzie River area. Pike (1892: 45-46) stated that the Mackenzie River was the western limit of herds to the eastward, but that "...not many years ago they are known to have crossed the Slave River in the neighborhood of Fort Smith." He stated further,

> ...they keep a more easterly route than formerly, as they seldom come in large quantities to the Mackenzie River, where they used to be particularly numerous in winter. This is in great measure accounted for by the fact that great stretches of the country have been burned....

Russell (1898: 226) observed with regard to that area, "They seem to have moved eastward, as they have entirely deserted the timbered country along the Mackenzie River.", although he noted that the animals were still abundant to the westward "...along the barren coast and in the mountains south of it." These observations imply that there was contact along the Mackenzie River between the caribou of Region IV and those farther to the east in Canada during the period prior to 1900. Yet by 1902 Grant (1903: 186) was able to state,

> ...the Mackenzie River, throughout its entire length, including a belt of land one hundred miles wide along its banks, is uninhabited by caribou, and appears to form the western limit of the Rangifer arcticus. To the west of the river the caribou are nearly twice the size attained by those on the east....

To the west along the coast apparently the caribou were not consistently numerous, because there were no permanent Eskimo villages between Pt. Barrow and Herschel Island (U. S. Census Office, 1893: 130).

Farther to the south the animals also were reported numerous, and it seems apparent the movement pattern in the 1890's was quite similar to that observed today. Funston (1896: 103) noted at Rampart House on the lower Porcupine River during the winter of 1893-94 that, "Large game is abundant

and I have seen 2,000 caribou in one herd." Russell (1898: 227) stated that "Rampart House was a 'deer post', being situated in a pass traversed semiannually by the caribou." On the other hand, caribou were rare farther downstream toward Fort Yukon and along the lower Black River (O. J. Murie, 1935: 64). Richardson (1900: 750) noted, however, that in the winter of 1897-98 one family of Indians "brought considerable caribou meat" into Fort Yukon for sale, yet the same family starved to death the following winter from lack of food. Preble (1908: 138) quoted John Firth of Hudson's Bay Company as saying that the herds of caribou west of the Mackenzie had a semiannual movement to and from the sea-coast--south in August, north in March.

To the west, caribou were common seasonally in the Ray Mountains, based upon the fact that natives along the Yukon River made annual hunts to the north during the fall and early winter (Schwatka, 1885a; Cantwell, 1902). Schrader (1900) reported that caribou were not abundant in the mountains adjacent to the upper Chandalar River in the summer of 1899, but that seasonal migrations brought caribou into and through the area. As noted in the discussion of Region III, O. Murie (1935: 65, 67) stated caribou were extremely scarce in the Wiseman area of the upper Koyukuk River in 1898, and that "Later, caribou were brought... all the way from the East Fork of the Chandalar, which became a favorite hunting ground."

During the early 1900's caribou continued to be numerous in the northeastern portions of Region IV. Harrison (1908) reported that many caribou were killed near Herschel Island in the winter of 1906, inland along the northern foothills of the British and Richardson Mountains. In the spring of 1907 Leffingwell (1919: 63) reported caribou abundant along the coast east of the Canning River, but were scarce during 1911-1914. He noted also the lack of villages between Barrow and Herschel Island, stating further (p. 66) that inland Eskimoes formerly were abundant, but were forced to come to the coast for lack of game. During this period the caribou were becoming more numerous on the south slopes of the eastern Brooks Range (Anderson, 1909, 1910, 1913; Stefansson, 1913; Leffingwell, 1919). In January, 1909, Anderson (1910: 136) encountered many caribou at the head of the Hulahula River in the Romanzov Mountains moving eastward in long lines. Keele (1910: 25) noted in 1908 that caribou assembled in large numbers in the northern part of the Mackenzie Mountains, which lie south of the upper Peel River. To the east of that region, it was reported by Hornby (1934: 106) that in 1909 caribou from east of the Mackenzie River moved through the Franklin Mountains as far west as the river itself. Yet, there is no evidence of movement across the Mackenzie in either direction at that time. In 1907, Harrison (1908: 264) reported that caribou were still scarce along the Mackenzie in the vicinity of the mouth of the Peel River.

Field trips by surveyors with the International Boundary Commission during 1911-1913 revealed that caribou were abundant along the Firth River in June and along the British Mountains (International Boundary Commission, 1918: 283). Williams (1925) noted that caribou were abundant along the Black River during the winter of 1910-11, and during the summer of 1911 found many shed antlers along the ridges north of the Black. Cairnes (1914: 19) stated that "Between Porcupine River and the Arctic Ocean, there are also vast herds of Barren Lands caribou which trek to the south of the Porcupine after the 'freeze-up' in the autumn." Meanwhile, to the west Maddren (1913: 19) and Eakin (1916: 21) reported caribou present but not abundant in the region lying between the Koyukuk and Chandalar Rivers. Thus, throughout the early 1900's it appears that the caribou of Region IV were concentrated at the center of habitation, with perhaps a shift in range utilization away from the coast toward the interior.

By 1917, however, caribou were starting to move into the middle and lower portions of the Chandalar River (Stuck, 1920: 19). Riggs (1920: 6) estimated 60,000 animals present in herds along the northern Alaska-Yukon boundary; O. J. Murie (1935: 66) considered this estimate to be conservative. Mertie (1925: 222) found caribou to be common along the lower and middle portions of the Chandalar River during the summer of 1923.

In the fall of 1924, as has been mentioned already (O. J. Murie, 1935: 64), a huge migration of animals from the northeast moved southwestward into and beyond the Ray Mountains. Throughout the 1920's caribou were numerous in the upper Koyukuk and Chandalar River drainages. In 1925 Murie (1935: 64) noted that caribou were killed near Fort Yukon, the first time in the "last one hundred years", according to a local Indian. U. S. Geological Survey parties along the Chandalar and Sheenjek Rivers in 1926 and 1927 reported caribou as plentiful (Mertie, 1929, 1930). Marshall (1933: 166) reported the natives in the Wiseman area spent most of the summer hunting caribou in the mountains to the north and east. To the far northeast, Porsild (1945: 20) stated that caribou had been scarce in the Mackenzie Delta region for "...a number of years preceding 1927...although some were obtained each winter in the mountains west of McPherson and south of Herschel Island." In the fall of 1927, however, he reported as follows (p. 20):

> ...in October, the low hills between the forested delta and Richardson mountains were literally covered by a vast herd of caribou slowly moving in a southerly direction. This migration was thought to have come from interior northeastern Alaska... turned south following the eastern slopes of the Richardson mountains....a few animals may actually have crossed the Mackenzie river near Point Separation or at Arctic Red river....By January this herd, which by some observers was estimated at 'millions of head', had become divided into numerous smaller herds....

From the above observations it would appear that during the 1920's there were two major groups of caribou in Region IV. One ranged the Endicott and Philip Smith Mountains, and eastward onto the Chandalar River drainages. The second group occupied the center of habitation to the northeast. During this period, also the sub-populations of Regions II and V were quite large, and emigrations were occurring to the northward. The northward movement of McKinley caribou in the fall of 1927 has already been referred to (Alaska Game Commission, 1928; Glaser, 1950); that winter, 1927-28, caribou were extremely numerous in the Wiseman-Ray Mountains region, at the same time that Porsild (see above) reported the huge herd near the Mackenzie Delta. O. J. Murie (1935: 71) noted the intermingling of caribou between Regions IV and V at the heads of the Porcupine and Peel Rivers.

In the winter of 1928-29 the Alaska Game Commission (1929c: 23) reported, "More caribou have wintered...than for many years, possibly coming down from the Yukon and Chandalar country," in the Fairbanks district. The following year, however, it was noted (1930c: 29) the Chandalar-Arctic migration did not occur, but that caribou were numerous north of the Endicott Mountains and a large number of caribou had crossed the Yukon River between Fort Yukon and Woodchopper; the report also stated that "...the larger herds are being diverted closer and closer toward the

Yukon Flats." Farther to the north, Porsild (1945: 20) stated that caribou were abundant in the Mackenzie Delta region in the winter of 1931-32, and "A few animals crossed on the ice...landing on the eastern mainland...." The following two winters the animals were scarce, but were abundant in the Richardson Mountains during the summers of 1933 and 1934. Except for the few animals known to have crossed the Delta to the east, Porsild stated (p. 20) that "...no caribou were seen or reported east of the delta during the years of my resident." (1927-28, 1931-34).

During the early 1930's the caribou migrations in Region V to the south dwindled steadily in size, and it appears likely that animals were moving into the arctic at this time. Alaska Game Commission reports noted an ever increasing number of caribou wintering near Fort Yukon and both on and around the Yukon Flats. Regular migrations took place across the Yukon River between Forth Yukon and Woodchopper late each fall, but these apparently stopped about 1935 (Alaska Game Commission, 1935c: 34). In September of 1939, however, there was another large run of caribou moving to the southward at Woodchopper, and the previous winter there had been large numbers of animals "...all through the Yukon Flats" (1939c: 35). This was the last report of large numbers of caribou near Fort Yukon on the Yukon Flats. The same winter, 1938-39, White and Rhode (1939: 5) reported the entire upper drainage of the Kandik River to be

"...alive with caribou and wolves." It is assumed likely that most of the caribou movements and distribution noted in this paragraph pertain mostly to the sub-population of Region IV (Porcupine herd).

There is little information concerning caribou distribution in the north during the 1930's, although, as noted earlier, Collins (1937) did report a large wintering concentration in 1936-37 along the foothills between the Kuparuk and central Colville Rivers. These animals might well have been from the central Brooks Range group, which at this time was shifting away from the southern regions (e. g., the Wiseman area). To the northeast caribou were still rather abundant in 1942, according to Clarke (1944: 101), and with regard to the area west of the Mackenzie Delta he stated that these animals "...customarily migrate along the coast south of Herschel Island in the summer. In autumn they turn south....In the autumn of 1942 they did not appear...." He also noted that a large migration of barren-ground caribou came from the northeast into the Fort Good Hope area on the Mackenzie River during the winter of 1941-42, although he did not mention any crossing to the westward. In 1943 the Alaska Game Commission (b and c) reported that caribou migrations in interior Alaska had "fallen to an all time low", and there were "...many indications that the caribou herds are moving into the Arctic ranges in a northwesterly drift from the

interior." In 1945 a "vast migration" of caribou was reported at Aklavik, on the west side of the Mackenzie Delta, and again in 1947 (Alaska Game Commission, 1946b, c; 1948c). At the same time caribou remained numerous in the Endicott Mountains. Munro (1953) stated that many "thousands" of caribou were observed on the east slopes of the Richardson Mountains, just west of the Mackenzie River, in 1949 and 1951. Yet in 1953 he estimated the main population at only 30,000-40,000 animals, ranging the drainages of the Porcupine, Firth, and Chandalar Rivers. Meanwhile, Scott et al., (1950: 623) had reported a wintering herd of about 20,000 animals along the East Fork of the Chandalar River in late winter, 1949, which moved northeastward in early spring. The same authors reported the bulk of the caribou in the Alaskan arctic to be located in the western Brooks Range.

The above information suggests that the population in northeast Alaska dwindled considerably in size during the late 1940's. A shift in the population to the west or east is quite possible, but cannot be documented. An emigration eastward or southeastward farther into Canada could have occurred easily without detection, even though Banfield (1954) and Kelsall (1957a) made no mention of a possible influx of animals into the region east of the Mackenzie River during that period. The Canadian studies did not begin until 1948, however, and little was known about caribou movements and numbers before then (Banfield, 1951). On the other hand, there appears to be no precedent for

such an exchange of animals, in spite of the fact that large numbers of caribou from both the east and west have reached the Mackenzie from time to time. But then, in such a vast, largely uninhabited region, a sudden large-scale movement across many portions of that river would not likely be observed, nor would the change in total numbers apt to be fully appreciated. Such problems of observation exist even today in many areas of caribou habitation in Alaska and in northern and western Canada. A shift of animals to the west from Region IV also was quite possible. The large population already present in the central Brooks Range and farther west easily could have absorbed many animals from the east without any obvious change that could be readily detected by the usual field methods of observation. It seems evident to me that there was a "drastic" decline in caribou numbers in Region IV sometime prior to 1952, and that a population shift seems the most likely answer. The direction of this shift remains in doubt, other than it must have been either eastward or westward, because populations to the south remained small.

Since 1953 the population in Region IV appears to have expanded steadily. Alaska Game Commission reports (d) during the 1950's indicated that the main population remained in the center of habitation. Occasionally, segments of the herd wintered in Alaska along the upper reaches of the Chandalar River, but each

spring they moved northeastward to the calving grounds on the arctic slope. The bulk of the herd has wintered each year in Canada in the area encompassing the upper drainages of the Black, Porcupine, and Peel Rivers, southward to the Ogilvie Mountains. Large movements near the Mackenzie Delta were reported in early winter during 1953 (Scott, 1954), 1957 (Olson, 1958), and 1958 (Olson, 1959). During the winter of 1957-58 there were large numbers of caribou along the entire arctic slope, between Point Barrow on the west and Barter Island on the east (Olson, 1958). At the same time it was noted there were relatively few animals on the south slopes of the Brooks Range in Region III and those caribou to the south in Region IV were fewer in number and were wintering farther to the north and west than usual. Such a distribution pattern would have permitted an interchange of animals between the eastern and western arctic, but there was no evidence of such occurring. During 1957 and 1958, Olson (1957; 1958) expressed concern over the dwindling numbers of animals in the Fortymile herd of Region V, and implied that an emigration probably had occurred into the Porcupine herd of Region IV. I recorded such a movement in the spring of 1964, when numerous trails in the snow were followed northward by airplane from the wintering grounds of the Fortymile herd to as far as Old Crow Flats. The trails continued northward beyond that point, and the calving concentrations in Region V that spring were

limited to several thousand animals which had spent the winter in the western Tanana Hills. Whether such emigrations actually constituted permanent shifts in the sub-populations remains unknown. It is quite possible that a certain proportion of these animals returned in later months or years. In June, 1961, I censused the calving grounds of Region IV and estimated a population of 110,000 to 117,000 animals (Skoog, 1962: 4; 1963a: 10). I also determined there was but one calving area being utilized and therefore that Region IV had but one sub-population--the Porcupine herd. A substantial increase had occurred since 1953.

Prior to 1900 the sub-population of Region IV seemed to be rather large. Caribou also were abundant to the east of the Mackenzie Delta and there may have been a periodic exchange of animals across the Mackenzie River. During the early 1900's the herd remained large at the center of habitation, but had shifted away from the coast, and segments also were shifting toward the Endicott Mountains on the west. In the 1920's and 1930's there were essentially two herds in Region IV: one ranging the center of habitation in the northeast, and the other occupying the central Brooks Range, i. e., the upper drainages of the Koyukuk and Chandalar Rivers northward to the arctic slope. There was an influx of animals into the arctic from Regions II and V during and after the late 1920's, and there may have been an interchange between Regions III and IV as well. By the mid-1940's the sub-population in Region IV was quite large, but by the early 1950's had dwindled considerably. It seems likely that a shift in numbers to the east or to the west had occurred. Since about 1953 or earlier there has been a steady buildup in numbers, and evidence exists for further immigrations from Region V on the south. The central Brooks Range "herd" disappeared as a separate group during the 1950's, presumably joining those to the westward, and by 1964 the Alaskan arctic contained but two sub-populations: the Arctic herd of Region III and the Porcupine herd of Region IV, each utilizing a separate, distinct calving area. No other calving areas were evident in those regions.

Region V. Eastcentral Alaska.--Records of the caribou distribution in this region are few for the period prior to 1900, but there are several accounts which permit an interpretation. During this early period it was evident that the bulk of the subpopulation ranged to the eastward, extending southeastward to the Whitehorse-Skagway area. In the summer of 1883, Schwatka (1885a, b) reported that large herds seasonally crossed the Yukon River near the present townsite of Eagle, and that the animals "abound in quantities" throughout the Klondike River area. Dawson (1888) noted that caribou were abundant everywhere along the drainages of the Pelly and Lewes Rivers, tributaries to the upper Yukon River in the Yukon Territory. Schwatka (1894) made several pertinent observations in 1893 on another trip down the Yukon River. He found (p. 91) that caribou were numerous in the Chilkoot Pass region north of Skagway, and noted (p. 109) that along the river draining Lake Bennett was a "place where the caribou cross" (near the present town of Carcross). Large migrations of caribou crossed there and also near Indian River (p. 244), about 50 miles south of the present site of Dawson. These observations suggested a large caribou population at that time (the 1880's and early 1890's), and probably earlier, because of the regular crossings known to the Indians of the region.

Along the upper Tanana River to the west, however, it would appear that caribou were scarce, because the natives there " ...clothed themselves almost exclusively in tanned moose skins...." (U. S. Census Office, 1893: 126). The military reconnaissances of that region during the late 1880's and 1890's also reported a scarcity of caribou there. H. T. Allen (1900: 437-448) in 1885 found the natives of the Mentasta Pass-Tetlin Lake area in near-starving condition because of the lack of game, and he reported a scarcity of big game all along the Tanana River; only three caribou skins could be obtained in the Tetlin area for use in making a boat. This scarcity of caribou was evident still in 1898 (Glenn and Abercrombie, 1899), even into the upper drainages of the South and Middle Forks of the Fortymile River. During the winter of 1898-99 the Mentasta Indians starved to death (all but two), and Abercrombie (1900: 98) reported the whole area devoid of caribou. He also noted a caribou drive-fence on the Mosquito Flats, near the Indian village of Kechumstuk, along the upper reaches of the South Fork of the Fortymile River. The fence seemed to be in good repair and apparently had been used in recent years--a definite indication of caribou abundance and of regular, seasonal movements. Murie (1935: 3) observed this fence in 1921, and estimated it had not been used since about 1895 based upon talks with local Indians.

By the early 1900's caribou had become scarce in the Whitehorse-Skagway-Haines district, and the wintering animals remained farther to the northwest. Osgood (1909: 13) stated that a large herd ranged the Tanana Hills in 1903, but that few crossed the Yukon River anymore, as they once did in the past. He noted that the "older" Indians referred to an old crossing of the Yukon near Eagle. Evidentally the herd then, as in recent times was using its main migration path, which extended southeastward along the slopes adjacent to the Sixtymile River and crossed the Yukon at various places above Dawson. Osgood's observations pertained mostly to the Eagle-Dawson area, and below, although he did mention seeing abundant caribou sign in the lower Pelly River area during late September, 1903. It is difficult to assess the relative numbers of caribou present in the herd then, but Osgood (1909: 13) stated, "Doubtless the present herds are comparatively small, but they are still large enough to be worth seeing." This observation seemed to imply a decrease in numbers from earlier times. Yet, Wickersham (1938: 51) noted in October, 1900, the "great herds of caribou browsing" along the ridgetops south of Eagle, and Higginson (1926: 441) stated that in the winter of 1907-08 the caribou "...ranged in droves of many thousands--some reports said hundreds of thousands--through the hills and valleys of the Stewart, Klondike, and Sixty-Mile rivers...." In the winter of 1904, Selous (1907: 307) reported that "...fifteen hundred caribou were killed by meat-hunters during the autumn migration across the upper waters of the

Klondyke River...."; also, in late autumn, 1904, he reported a large migration of caribou moving southward across the Yukon River, probably just above Circle. These animals might have come from Region IV. The heavy trails observed by Osgood (1909: 49) in the Ogilvie Mountains in July, 1904, could have been the results of seasonal movements by Region IV caribou, also, for these animals wintered periodically in the Ogilvies and the population was high in the early 1900's. Higginson (1909: 441) noted the rarity of caribou in the Carcross area south of Whitehouse, where previously large seasonal migrations had occurred each year.

During the 1910's caribou numbers must have been increasing rapidly, for tremendous herds were being sighted and major movements occurred in widely separated areas. Palmer (1941) stated that five large fall-runs of caribou occurred in the Fairbanks-Circle region between 1906 and 1913. In October, 1909, Stuck (1914) estimated about 100,000 animals crossed Mosquito Fork and Kechumstuk Flats. One winter, about 1912, the same man (Stuck, 1917: 83) observed "...the entire bed of the Charley River, from bank to bank, and even up to the first mountain benches on either side whenever they were accessible, for fifty miles, trodden hard and solid by innumerable hoofs of caribou...." The increase of caribou in Region V might have resulted in part from an influx of animals from Region IV. In the latter region the caribou were shifting away from the arctic coast to the southward, and

were extending both into the Ogilvie Mountains as well as into the Chandalar River country on the west. Eakin (1913: 13) noted in 1911 that caribou often ranged into the Rampart area, between the Tanana and Yukon Rivers, " ...during their winter migrations but are rarely seen in summer except in the mountainous areas north of the Yukon," (i. e., the Ray Mountains). Sheldon (1911) observed in the Ogilvie Mountains that the main group of caribou passed southward through the mountains in November and December, and returned northward in March; this observation suggested that the animals probably were moving into the Dawson area on the south. In November, 1915, Brownlee (1916) recorded a large southeast movement along the mountains about 25 miles west of Dawson. Such a movement would have brought the animals into the Sixtymile River area, as might have been expected at that time of year. The Governor's report for 1918 (Riggs, 1919: 4-5) noted the caribou had greatly increased; in the fall of 1918 "unprecedented" numbers were observed near Fairbanks and in the Fortymile country. In the winters of 1918-19, 1919-20, and 1920-21 large numbers of caribou moved southeastward into Region VI across the Tanana River to the head of the Delta River, and perhaps beyond (O. J. Murie, 1935: 72).

By the mid-1920's the caribou in Region V probably had reached peak numbers. In the fall of 1920 Murie (1935: 6) estimated 568,000 animals in a migration northeast of Fairbanks. Movements were widespread and in various directions. The main fall movement continued to the southeast, with the animals wintering in Canada along the hills adjacent to the Ladue, Sixtymile, Klondike, Stewart, Pelly, and White Rivers. In the winter of 1924 large numbers extended as far as Whitehorse and the summits of the coast range above Skagway (Murie: 77) for the first time since before 1900. To the west, many caribou also crossed the Tanana River into Region VI through Isabel and Mentasta Passes, ranging as far as Copper Center and the Lake Louise Flats. On the east, the animals were intermingling with those of Region IV at the heads of the Porcupine and Peel Rivers, and probably in the Ogilvie Mountains as well (Murie: 71). To the northwest, seasonal movements occurred at Nenana across the Tanana River during the 1920's (personal communication with a long-time resident of Nenana, A. Linder) and regular crossings of the Yukon River occurred between Stevens Village and Rampart (personal communication with a long-time resident of Rampart and Fairbanks, G. A. Gasser). Mason (1924: 171, 179) reported a huge run of caribou crossing the Yukon River above Circle, from the north, in September, 1920, stating, "The river boats had been seeing the caribou cross for days....the bank was a seething mass

of running beasts, coming across on their way south." There seems little doubt that during the 1920's Region V supported a large number of caribou, which ranged out in all directions. Bone (1923: 3) stated the migratory herds were the greatest known in the history of the interior and that "The total number of caribou in Alaska is variously estimated from 500,000 to 1,000,000, but these figures are guesswork necessarily." O. J. Murie's 1920 estimate noted above was the only one that attempted to assess numbers in a systematic fashion. He decided later (1935: 6), however, that "In the light of subsequent experience this figure seems conservative and it is safe to say that the herd numbered well over half a million, possibly much nearer a million." The total for Alaska and the Yukon Territory be believed (p. 7) might "...number anywhere from 1 to 2 millions."

At the end of the 1920's and during the early 1930's the distribution and movement pattern of the caribou in Region V changed. The movements southwestward into and beyond the Isabel and Mentasta Pass areas of Region VI ceased, the last such movement occurring in 1931 (Scott _et al._, 1950; Alaska Game Commission, 1935c: 80). The main northwest-southeast pattern remained, but there seemed to be an ever-increasing movement to the northeast as well. Alaska Game Commission reports noted that the Fort Yukon-Circle areas was utilized as a wintering area

during 1932-1935, apparently by caribou from both Regions IV and V. Mertie (1932: 367) stated that in 1930 large numbers of caribou still migrated through the Ogilvie Mountains each fall. In 1936 the caribou again extended far to the southeastward, wintering near Kluane Lake (Rand, 1945: 82). The main trend, however, seemed to be toward the northeast, and crossings of the Yukon River between Fort Yukon and Woodchopper were common until about 1935 (Alaska Game Commission, 1935c: 34); another crossing occurred in September, 1939 (1939c: 35). After 1939, caribou once again became scarce near Fort Yukon; the population in Region V probably had reached a low point. The remaining animals occupied the center of habitation and their movement pattern was directed primarily southeast-northwest. Alaska Game Commission reports all expressed the opinion that large numbers of caribou had moved into the arctic regions. About this time, also, the sub-population of Region IV was approaching a high point in numbers. The northward shift seems quite probable even though direct observations are not available.

During the 1940's the herd seemed to increase steadily, and the southeast-northwest movement pattern was maintained. Calving took place to the northwest and for the most part the animals wintered to the southeast. In June, 1953, I estimated the herd at 40,000 animals (Skoog, 1956: 65), and the annual herd increment remained high during the next few years. During

the winter of 1956-57 the major portion of the herd wintered in the Ogilvie Mountains north of Dawson. In May, 1957, a large portion of the wintering population did not return to Alaska, and it is thought that many animals (perhaps 30,000) went northward with the Porcupine herd. Since then, the animals have remained farther to the south during the spring and early summer. In the winter, the herd sometimes has broken into several segments, one wintering to the north and another to the west, with the main segment to the east and southeast as usual. In the spring of 1964 a large portion of the Fortymile herd once again moved northward with the Porcupine group (Skoog, personal observations). At present there remains but one calving area, therefore but one sub-population called the Fortymile herd by the author.

The historical information examined suggested that prior to 1900 the sub-population in Region V was of "moderate" size and ranged farther to the east and southeast than now. It is presumed that the seasonal migrations noted in the Whitehorse-Skagway area were part of this herd's movement pattern. Caribou were scarce to the west along both sides of the Tanana River Valley, but an Indian drive-fence at Kechumstuk indicated a large population must have occupied the center of habitation. During the 1900's the herd expanded steadily and reached a huge size by the mid-1920's. Part of this increase may have resulted from an influx of animals from Region IV. At peak numbers the animals ranged in many directions and the movements became somewhat erratic. On the southwest, seasonal fall movements brought many animals into Region VI, via the Alaska Range and Isabel and Mentasta Passes, where they wintered. Many continued to winter in Canada on the southeast, and in 1924 extended as far as Whitehorse and the summits of the Coastal Range above Skagway. Intermingling with caribou from Region IV occurred commonly on the east and northeast, and movements also extended

northward across the Yukon River, below Stevens Village. During the early 1930's the southwest movements to Region VI stopped, and a shift in animals to the northeast was taking place. By the late 1930's the sub-population had been reduced considerably in size, and was ranging the center of habitation, returning to the established southeast-northwest movement pattern. The herd increased steadily, but in the spring of 1957 apparently lost many animals to the Porcupine herd in Region IV. Another such emigration occurred in the spring of 1964.

Region VI. Southcentral Alaska.--Observations made in the late 1800's indicated that caribou once had been abundant in this region, based mainly upon the presence of Indian drive-fences. Such fences were found along the upper Copper River above Gakona in 1898 (Glenn and Abercrombie, 1899: 362) and along the Chitina River valley in 1899 (Rohn, 1900). In the latter instance Rohn noted that caribou must have been quite abundant, judging from the large number of shed antlers found, in addition to the remains of traps and fences of the natives. The shed antlers indicated that the animals had been present there in the winter. To the present day, however, caribou have not occurred again along the Chitina River. Because of the rather marginal habitat in that isolated valley, with its rather deep, frequently wet snows, it seems unlikely that caribou would range into that area (at regular intervals as implied by the drive-fences) unless the population toward the northwest (center of habitation) were quite large and its seasonal movements had become widespread. The other drive-fence noted, along the upper Copper River, probably was used about the same time. In recent years a large segment of the Nelchina

herd has moved through this section of the Copper River during early and late winter, probably much as it did when the drive-fence was being used actively. Other evidence for a large population sometime prior to 1900 was obtained from an old (70 yrs.+ in 1962) Indian of the Tazlina area, on the southern edge of Lake Louise Flats. In talks with this person, Jimmy Secondchief, the author discovered that the man's immediate ancestors had hunted caribou at Clarence Lake, along the upper Susitna River. They drove the caribou into the lake and then speared them from canoes as the animals swam. This type of hunting, too, probably would not have existed had not the caribou population been rather large and its movements rather regular.

The presence of caribou on the Kenai Peninsula during this early period also might have been an indicator of a former high population farther to the north. This area, as well as the Chugach Mountains on the north through which the animals would have had to pass in order to reach the Kenai, can be considered as marginal habitat for caribou, because of the precipitous terrain, deep snows in the mountains, and rather limited suitable areas above timberline (i. e., extensive sedge-meadow and/or heath-lichen stands). There is no record indicating that caribou were ever particularly abundant on the Kenai. Petrov (1881: 38) mentioned the natives there hunted caribou in the interior, but from his comments it would appear that moose and fish provided

most of the protein food. At any rate, by 1900 the animals had become quite scarce and A. J. Stone stated they " ...will doubtless soon be exterminated," (Osgood, 1901: 61). Neither Osgood (1901) nor J. A. Allen (1904) were successful in locating caribou in 1900 and 1903, respectively, although both noted recent evidence of the animals' presence, as did Radclyffe (1904) in 1903 also. Lutz (1956: 85) stated the last known record of a caribou being sighted on the Kenai was in 1912. Palmer (1941) suggested that the widespread fires on the Kenai in the late 1800's (1871, 1883, 1891) were in large measure responsible for the disappearance of caribou. To certain extent this opinion might be true, for certainly the fires destroyed a large portion of the winter range, which in this area was located mostly in the spruce forests. I concur more with O. J. Murie's (1935: 77) statement, however, that, "The Kenai Peninsula seems to be simply an overflow area that probably often received an influx of caribou from unusual migratory movements of interior herds." In this respect, then, the Kenai Peninsula, like the Chitina River valley mentioned earlier, would be utilized only as a result of high population pressures at the center of habitation.

At what period the population in Region VI reached a high point remains unknown. By 1885, however, there were few caribou to the southeast along the Chitina, Tazlina, and Copper Rivers, for H. T. Allen (1900) reported all the natives were in

near-starving conditions and his expedition was not able to secure meat. Later expeditions, in 1898 and 1899, reported similar conditions in this portion of Region VI (Glenn and Abercrombie, 1899; Abercrombie, 1900; and Rohn, 1900), although a few caribou were known to be present in the Mentasta Pass area. Rohn (1900) noted caribou were taken then (1899) only along the northwest border of the Copper River valley (presumably the Lake Louise Flats or perhaps farther to the northwest). H. T. Allen (1900: 413) referred to the diary of a Russian explorer named Sereberinikoff, who in 1848 reported four caribou were killed at Tazlina Lake, but hunger was present in all the native villages along the Copper River drainage. This observation suggested that the abundance of caribou along the Copper and Chitina Rivers, indicated by the Indian drive-fences, probably occurred between 1848 and 1885. The fences examined in 1899 by Rohn (1900) were in too good condition not to have been used since before 1848, and the natives would not have been starving had the caribou been present and the fences operated.

With this admittedly scanty evidence I have concluded there was a high population of caribou in Region VI sometime during the period 1848-1885. Large numbers extended seasonally into the main Copper River valley, as they are doing today, and even reached the Chitina River valley. It is quite possible segments extended southward to the Kenai Peninsula as well, and

may have been the immediate ancestry of the caribou noted there later in the 1800's. It would appear significant that DeLaguna (1934), in her archeological investigations of the Kenai area, did not find caribou bones in the middens excavated while finding moose bones common. This piece of evidence lends support to Murie's idea of the Kenai being simply an "overflow" area, which periodically supported a caribou population.

By 1900 it appears the caribou population had decreased and remained mostly within the center of habitation. Osgood (1901) observed caribou were common in 1900 along the lower Susitna River and their skins were often brought to the coast as trade items (trading posts at Tyonek and Knik). The reports of Glenn and Abercrombie (1899) noted caribou were quite plentiful in 1898 in the mountains east of the lower Susitna and along the Talkeetna River. It was stated (p. 285) concerning the upper Talkeetna River, "The uplands are completely covered by a thick matting of reindeer moss, and caribou signs are seen on every hand." In Broad Pass to the northwest caribou sign was particularly abundant, and further comments were made regarding the abundance of lichens on the above timberline areas (p. 270).

In 1898 Captain Glenn of the U. S. Army (Glenn and Abercrombie, 1899) traversed the southern portion of the Talkeetna Mountains, moving northeastward from the lower Matanuska River across the mountains adjacent to Caribou Creek, down the Little Nelchina River, across the Lake Louise Flats to Tangle Lakes, and down the Delta River almost to the Tanana River. This journey crossed what is today considered to be an important segment of the Nelchina caribou herd's range. He noted (p. 59) on August 4, 1898, upon leaving the Matanuska River, "In passing Hicks Creek we left the moose country to our rear and passed into the caribou country, the signs of which were quite abundant. Reindeer moss abounds in all of the sections traversed today." Caribou sign was plentiful throughout the mountainous area until he reached the Lake Louise Flat. In crossing these Flats he noted the entire flat had been burned a long time previously and " ...none of the Indians we encountered remembered it as being in any other condition than it is at the present time. It was covered with a growth of dead spruce that was evidently killed at the time of the fire." By then, however, the lichen cover was abundant throughout; he mentioned no sign of caribou, but such would not be expected during the summer in that area. In the Tangle Lakes-Fielding Lake highland to the northeast he again noted the abundance of caribou sign, and encountered a band of Copper River Indians

who were hunting caribou. In regard to this area he stated (p. 77), "Game signs, including moose, caribou, bear, wolf, and fox, were more abundant here than at any place we had passed over...."

Mendenhall (1900), who was leader of a separate party attached to Glenn's command, stated (p. 339) that the Indians living along the upper Matanuska River and in the Tazlina area penetrated the Susitna River basin to hunt caribou. These Indians would have been of the same group to which Jimmy Second-chief (whose comments were noted earlier) belonged; Clarence Lake lies along the middle portion of the Susitna River. Mendenhall also remarked (p. 337) caribou were abundant along the northern base of the Talkeetna Mountains, in the hill country of the middle Susitna, and on the uplands along both flanks of the Alaska Range. In regard to the last named area, he probably was referring to the Isabel Pass-upper Delta River area to the northeast in Region VI. Earlier that year (1898),Mendenhall had passed through part of the Chugach Mountains, along the Eagle River, which lies to the east of where Anchorage is now located. He mentioned (p. 275-280) no sign of caribou, and noted that the Indian camps passed had an abundance of moose and sheep hides. The lack of caribou in this section of the Chugach Mountains, immediately north of the Kenai Peninsula, was to be expected because of the marginal habitat.

In a further comment with regard to this period of time, Glenn (1900) in his report on explorations during 1899 stated (p. 732) that caribou " ...are found in the foothills of the Matanuska and Sushitna Rivers, also in the Alaska range, but seem to be very abundant in the section of country between the headquarters of Indian Creek and the Tanana River." He referred here to the northwest portion of Region VI, the mountains between the Susitna River and the upper Nenana River--presumably Indian River, Portage Creek, Jack River, Wells Creek, Yanert Fork, Broad Pass, etc. The caribou distribution in 1900, as interpreted from the observations of Glenn's explorations in 1898 and 1899, thus resembled closely that encountered today. The animals appeared to be spread throughout the center of habitation, with concentrations toward the northwest.

This abundance of caribou in the northwest might well have been associated with the subsequent increase in numbers in the McKinley herd, as noted in the discussion of Region II. Sheldon (1930) reported caribou abundant along the Toklat River in 1906-07, and similar observations were made by Browne (1913) during 1912. An interchange of animals between Regions II and VI may have occurred, with a continued movement pattern directed seasonally back into Region VI along the upper Nenana River drainages. Moffit (1914, 1915) noted that Valdez Creek, tributary to the uppermost portion of the Susitna River (about 50

miles east of Broad Pass), once had been a favorite hunting ground for caribou, but the gold miners there in 1913 stated the animals had not reached there for several years. He remarked (1915: 20), "The Indians of the upper Susitna spend a large part of the year hunting on Jack River and on the Yanert Fork of Nenana River. These two localities are considered the choice hunting grounds of the region, and Yanert Fork is the better of the two." Apparently the large migrations east and west from the McKinley area had not yet begun.

Elsewhere, Chapin (1918) reported caribou plentiful along both sides of the middle portion of the Susitna River during the summer of 1915. Today this area remains one of the most important of the summering areas for the Nelchina herd. He also sighted large herds that year farther to the south, along the Oshetna and Little Nelchina Rivers. In 1915, caribou remained absent from the Chitina River valley on the southeast, and Moffit (1918) reported only the scattered remains of old shed antlers. To the northeast of the Chitina River, across the Wrangell Mountains, Moffit and Knopf (1910) had found caribou to be common in the mountains adjacent to the upper Chisana and upper White Rivers in the summer of 1908. That area seems to have contained a small herd of caribou throughout the 1900's, but relatively little is known about its movements or possible connections with other herds.

During the late 1910's and the 1920's the adjacent sub-populations in Regions II and V reached peak numbers and many animals moved into Region VI seasonally, usually arriving in the fall and departing in the spring. The movements through Isabel and Mentasta Passes on the northeast were in full swing by 1918 (O. J. Murie, 1935: 72). These brought Region V caribou into the Mentasta-Nabesna River-White River area, the north slopes of the Alaska Range between Mentasta and Isabel Passes, and probably the north slopes west of the Delta River. Once through the Passes the caribou ranged as far as Copper Center, probably extending onto the lower Chitina River as well; they moved into the Tangle Lakes-upper Maclaren River area, and very likely large numbers reached the Lake Louise Flats. Frank Glaser (1950) estimated some 300,000 animals of the Fortymile herd moved into Region VI during the fall of 1921. Similar estimates of numbers were noted later in the 1920's in various reports of the Alaska Game Commission regarding caribou moving southward past Big Delta toward Isabel Pass. Major movements into the Broad Pass area by McKinley caribou apparently did not begin until about 1925 (A. Murie, 1944: 146). These animals moved eastward into the mountains adjacent to Broad Pass, Jack River, Yanert Fork, and the upper Nenana River, frequently crossing Monahan Flat and reaching Valdez Creek and the upper Maclaren River. There may have been contact with the animals of

Region V that came from the east via Isabel Pass. All of these major movements--through Broad, Isabel, and Mentasta Passes--stopped after 1931. Apparently the winter of 1931-32 was the last in which large numbers of caribou from Regions II and V were present in Region VI (Alaska Game Commission reports, 1930-33, a and c). To what extent remnant groups of caribou remained in some of the areas traversed by these huge migrations is not known, although it seems evident that no large groups remained. Three small herds remaining today may be "relics" of these large scale movements during the 1920's: the Delta herd, on the north slopes of the Alaska Range; the Mentasta herd, in the Mentasta-Mt. Sanford area; and the Chisana herd, along the upper stretches of the Chisana and White Rivers.

The Nelchina herd may have been augmented by animals from Regions II and/or V, but the magnitude of the immigration if such did occur remains unknown. On the other hand, it is quite possible that the herd lost animals instead; such large seasonal migrations from Regions II and V easily could have pulled animals with them during the return movements each spring. It is evident, however, that the center of habitation has contained caribou throughout the period for which historical records are available. Capps (1927a) found that caribou were common along the adjacent mountains of the upper Matanuska River valley

during the summer of 1924, but were not abundant. Such is the typical situation today also: that area long has been known to be the summering grounds for various numbers of bulls, the main herd remaining farther to the north (Alaska Game Commission reports; Skoog, personal observations; various big game guides working that area). In September-October, 1929, some 6,000 caribou were sighted by guides in the Chickaloon River area, a northern drainage of the Matanuska River from the Talkeetna Mountains; these animals occurred in this southern portion of the region at the same time the movements from Regions II and V were occurring to the northeast and northwest (Alaska Game Commission, 1930a: 20). In 1931 the Alaska Game Commission (1932a and c) reported caribou as numerous in the Talkeetna Mountains, especially along the Little Nelchina River, Caribou Creek, and the upper Susitna River. The same year they were reported as abundant in the Mentasta-White River area, with a few wandering southwestward as far as Copper Center. All reports of the Alaska Game Commission during 1932-1935 noted the general lack of caribou in the eastern portion of the region, except for a small herd in the White River area; the north slopes of the Alaska Range contained a fair number of caribou, but these did not seem to range to the southward; in the Talkeetna Mountains the animals were reported as having dwindled in numbers. In 1936 (Alaska Game Commission, 1936c: 84) a game warden reported, "The Nelchina herd

is....wintering in the Talkeetna Mountains from where they disappeared last year." In June, 1936, the McKinley herd again invaded the northeast portion of Region VI, south of Broad Pass, but returned westward by July (Alaska Game Commission, 1936c: 55). During the winter of 1937-38 large numbers of caribou occurred in the Talkeetna Mountains, "....in numbers exceeding anything formerly seen," (Alaska Game Commission, 1938c). At the same time the animals were extremely scarce along the entire Copper River drainage, but a few were present in the Chisana River-White River area. The following year the Nelchina caribou were thought to have moved elsewhere, and were considered as scarce in the Talkeetna Mountains once again. On the other hand, the herd simply might have changed its movement pattern, and wintered farther to the north. Observations during this period did not cover extensive areas which remained relatively inaccessible.

During the 1940's the sub-population in Region VI remained rather low, with the Nelchina herd being the largest group present. In the early winter of 1945 an estimated 10,000 animals were reported ranging the foothills of the Talkeetna Mountains west of Lake Louise (Alaska Game Commission, 1945c). This observation represented the first in which Nelchina caribou were known to have moved onto the Lake Louise Flats, which later became an important wintering area for several years. In 1949, the following estimates were made for the four herds in Region VI

(Scott et al., 1950: 617-618): Nelchina, 4,000; Delta (north slopes of Alaska Range), 300; Mentasta (Mentasta-Mt. Sanford), 50; and Chisana (Chisana River-White River), 100. Subsequent knowledge indicated that the methods used for estimating caribou numbers at that time (extensive, aerial total counts) probably were grossly under-estimating the actual numbers (Watson and Scott, 1956). Nevertheless, the locations recorded for the herds were valid, and it is interesting to note that the distribution has not changed since then except for the utilization of a greater area, with increasing numbers.

Since then, and probably starting before that, there has been a steady increase in the size of the Nelchina herd. Intensive censuses in 1955 and 1962 revealed 40,000 and 71,000 animals, respectively. Comparable censuses have not been made of the other three herds, but 1964 estimates (Skoog, unpublished data) indicated 5,000 animals each for the Delta and Mentasta herds, and 3,000 for the Chisana. All three have remained essentially within the areas recorded for them in 1950. The Nelchina herd, however, has expanded its range considerably as the numbers increased. Since 1956 the animals have shifted their winter range primarily to the northwest, but also to the southwest, southeast, and northeast, and the herd has split into several wintering segments. Large numbers moved northward through Isabel Pass in the winters of 1956-57 and 1961-62;

eastward to Mentasta Pass in 1961-62, 1963-64, 1964-65, and in 1965-66; and northwestward into Broad Pass and Mt. McKinley Park in 1959-60, 1961-62, 1962-63, 1963-64, and 1964-65. These rather erratic, widespread movements have brought the Nelchina caribou to and beyond the boundaries of what previously had been considered their "home range". The Mentasta herd has been "swamped" on several occasions, and contact has been made with the Delta and McKinley herds. Thus far, however, the writer knows of no loss of animals from the Nelchina herd. Such losses undoubtedly will occur, however, if the herd continues to expand. At present the four herds in Region VI remain intact, each with its own calving grounds: Nelchina, Delta, Mentasta, and Chisana.

My interpretations of the available records for caribou distribution in Region VI indicate there probably was a high population at the center of habitation sometime between 1848 and 1885. Evidence for this high rests upon the presence of Indian drive-fences on the Copper and Chitina Rivers and of caribou on the Kenai Peninsula. The writer concurs with O. J. Murie's opinion (1935: 77) that the Kenai Peninsula probably was an "overflow" area that received caribou periodically as the herds farther north became large in size and expanded their movement patterns. By 1900 caribou remained numerous throughout the Talkeetna Mountains; apparently they were most abundant to the northwest. During the 1920's peak numbers were reached in herds of the adjacent Regions II and V, and seasonal migrations brought many thousands of animals into Region VI during the winter via Broad, Isabel, and Mentasta Passes. These migrations ceased after the winter of 1931-32. How they affected the number of caribou in this region is not known; there could have been a gain of animals, or a loss. It is only known that there still remained a substantial number of animals (Nelchina herd) at the center of habitation,

which seems to have supported a caribou population throughout the time for which historical records are available. In addition, remnant herds remained on the north slopes of the Alaska Range (Delta herd), in the Mentasta-Mt. Sanford area (Mentasta herd), and in the Chisana River-White River area (Chisana herd). A low in the sub-population of Region VI probably was reached during the late 1930's or early 1940's, but since then the four herds have increased steadily in size. The three small herds have remained essentially in the same areas. The Nelchina herd has expanded greatly, however, both in numbers and in range. Widespread movements have occurred which have taken animals to and beyond the "normal" limits of the herd's range on numerous occasions. Although the herd still utilizes essentially one calving area (now enlarged), in winter it ranges over several, widely separated areas. The northwest portion of the region has been utilized most heavily in recent years, and the animals have extended well into Mt. McKinley Park. In 1965-66, however, large numbers moved southeastward during the winter onto the drainages of the Tetlin and Nabesna Rivers. It seems likely that if the herd continues to increase in size, an emigration eventually will occur into adjacent regions.

Present Herds.

At present, eleven distinct caribou herds have been recognized by the writer in Alaska, based upon the existence of separate calving grounds. Six of these are considered to be the main sub-populations of the six caribou regions designated earlier; these occupy the centers of habitation. The other five range in somewhat marginal habitat and can be considered as remnant herds which have remained since previous population highs in the regions in which they occur or in adjacent regions. The names and approximate locations of these herds, as depicted in Figure 2, are as follows:

Region I (Southwest Alaska)--Alaska Peninsula; the Unimak group and that southwest of Port Moller both are considered here as being temporary offshoots of the main herd.

Region II (West Alaska)--McKinley, plus two remnant herds: Beaver, located in the Beaver Mountains west of McGrath; and Mulchatna, ranging the drainages of the Mulchatna and upper Stony Rivers. Other animals reported from time to time in various parts of the Kuskokwim and Sischu Mountains and in the Rainy Pass area probably belong to one of the three herds listed.

Region III (Northwest Alaska)--Arctic; so far, essentially one calving area continues to be used, and therefore but one herd is designated. In addition there is a group of about a thousand animals at the base of the Seward Peninsula whose status is unknown; these animals possibly may be feral reindeer, or merely a remnant group from the Arctic herd.

Region IV (Northeast Alaska)--Porcupine; no remnant herds.

Region V (Eastcentral Alaska)--Fortymile; no remnant herds in Alaska, possibly some in Yukon.

Region VI (Southcentral Alaska)--Nelchina, plus three remnant herds: Chisana, located on the northeast slopes of the Wrangell Mountains; Delta, ranging the north slopes of the Alaska Range; and Mentasta, in the Mentasta Pass-Mt. Sanford area.

The distribution and status of each herd are discussed briefly below. Those which are most accessible to the Nelchina herd (the study population) include the Chisana, Delta, McKinley, and Mentasta herds.

Alaska Peninsula Herd.--At present the main caribou population is north of Port Moller, in the center of habitation of Region I, ranging between Port Moller on the southwest to the Naknek Lake and river system on the northeast. The main wintering grounds are in the vicinity of Becharof Lake, mostly in the hills to the north. The calving grounds are located in the southwest, primarily between the Bear and Meshik Rivers. In summer the herd ranges from Port Moller to Port Heiden, on both sides of the Peninsula. A census by the author in June, 1960, indicated a population of 7,000 animals (calves excluded) to the northeast of Port Moller (Skoog, 1961: 11). Since then, with good calf crops and mild winters, the herd has increased steadily; assuming an annual increment of 10 percent I estimated this sub-population at 10,300 animals (calves excluded) for June, 1964.

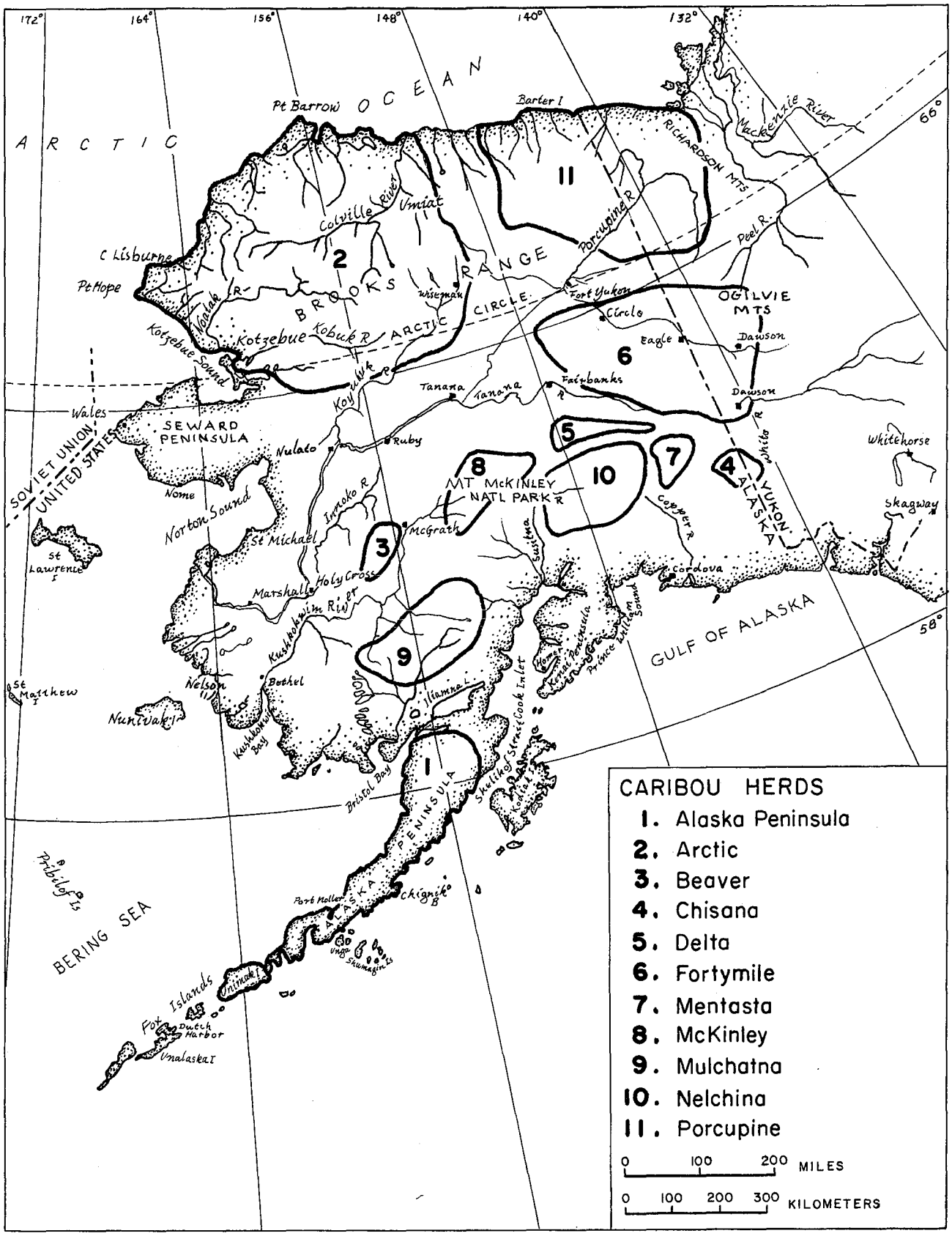

Figure 2. Approximate locations of the main caribou herds in Alaska, 1968.

The animals to the southwest of Port Moller actually are divided into two groups, one on the mainland and the other on Unimak Island. An interchange of animals occurs sporadically across Isanotski Strait, but the relatively low numbers at present makes this exchange rather infrequent. Little is known about the seasonal distribution of these animals, but those on Unimak probably calve in the vicinity of Urilia Bay and those on the mainland, in the Black Hills near Cape Leontovitch, based upon past observation by O. J. Murie (1959). In June, 1960, I estimated 1,000 animals to the southwest of Port Moller, including Unimak Island. In 1963 personnel of the U. S. Fish and Wildlife Service tallied nearly 1,000 caribou on Unimak Island (personal communication with Robert D. Jones, Refuge Manager, Aleutian Islands National Refuge). The estimate in June, 1964, based on an annual increment of 10 percent since 1960, was 1,400 animals (excluding calves).

Arctic Herd.--This caribou herd presently is at a high level and is well distributed throughout the whole of Region III. The main wintering grounds are to the south and extend from the Waring Mountains, Baird Mountains, and lower Koyokuk River, eastward to the Wiseman area. The main calving grounds are located along the upper portions of the Colville and Utukok Rivers. In summer the animals spread out over a wide area extending from

Cape Lisburne on the west to the Colville River on the east, generally north of the Brooks Range, and occasionally northward to Point Barrow. In the winter of 1963-64, a large segment of the Arctic herd wintered to the east and southeast of Bettles between the Koyokuk River drainage and the Yukon River (Skoog, personal observations).

The sub-population in northwest Alaska probably is approaching a peak at this time. Lent (1966b) estimated that in the summer of 1962 there were between 175,000 and 200,000 animals in this herd. In the spring of 1963, the writer, using mostly Lent's data plus additional observations, estimated the Arctic herd must number at least 200,000 animals.

During the winter of 1963-64 large numbers of caribou moved through the lower Kobuk and Kotzebue Sound areas, accessible to many of the settlements in that area. An attempt was made by the Alaska Department of Fish and Game to obtain harvest figures for that period. The results indicated that at least 25,000 animals were killed between September, 1963, and April, 1964. If one were to assume that one out of every ten animals in the herd had been killed that winter, it would mean that the original population was approximately 250,000 animals. In view of the wide distribution of the movement of these caribou to the wintering grounds, especially since such a vast number of animals moved southward east of the main settlements, it seems quite doubtful

that the people could possibly have killed 10 percent of the animals. This type of reasoning implied that there probably was a much greater population in the northwest arctic than had been supposed. As such, the writer placed the minimum estimate for this herd at 300,000 animals (calves excluded) for June, 1964. It is not known at present whether or not the herd is continuing to increase; the relatively high incidence of morbidity found in recent years (Skoog, 1963b: 5) may indicate a reduced vitality and lowered annual increment.

Beaver Herd.--This small remnant herd inhabits the Beaver Mountains, which lie just to the westward of McGrath in Region II. Not too much is known about the distribution of these caribou during the various seasons, and the animals frequently are widely dispersed in small groups. The main wintering grounds seem to lie to the west of the Beaver Mountains primarily along the drainage of the upper Dishna River. Since above timberline areas are relatively scarce in this locale, I suspect that the main calving area lies in the midst of the Beaver Mountains. It is possible that animals sighted both southward toward Aniak and northward along the Nixon Fork may be from this herd. A survey of this group by the author in January, 1964, indicated a population of approximately 3,000 animals.

Chisana Herd.--During the high population level of Region V in the late 1920's and early 1930's, great numbers of caribou moved into the upper drainages of the Nabesna, Chisana, and White Rivers each fall. When the movements ceased in the early 1930's remnant groups of caribou probably remained on these northeastern slopes of the Wrangell Mountains. This herd is thought to have been derived from such groups. Little is known of the seasonal distribution of this herd, but its approximate range includes the mountains and foothills from the Nabesna River southeastward to the upper White River, extending northeast to the timbered lowlands of the upper Tanana River and of the middle White River. This range lies in the eastern corner of Region VI. It is thought that the main calving area lies between the upper Chisana and White Rivers, in the rolling hills to the north of Ptarmigan Lake. The wintering grounds probably are along the spruce-covered slopes to the northeast, and in the alpine areas.

The size of this herd has remained quite small since the mid-1930's, and was estimated at only 50 animals in 1949 (Scott *et al.*, 1950). That estimate probably was low, however, because adequate information was not available. Current information from guides in the area suggested that the population has been increasing steadily. Based upon that and upon brief aerial surveys, I estimated the herd at 3,000 animals (calves excluded) in June, 1964.

Delta Herd.--This remnant herd ranges the north slopes of the Alaska Range from the upper Wood River on the west to the Robertson River on the east, located in the northern portion of Region VI. The animals possibly are descendants from groups remaining after the high density of the Fortymile herd in the early 1930's. At that time a major segment of the herd moved through Delta Junction southward onto the north slopes of the Alaska Range and through Isabel Pass to beyond Paxon. This movement ceased about 1932, and animals have been reported in the area ever since. At present the main wintering grounds are located along the middle drainages of Little Delta River and Delta Creek. The calving takes place to the southward in the above-timberline areas drained by these streams. This herd has remained small since the 1930's and only in recent years has an increase been evident. In part, this increase may have been due to an ingress of animals from the Nelchina herd. In June, 1964, I estimated that the herd contained at least 5,000 animals (calves excluded).

Fortymile Herd.--The Fortymile herd constitutes the main population of Region V, and has been one of the most important herds in Alaska since prior to 1900. The traditional wintering grounds of this herd extend from the Fortymile area of Alaska eastward into the Ogilvie Mountains north of Dawson, and southeastward into the Sixtymile River area and the western portion

of the Dawson Range. The calving grounds extend from the White Mountains on the northwest to the highlands at the heads of the Salcha, Chena, and Charley Rivers. The main summering grounds are the rolling mountains and hills between the Yukon and the Tanana Rivers, encompassing the upper portions of the Chena, Salcha, Charley, Goodpaster, and Fortymile Rivers.

In April, 1963, the herd was estimated to contain approximately 30,000 animals. During the winter of 1963-64 the main portion of the herd wintered in the Ogilvie Mountains north of Dawson. In May, 1964, during aerial reconnaissance flights I found that most of these animals had moved northward into Region IV. All that remained on the Fortymile range then were several thousand animals that had wintered to the west in the upper Goodpaster River area, plus an undetermined number to the southeast. Subsequently it became apparent that many animals had returned to the region, and once again the herd is thought to number 30,000-40,000 animals.

Menasta Herd.--This small remnant herd is located in the northeast portion of Region VI, extending from the Mentasta Mountains southward onto the western slopes of the Wrangell Mountains. It is thought that this herd was formed at the same time as the Chisana herd and under the same circumstances, i. e., remnant groups of animals remaining after the large

movements of the Fortymile herd ceased about 1932. The herd does not range very far, wintering on the alpine areas and sparsely covered spruce flats surrounding Tanada Lake and calving on the slopes of Mount Sanford above timberline. The population seems to be increasing slowly, and it may have received an increment of animals from the Nelchina herd in recent years. The estimate for this herd in June, 1964, was 5,000 animals (calves excluded).

McKinley Herd.--This herd presently ranges the northern half of the center of habitation for Region II, extending from McKinley Park on the east to the north fork of the Kuskokwim on the west and to Rainy Pass on the south. The main wintering grounds encompass the spruce-covered flats near Lake Minchumina, extending southward onto the slopes of the Alaska Range. The calving grounds used most are located on the rolling hills above timberline between the Savage and Toklat Rivers. At present the herd seems to be increasing steadily and in June, 1964, I estimated it to number about 14,000 animals (calves excluded).

Mulchatna Herd.--This herd occupies the southeastern portion of Region II, ranging the upper portions of the Mulchatna and Stony Rivers. Little is known about the seasonal distribution of this herd. Large numbers of animals have been seen in winter near Whitefish Lake; in the winter of 1963-64 about 2,000 animals were reported in the Taylor Mountains. The calving area is unknown, but is thought to be somewhere in the hills northwest of

Lake Clark. Observations made by the author, plus reports from local residents and guides, suggested that this herd has been increasing slowly; I estimated the populations in June, 1964, at approximately 5,000 animals (calves excluded).

Nelchina Herd.--The Nelchina herd constitutes the main population of Region VI, and ranges predominantly over the center of habitation. The present wintering grounds are located mainly in the western half of the Nelchina range in the alpine areas adjacent to the Talkeetna River, Deadman Lake, and the upper Nenana River. The traditional calving grounds extend from Clarence Lake on the upper Susitna River southeastward to the upper Tyone Creek. In recent years this herd has made extensive movements into new areas, such as Mentasta Pass on the east, Isabel Pass on the northeast, and the Windy Pass-Yanert Fork region to the northwest. As the population increases these movements are expected to become increasingly diverse and extended; eventually an emigration to adjacent regions undoubtedly will occur. A census in February, 1962, disclosed that the population contained at least 71,000 animals. This herd has been the principal study population of the author since 1955 and will be discussed in detail later. In June, 1964, assuming a continued 9 percent annual increment, I estimated the size at 86,000 animals (calves excluded).

Porcupine Herd--This group of caribou ranges over the center of habitation of Region IV, extending from the upper Porcupine River northward to the Arctic Ocean and westward to the Canning and Sheenjek Rivers. The main wintering grounds encompass the upper drainages of the Porcupine and Peel Rivers, southward to the Ogilvie Mountains. The main calving area is located on the north slopes of the eastern Brooks Range, along the foothills of the Romanzof and British Mountains. This herd has been increasing steadily since the early 1950's, and is reaching a high point in its population. In June, 1961, a census by the author revealed that the herd numbered at least 110,000 animals (calves excluded). In the spring of 1964, it received an increment of about 15,000-20,000 animals from the Fortymile herd of Region V to the south, but many of these probably returned southward later, perhaps together with others of the Porcupine herd. Observations in eastern Alaska and adjacent Yukon have been too few in recent years to ascertain what fluctuations may have occurred. The historical information presented earlier, however, indicated a rather frequent interchange of animals between this herd and the Fortymile herd. Such interchanges probably will continue as long as either population of Regions IV or V remains high, facilitated by the overlap which occurs on the wintering grounds when both herds utilize the Ogilvie Mountains. I estimated the Porcupine herd at 140,000 animals (calves excluded) in June, 1964.

Alaska's caribou population today is distributed throughout the major portion of the regions lying north of the "Panhandle". The only sections without caribou are the Bering Sea coast between Dillingham and Kotzebue, many of the drainages of the lower Yukon and lower Kuskokwim Rivers, the Yukon and Tanana Flats, and the area bordering Cook Inlet and Prince William Sound, including the Chugach Mountains. All information available indicates that Alaska's caribou population is increasing steadily. The only herd that appears to be in danger of a population decline is the Arctic herd of northwest Alaska, where the animals generally are in poor condition and have a relatively high incidence of morbidity (Skoog, 1963b: 5); these factors may seriously hamper the productivity of the herd. Thus far, however, the herd has continued to have good calf crops and probably is increasing slightly or at least holding its own. The loss of animals in the Fortymile herd in recent years appears to be merely a shift of animals northward. I have estimated Alaska's total caribou population, as of June 1, 1964, at approximately 600,000 animals (calves excluded).

POPULATION CHANGES

The historical data examined indicated that Alaska's caribou population has fluctuated widely during the past 100 years or more. Even though the centers of habitation have been utilized continuously during this period, definite shifts in distribution and numbers have occurred both within and between the six regions designated. Individual herds have expanded and declined in size; few have remained stable for very long. As the herds increased, their movements have become increasingly complex, more erratic in timing, and more extensive in scope, with the opposite occurring as the herds declined. Major emigrations from one region to another have taken place when peak numbers were reached; other emigrations have occurred when animals from adjacent regions have intermingled during the winter. Such a dynamic movement pattern has characterized Alaska's caribou population. Indeed, such a pattern may well be a characteristic of caribou populations in general. Before proceeding with this discussion section, it might be well to quickly summarize the historical data relative to the five time-periods mentioned earlier.

During the period prior to 1875 it was apparent that a large herd ranged the Bering Sea coast from Kotzebue Sound on the north to Bristol Bay on the south. Another large herd moved along the entire Alaska Peninsula (Region I), ranging northward well into the Taylor Mountains and Mulchatna River drainage (Region II). In the arctic (Regions III and IV), caribou were plentiful along the coastal-plain year-round, but there seemed to be no indication that the sub-populations of these two Regions were at peak levels. The emigration of inland Eskimoes from the Meade River area suggested that the animals decreased in abundance in the northwest sometime between 1840 and 1880. East central Alaska (Region V) probably had a moderately high population in the eastern portion (Whitehorse area, Yukon), based on known caribou "crossings", while the sub-population of south central Alaska (Region VI) probably attained a peak level sometime between 1848 and 1885. In the latter region, a herd also was present on the Kenai Peninsula, which is thought to be an "overflow" area for large populations farther north. Alaska's caribou population was at a high level, with the center of abundance to the south and west.

By the next period, 1875-1895, considerable changes obviously had occurred. A large herd remained at the base of the Alaska Peninsula, but it no longer migrated to the southwest end. During the 1880's the seasonal migration across the

Kvichak River ceased, and apparently many of the animals stayed to the north (Region II). The huge numbers of caribou present earlier along the Bering Sea coast had largely disappeared by the late 1870's. Many of these probably had moved northward or eastward. To the east, there was evidence of caribou abundance along the Kuskokwim Mountains and the west slopes of the Alaska Range (Region II). To the north (Region III), caribou had become abundant again on the arctic slopes year-round, while remaining scarce to the south, in the Baird Mountains and the drainages of the Kobuk River. The northeast portion of Alaska (Region IV) continued to support large numbers of caribou, which were especially numerous along the arctic coast during the 1890's. In east central Alaska (Region V) the sub-population was shifting westward from the Whitehorse area, where caribou became scarce by the late 1890's. Caribou were particularly scarce along the Tanana River to its head and along the entire Copper River drainage (Region VI). The animals had mostly disappeared from the Kenai Peninsula, and only a moderately sized herd remained in the Talkeetna Mountains. Some of the animals from this region may have moved into the northeastern portion of Region II, where caribou apparently were numerous at this time. The information available suggested that Alaska's caribou population had become reduced in size by 1895, although the evidence is not conclusive. It is quite possible that the population may have shifted to more

isolated areas, as compared with the Bering Sea coast where travellers commonly were present to view any large-scale caribou movements that might occur. Farther inland such observations were not possible. The center of abundance probably encompassed central and northeastern Alaska.

Nevertheless, the numerous explorations by the Army Signal Corps and the U. S. Geological Survey during the late 1890's and early 1900's gave no indication of particularly large numbers of caribou in any of the interior areas. The period of 1895-1925 seemed to mark the growth of Alaska's caribou population from a "low point" about 1895 or so to a peak in the late 1920's. It is pertinent to note this increase occurred during the height of Alaska's early development, when miners penetrated every drainage, roads and towns were constructed, and forest fires destroyed vast acreage. The caribou remained absent from the Bering Sea coast. The Alaska Peninsula herd shifted to the southwest, and maintained a rather stable low-level during this period. Only remnant groups were present in the Kuskokwim Mountains (Region II) by the early 1900's, and only deep trails remained to attest to the former abundance there. Many of these animals possibly had crossed the Yukon and moved northward. The center of abundance for this region lay to the northeast (McKinley herd); there the animals increased steadily and had reached peak numbers in the mid-1920's. In the northwest (Region III) the

caribou shifted again away from the northern coastal plain to the central Brooks Range, and farther east. The numbers remained low to the west and south. In the northeast (Region IV) the animals also moved away from the coast, shifting westward to the central Brooks Range and also southward toward Region V. The latter region's sub-population increased rapidly during this period and by 1920 was estimated at a minimum of 568,000 animals by O. J. Murie (1935). Movements were widespread and contacts were made with the herds in Regions IV and VI. The herd in south-central Alaska (Region VI) remained rather small in size during this period, but during the late 1910's and the 1920's it received an influx of animals from Regions II and V seasonally. It seems apparent that Alaska's caribou population had attained a peak level in the mid-1920's, the center of abundance being to the east.

The next period, 1925-1945, was one of steady decline in caribou numbers, and again the distribution shifted. A series of bad winters (snow-crusted conditions) in the 1930's reduced the Alaska Peninsula (Region I) herd; a low point of only a few thousand animals was reached in the early 1940's, with the herd once again shifted to the northeast end. The McKinley herd (Region II) became reduced in numbers also, mostly because of emigrations northward into Region III during the late 1920's and the 1930's. The herd seemed to stabilize at about 30,000 animals during the

late 1930's and early 1940's. Elsewhere in Region II caribou were relatively scarce; they remained absent from the Bering Sea coast. The sub-population of northwestern Alaska (Region III) received an immigration of animals from Regions II, IV, and V during this period. At first the center of abundance remained in the central Brooks Range, but during the late 1930's shifted farther to the west. The herd was increasing in size, and by the mid-1940's had started to winter in the Baird Mountains and along the Kobuk River drainages to the south; once again caribou were seen along the northern Bering Sea coast. In northeastern Alaska (Region IV) the sub-population also received immigrations of animals from Region V, and had reached peak numbers by the early 1940's. It was clear that many of the animals had moved northward from east central Alaska. This emigration took place during the 1930's, and by the early 1940's the sub-population in Region V had reached a low point. In south central Alaska (Region VI) the sub-population probably reached its lowest level sometime during the late 1930's, perhaps in part due to an emigration to the northwest. At the close of this period (the early 1940's) there was much concern expressed in the reports of the Alaska Game Commission regarding the great decrease in caribou numbers since the late 1920's. Certainly all the herds south of the Brooks Range were at low levels, yet the arctic herds had increased

substantially. Nevertheless, it seems likely that Alaska's total population had declined in numbers, and had reached a low point during the mid-1940's. The center of abundance had shifted to the Arctic, particularly the northeast.

During the final period, 1945-present, the caribou numbers in Alaska generally have shown a steady increase. The sub-population in Region I has remained rather low, but definitely has been increasing in size. The McKinley herd (Region II) has declined in numbers since the 30,000 estimated by A. Murie (1944) in 1941 to the 14,000 estimated by me in 1964. There is no obvious explanation for this decline. To the northwest (Region III) the sub-population is at peak numbers, and its seasonal movements extend in all directions. A change seems imminent there in the near future. In the northeast (Region IV) the sub-population declined rapidly from the peak numbers in the 1940's to reach a low point in the early 1950's. An emigration undoubtedly occurred either to the eastward farther into Canada or to the westward into Region III. Since then, however, the herd has increased steadily, received immigrations from east-central Alaska, and once again is approaching a high point. In Region V the herd increased during the late 1940's and early 1950's, but lost animals to the north in 1957 and 1964. At present the herd appears to be of "moderate" size, with no obvious decrease or increase noted. In south-central Alaska

the main herd (Nelchina) has increased steadily during this period and is approaching peak numbers. Its movements have become widespread and somewhat erratic, and animals are extending into adjacent regions. A change is imminent here, too. At present, the center of abundance for Alaska's caribou population remains in the Arctic, but shifted now to the northwest.

Shifts in Distribution.

Nomadism appears to be a species characteristic of *Rangifer tarandus*, and the home range of a population would be difficult to define except in a temporary sense. The continual movements of the herds occasionally result in losses or gains due to straying and/or emigrations. This behavioral trait has plagued reindeer herders for centuries. Unless the animals are watched closely many of them are apt to leave their range and join other nearby reindeer or caribou herds or simply move into a new region. Such losses have occurred rather commonly during the history of the reindeer industry in Alaska; in fact, these often have been cited as one of the main causes of the rapid decline in reindeer numbers during the 1930's (Jackson, 1892-1898; Hadwen and Palmer, 1922; Burdick, 1940; Rood, 1942; Lantis, 1950; Hanson, 1952; Sonnenfeld, 1959). Bogoraz (1904) noted this problem among the Chukchee reindeer herders in eastern Siberia. Krebs (1959), in analyzing the records for the reindeer of the Mackenzie River delta, observed that straying and shifts in animals between the various herds constituted the most important cause of the population changes that occurred during the period 1938-1958.

Among caribou such changes are commonplace, and these have been documented for Alaska in a previous section. Major anomalies in the movement patterns of caribou herds, as well as

population shifts, the occupation of new ranges, emigrations, and the interchange of animals between herds, have been observed in Canada, also. Clarke (1940) and Banfield (1954) suggested that the intermingling of two or more caribou herds occurred on occasion. Banfield (1951) also noted the great changes in range utilization that had taken place since earlier historical times. Kelsall (1955) observed the intermingling of the Radium and Great Bear herds during the winter of 1952-53 along the Great Bear River (outlet from the lake to the Mackenzie River); the following spring that portion of the Radium herd moved northward with the other. He stated (p. 556), "Whatever ranges the Radium animals ultimately reached, they would not have been less than 300 miles distant from those on which they originated." Kelsall (1955) also described what he termed a "population shift" as occurring in one area of northwestern Canada, where the wintering population of the Radium and Rae herds dwindled from an estimated 215,000 animals in 1949 to only 35,000 in 1954: the decline was accountable only in terms of "....a shift of the caribou population from west to east." In the same paper (1955: 558) he noted another major shift, "The main body of animals apparently continued east and spent the following winter 300 to 400 miles east of the ranges which they had occupied for the previous several years. In doing this they re-populated, in a spectacular manner, areas which had been nearly devoid of caribou for fifteen years and more." These few observations

are quite consistent with those which have been recorded for Alaska's herds. Table 13 presents a summary of the major shifts that have occurred in the distribution of caribou in Alaska during the past 100 years. The data which have been presented illustrate well the erratic, shifting nature of caribou populations through time and space.

Table 13. Summary of major shifts in distribution of Alaska caribou during past 100 years. *

REGION	HERD/AREA	TIME	SHIFTS IN DISTRIBUTION NOTED
I	Alaska Peninsula	Late 1870's	Movements to SW of Port Moller stopped; center of abundance in NE.
		1880's	Movements across Kvichak R. stopped; emigration of animals N into Reg.II.
		ca.1900	Center of abundance shifted to SW.
		Early 1940's	Center of abundance shifted to NE.
II	Lower Kuskokwim River	1870's	Movements of Norton Sound herd (Reg. III) N-S across lower Yukon & Kuskokwim R's. stopped; many probably remained in II; center of abundance in south half of Reg. II.
	Kuskokwim Mountains	1880's	Probably emigration N across Yukon R. into Reg.III from Kuskokwim Mts.
	Mulchatna herd	1880's	Movements to Alaska Peninsula across Kvichak R. stopped; most of herd probably remained in upper Mulchatna R. area (Reg. II).
	Whole region	ca.1900	Center of abundance shifted to NE.
	McKinley herd	1906	Large movement across Yukon R. at Tanana.
		1925-31	Extensive annual movements E into Reg. VI; return each spring.
		1927	Emigration N into Reg. III.
		1932	Eastward movements stopped; winter range now to W.
		Early 1930's	Further emigrations N into Reg. III; center shifted S toward Rainy Pass.
		Late 1930's	Center shifted back to NE.
III	Arctic herd	1837	Abundant on arctic coast year-round.
		After 1837	Probably shift away from arctic coast.

* See Fig. 1 for geographic references.

Table 13. (cont.)

REGION	HERD/AREA	TIME	SHIFTS IN DISTRIBUTION NOTED
III	Norton Sound herd	1860's	Abundance in Norton Sound area and along lower Yukon & Kuskokwim R's.
		Early 1870's	Movements N-S across lower Yukon & Kuskokwom R's. stopped; herd left area; probably emigrated E into Reg. II and/or N into Arctic.
	Arctic herd	1883	Animals had returned to arctic coast.
		Late 1890's	Shift away from arctic coast, S and perhaps E; center of abundance along upper Colville R.
		Late 1910's	Shift E to central Brooks Range; probably formed separate herd, embracing portions of both Reg. III & IV; reduced herd remained in DeLong Mts. & along upper Colville R.
	Central Brooks Range	Late 1910's	Received immigration from Reg. IV.
		1927	Received immigration from Reg. II.
		Early 1930's	Received further immigrations from II & IV, and possibly from V.
		1940's	Shift to W; herd no longer separate.
	Arctic herd	1940's	Began to winter on south slopes of Brooks Range & along Kobuk R.; began to appear along Bering Sea coast N of Kotzebue.
		1960's	Extensive movements to all portions of region, except Seward Peninsula.
IV	Porcupine herd	Early 1900's	Shift inland from arctic coast; movements extended far to S; possible emigration into Reg. V.
		Late 1910's	Shift of animals W into Central Brooks Range.

Table 13. (contd.)

REGION	HERD/AREA	TIME	SHIFTS IN DISTRIBUTION NOTED
IV	Porcupine herd	1920's	Intermingling with Fortymile herd of Reg. V; split occurred, with one portion comprising the Central Brooks Range herd, together with animals from Reg. III.
		1930's	Received immigration from Reg. V.
		Late 1940's	Large emigration either E into NW Territories of Canada or W into Reg. III, or both.
		1957; 1964	Received immigration from Reg. V.
V	Fortymile herd	Late 1800's	Shift in wintering grounds to W from Whitehorse area.
		Early 1900's	Probably received immigrations from Reg. IV.
		1920's	Huge population; widespread, erratic movements; seasonal movements into Reg. VI, return each spring; intermingling with animals of Reg. IV.
		Early 1930's	Shift in winter distribution to N & NE; movements to Reg. VI stopped.
		1930's	Emigration N into Reg. IV.
		Late 1930's	Main wintering grounds again to SE.
		1957; 1964	Emigration N into Reg. IV.
VI	Nelchina herd	1870's	Decline in numbers from previous high; possible emigration NW into Reg. II.
		1918-31	Received seasonal influx of animals from Reg. II & V; left each spring; some may have remained; movements stopped in 1932.
		1960's	Large population; widespread, erratic movements; winter movements extending into Reg. II and to border o of Reg. V.

Total Numbers.

An examination of the literature has provided a good historical picture of the caribou distribution in Alaska. The task is much more difficult, however, when attempting to evaluate the fluctuations in numbers that have occurred. Most observations prior to 1935 suggested a much greater caribou population than is present now, yet accurate figures were not available. These observations pertained mostly to the 1910's and 1920's when obviously a large caribou population inhabited east central Alaska where much of Alaska's human population also lived. What of earlier times and areas not frequented by the early settlers? The records examined have shown there were periods of abundance and of scarcity periodically in various locations, with the centers of habitation being more or less the focal points for caribou distribution. There is evidence for a population high in the 1860's and the 1920's, and a low in the 1890's and 1940's, and these appear to be rather well documented. Considerable fluctuations have occurred, of course, in the numbers within any one region. In Alaska as a whole, however, it is difficult to say how much the total population actually changed during the so-called "highs" and "lows". The extent of such changes could have been obscured by the population shifts.

The magnitude of Alaska's caribou population prior to the 1910's remains essentially unknown. Certainly the native "drive-fences" and the deep, well worn trails noted in various areas were positive indicators of large caribou numbers, as were the direct observations of "huge" herds, but these are not adequate for a population estimate. The writer has found only one observation for this period that permits an extrapolation. As mentioned earlier, Nelson had stated (Nelson and True, 1887: 286) that in June, 1867, Willaim Dall had seen "...over four thousand skins of reindeer fawns hanging up in a village near Anvik...." This figure, together with current knowledge of the structure of caribou herds, can be expanded to a total estimate for the Norton Sound herd. This herd was of large size and ranged the Bering Sea coast from the Seward Peninsula to Bristol Bay prior to 1875, making seasonal crossings of the lower Yukon and Kuskokwim Rivers. The 4,000 calf skins probably were taken during the southward movement along the hills west of Anvik or perhaps during the crossing of the Yukon River. I have made the following assumptions: 1) the natives killed not more than 10 percent of the calf crop, and 2) the total number of calves constituted not more than 25 percent of the total herd (see later section,"Population Structure", Part III). The calculation from these indicates a calf crop of 40,000 and a

total herd of 160,000 animals (including calves). Such a figure appears quite plausible, if one considers the various accounts written, together with the area involved. A herd of that size, moving along the relatively narrow "peninsula" of hills between Norton Sound and the Yukon River, easily could have elicited the remarks noted by Nelson (Nelson and True, 1887) and have made the deep trails observed in later years. The estimate provides a reasonable base for one to judge the various statements made by many authors regarding the Bering Sea caribou herds.

Any discussion of caribou numbers in Alaska necessarily must center upon O. J. Murie's (1935: 6) census of a major portion of the east-central (Region V) sub-population in 1920. That was the only estimate known to be based upon a systematic procedure of counting, as compared with the usual "eye-ball" estimates. In the fall of 1920 he witnessed a large migration headed southeastward across what is now the Steese Highway, the center of this movement probably lying about 70 miles to the northeast of Fairbanks. The migration took about 20 days to pass, covering a strip 60 miles wide. Murie tallied caribou passing across a one-mile strip of the main pathway (40 miles in width). "During 8 of the 20 days about 1,500 animals in the main herd passed each day....and during the remaining 12 days about 100 animals a day." These counts totaled 13,200 for the one-mile strip, and expanded to 528,000 for the 40-mile

strip. "Allowing an average of 100 a day per mile for 20 days over the (remaining) 20-mile strip traversed by scattered bands, one computes that 40,000 represents the additional number passing at the edges of the 'run'." The final estimate thus totaled 568,000 animals. Murie commented further,

> In light of subsequent experience this figure seems conservative and it is safe to say that the herd numbered well over half a million, possibly much nearer a million....but the other herds would add many thousands to the total for Alaska and Yukon Territory together. This total, then, may number anywhere from 1 to 2 millions.

Most discussions concerning the relative size of Alaska's caribou population, today as compared with the past, have been based to certain extent upon the above estimates by Murie. Admittedly his method of estimating the total numbers in the 1920 migration was subject to considerable error. He had no way of knowing how uniformly the animals were spread along the 40-mile stretch used in the main extrapolation, or whether any animals were doubling back. Today, an airplane could have provided that information quite readily. Yet, even a 100 percent over-estimation still would indicate a herd of some 300,000 animals. Later observations by various members of the Alaska Game Commission (Annual Reports, 1926-1932, a and c) also indicated a

huge population in Region V, and the vast migrations into Region VI during the 1920's lend further support. For example, during the fall of 1927 one warden estimated that over 400,000 caribou passed southward near the mouth of the Delta River (tributary of the Tanana River) during a four-day period, and 500,000 to 700,000 during the entire two-week period of the migration (Alaska Game Commission, 1928a: 27). No basis for the estimation was described, however, and the numbers could have been over-estimated considerably. Anyone who has attempted to estimate large numbers of any animal is readily aware of the problems involved.

There can be little doubt that the Fortymile herd of Region V had attained a peak level by the 1920's. The exact size of this sub-population will never be known; Murie's estimates of between 500,000 and 1,000,000 are the best available. The extent of the range being utilized at that time I computed as being a maximum of 100,000 square miles, and so the density of caribou would have been between 5 and 10 animals per square mile. These densities are minimal, of course, because they assume a uniform spread of animals on the range; certain areas, such as the wintering grounds, would have had much greater densities. In Alaska and the Yukon as a whole, based upon Murie's description of caribou distribution, I have computed a maximum

utilized caribou range of about 250,000 square miles. Murie's estimate of 1 to 2 million animals for this region indicated an average density between 4 and 8 per square mile. These population densities are discussed more later.

Starting in 1948 (and continuing since then) the caribou research studies were expanded greatly in Alaska. Management techniques were developed for detecting and evaluating changes in distribution and numbers. The airplane has played an important role in this development. At first, caribou censuses were made throughout the Territory by extensive aerial reconnaissances, and it was thought that reliable estimates could be obtained from such direct counts. This type of censusing formed the basis for Scott's 1949 estimate of 160,450 for Alaska's caribou population (Scott et al., 1950). Later work, however, revealed that this census method definitely resulted in a gross under-estimation of numbers. In 1952, the Fortymile herd was estimated at not over 10,000 animals; in the spring of 1953 an accurate tally of the calving segment was obtained and the total herd size (excluding calves) was computed to be not less than 30,000 (Skoog, 1956: 62-63). In November, 1954, the major segment of the Nelchina herd was estimated at 13,550 animals, not including a few areas of the range that were not examined (Watson, 1954). Just prior to the intensive aerial census in February, 1955, the maximum estimate for the herd among various