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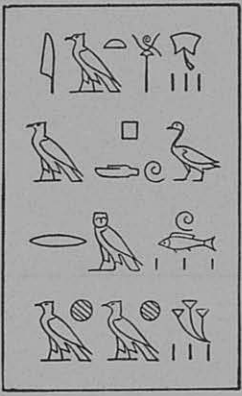

ECOLOGY OF THE TIMBER WOLF IN NORTHEASTERN MINNESOTA

by

VICTOR VAN BALLENBERGHE,
ERT W. ERICKSON, AND DAVID BYMAN

APRIL 1975 NO. 43

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Louis A. Krumholz, *Editor*
Water Resources Laboratory, University of Louisville, Louisville, Kentucky 40208

Consulting Editors for this Issue: **George B. Kolenosky, Ontario Department of Lands and Forests, Maple, Ontario**

Robert A. Rausch, Alaska Department of Fish and Game, Juneau, Alaska 99801

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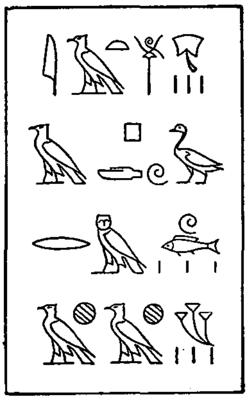

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FRONTISPIECE. An adult timber wolf (photo by James Brandenburg).

ECOLOGY OF THE TIMBER WOLF IN NORTHEASTERN MINNESOTA

Victor Van Ballenberghe,[1] *Albert W. Erickson,*[2] *and David Byman*[3]

CONTENTS

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INTRODUCTION

Alaska and northeastern Minnesota contain the largest and most significant timber wolf *Canis lupus* populations remaining in the United States. The status and management of wolves in Alaska have been discussed by Rausch (1964, 1971) and Harper (1970), but as of late 1974, wolves in Minnesota were not managed according to a statewide management plan and the ecological status of the species in the lower 48 states was largely unknown despite its official classification as endangered by the U. S. Department of the Interior.

The first ecological studies of the wolf in northeastern Minnesota were made by Olson (1938). Stenlund (1955) studied the wolf population on a 10,619-km^2 portion of the Superior National Forest and provided a valuable framework for subsequent studies. More recent ecological studies in the same area include those of Mech and Frenzel (1971) and Mech (1973). Prior to 1968 when the present study was initiated, no published accounts contained recent population data with management implications.

The purpose of this study was to gather data on the ecology, food habits, population density, and vital statistics of the wolf population on a portion of the 31,000-km^2 primary wolf range (Stenlund 1955) in northeastern Minnesota. Field work was conducted largely during the snowfree seasons of 1969, 1970, and 1971, but 178 of 625 man-days of field work occurred in the winters of 1969–1970 and 1971–1972.

ACKNOWLEDGMENTS

This study could not have been conducted without the substantial financial support of the Special Projects Foundation of the Big Game Club of Minnesota and Mr. Wallace Dayton, Wayzata, Minnesota. The cooperation of the Minnesota Department of Natural Resources and the U. S. Forest Service is acknowledged. Dr. U. S. Seal, Minneapolis Veterans Administration Hospital, analyzed blood samples from wolves and provided financial support for the senior author during preparation of the manuscript. Drs. J. R. Tester and D. B. Siniff reviewed portions of the manuscript and provided numerous helpful suggestions.

Lloyd Scherer, Lutsen, Minnesota, generously contributed his recollections of past wolf activities near Lutsen and permitted use of his land for research purposes. Carl Frank, Rochester, Minnesota, spent many hours afield at his own expense and contributed immeasurably to the data on numbers of wolf pups by recording howls of wild wolves and assisting in their analysis. William Peterson helped conduct deer pellet group surveys in the Jonvick deer yard and shared the resulting data.

THE STUDY AREA

This study was conducted in 2,606 square kilometers of primary timber wolf range in the Superior National Forest of Lake and Cook counties, Minnesota (Fig. 1). This area, between the Boundary Waters Canoe Area and the north shore of Lake Superior, is largely federally owned, but about 20 percent of the area consists of county, state, and private holdings. Access to most portions of the study area was provided by a network of gravel roads and trails built for logging purposes.

The physiography of the area is characterized by gently rolling tableland in the interior with more prominent ridges occurring along the shore of Lake Superior. Elevations range from 183 to 701 m above sea level. Precambrian granites and gabbros form the bedrock and shallow clay, clay loam, sandy loam or peat soils are characteristic of the glacial till (Thiel 1947, Grigal and Arneman 1970). Intrusives and flows covered by ferruginous silty and clayey lake deposits are characteristic of the shore of Lake Superior (Flaccus and Ohmann 1964). Numerous lakes and streams cover about 15 percent of the surface of the interior.

Climate is cool-temperate (Hovde 1941) with an average annual precipitation of 75.4 cm at Isabella 1 NW (U. S. Dept. Commerce 1960–1971). Mean monthly

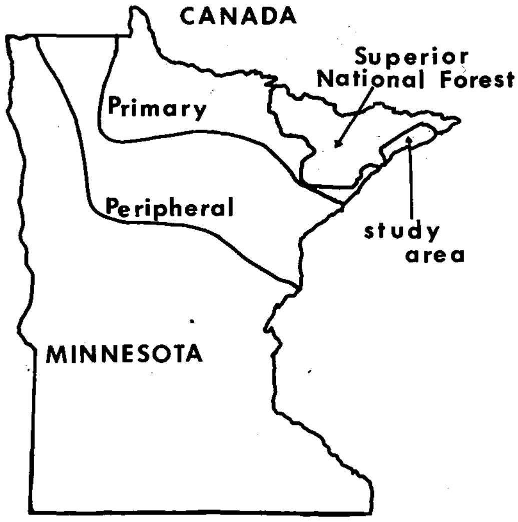

FIG. 1. Primary and peripheral range of the eastern timber wolf in Minnesota and location of the wolf study area.

TABLE 1.—TWELVE-YEAR AVERAGE MEAN MONTHLY TEMPERATURES AT ISABELLA 1NW AND GRAND MARAIS, MINNESOTA, WEATHER STATIONS, 1960–1971

Month	Isabella 1NW (°C)	Grand Marais (°C)
January	–15.5	– 9.7
February	–13.5	– 8.8
March	– 5.6	– 4.0
April	2.4	2.9
May	9.7	7.7
June	14.6	11.6
July	17.6	15.2
August	16.7	16.6
September	12.0	12.3
October	6.0	6.8
November	– 3.9	– 0.7
December	–11.2	– 6.8

temperatures at Grand Marais on the shore of Lake Superior are cooler in summer and warmer in winter than temperatures at Isabella 32 km inland (Table 1). The moderating effect of the lake is partly responsible for the occurrence of yellow birch *Betula lutea*–sugar maple *Acer saccharum* stands near the shore (Flaccus and Ohmann 1964) in an area predominantly composed of boreal conifer lake forest (Maycock and Curtis 1960, Buell and Niering 1957).

Extensive logging of the jackpine *Pinus banksiana* stands that originally dominated the upland sites has converted the vegetation into a mosaic of smaller stands of white spruce *Picea glauca,* black spruce *Picea mariana,* aspen *Populus tremuloides,* white birch *Betula papyrifera,* and balsam fir *Abies balsamea.* About 20 percent of the Isabella and Halfway districts of the Superior National Forest was cut between 1948 and 1967 (Peek 1971, unpublished doctoral dissertation, University of Minnesota, St. Paul, Minnesota). Large, continuous, lowland areas dominated by black spruce occupy portions of the western third of the study area but are more typical of southcentral portions of the Superior National Forest.

Moose *Alces alces,* deer *Odocoileus virginianus,* and beaver *Castor canadensis,* occurred in varying densities in the study area (Table 2). The entire study area lies within the northeastern Minnesota high density moose range (Ledin and Karns 1963) where Peek (unpublished doctoral dissertation) documented populations in excess of 0.8 moose per square kilometer. White-tailed deer populations have declined sharply in northeastern Minnesota since 1968 (Gunvalson 1971) but few data on the deer population exist for the study area. Spring deer densities of 4.9 to 5.3/km^2 occurred 129 km west of the study area in Itasca County in 1970 and 1971 (Table 2). An extensive winter deer yard has existed along the north shore of Lake Superior since the early 1900's (Krefting 1938, unpublished master's thesis, University of Minnesota, St. Paul, Minnesota; Erickson et al. 1961). Part of this, the Jonvick yard, occurred in the study area and supported 45 deer per km^2 in the winter of 1973 (Peterson 1973 pers. comm.). Active beaver colonies were numerous in the study area. Minnesota beaver population densities apparently increased statewide during 1971 (Stenlund 1971).

TABLE 2.—TIMBER WOLF PREY POPULATION DENSITIES IN NORTHEASTERN MINNESOTA IN OR NEAR THE WOLF STUDY AREA

Species	Census Area	Year	Population Density	Authority
Moose	Isabella[1]	1968–1969	0.6[4]	Peek 1971
		1969–1970	0.8	
Deer	Itasca Management Unit[2]	1970	4.9[5]	Karns 1971
		1971	5.3	
Beaver	Cascade River Drainage[3]	1969	0.3[6]	Stenlund 1971
		1970	0.3	

[1] 1,958 km^2 including the western one-third of the wolf study area.
[2] 6,066 km^2 in central St. Louis County, about 130 km west of the study area.
[3] 171 km of the Cascade River drainage located in the central portion of the study area.
[4] Moose per km^2, based on aerial surveys in early winter.
[5] Deer per km^2, based on spring pellet group surveys.
[6] Active colonies per kilometer of stream, based on aerial surveys in early autumn.

METHODS

Wolves were captured with steel-jawed foot traps, marked with radio transmitters (Fig. 2), and radiotracked from a light aircraft in this study. Trapping was conducted during the snowfree seasons of 1969, 1970, and 1971 to determine population characteristics including sex and age ratios, percentage of breeding females, and spacing of territories. Trapping methods followed those of Kolenosky and Johnston (1967) and utilized No. 4 Newhouse steel traps set on wolf trails or at scent posts and bait holes. Trap sets were made near logging trails and secondary roads on which wolf tracks or scats were observed. Captured wolves were anesthetized with intramuscular injections of phencyclidine hydrochloride (Sernylan, Parke–Davis Co.) and promazine hydrochloride (Sparine, Wyeth Laboratories) as prescribed by Seal and Erickson (1969). All wolves examined were classified as pups (less than 12 months), yearlings (12–23 months), or adults (24 months or older) on the basis of weight, upper canine length, and tooth wear. Teeth were not extracted from captured wolves for age determination since the single rooted premolars of many individuals were broken or missing. Pups captured prior to mid-October usually weighed less than 20 kg and had deciduous or partially erupted permanent canine teeth (Van Ballenberghe and Mech in press). Older wolves of both sexes that exhibited virtually no tooth wear were classified as yearlings. Females that displayed teat development similar to that of pups (teat elongation of 2 mm or less) were judged to be yearlings. Adult female wolves had elongated (5–9 mm), pigmented teats; those displaying signs of recent lactation were classified as breeding females. Adult females exhibiting tooth wear but no evidence of lactation were assumed to be nonbreeding adults.

All live-trapped wolves were marked with numbered metal ear tags, and 43 were fitted with radio transmitter collars. Collar weight and radio design were similar to those described by Mech and Frenzel (1971). Radio collars emitted pulsed signals in the 163 mHz range. All radio equipment was built by the Bio-Electronics Laboratory of the J. F. Bell Museum of Natural History, under the direction of Mr. V. B. Keuchle.

Instrumented wolves were radiotracked from a Cessna 172 aircraft according to the method described by Mech and Frenzel (1971). In addition, radiotracking from the ground was employed to determine locations of pups and the presence or absence of radiotagged adults at homesites. No effort was made to radiotrack wolves at night since flights could not be made, but daylight and dusk radio fixes were taken in addition to those obtained during midday

FIG. 2. Radiotransmitter collars, similar to the one being attached to this adult male, were used to determine the movements and territory boundaries of wolves in northeastern Minnesota.

in order to sample those periods of the day when adult wolves might be traveling. Home ranges for individual adult wolves were determined by the minimum area method (Mohr 1947) after plotting the radio fixes obtained with aircraft.

The presence and number of pups in each of 5 packs intensively studied by radiotelemetry in 1971 were determined by direct observation at rendezvous sites and by eliciting responses to human imitations of wolf howls (Pimlott 1960). Responses were recorded and replayed later if necessary to determine the number of individuals responding. The total number of wolves in each of the 5 packs was determined by howling responses and by direct observation of radiotagged wolves and their associates during the course of repeated aerial relocations. Best observations were obtained in December 1971 when a light snow cover was present.

Estimates of the density of the wolf population for all or part of the study area were obtained by delineating the location and boundaries of discrete pack territories, then determining the number of wolves per pack. Hornocker (1970) used a similar method to derive density estimates for mountain lions in Idaho. The territory boundaries of wolf packs not studied by radiotelemetric techniques were estimated by noting the location of capture, sex, and age of trapped wolves, and by observations from the air and ground of wolves and wolf signs.

Observed or reported instances of wolf mortality that occurred in the study area were recorded. Field personnel of the Minnesota Department of Natural Resources and the U. S. Forest Service contributed reports of tagged and untagged wolves killed in the area. Reported kills were subsequently examined, if possible, to determine the sex and age of the wolf and the cause of death.

Food habits of wolves were determined primarily from analysis of scats collected on roads and trails during other field phases of the study. Efforts to deliberately search wolf trails for scats were made June through September 1969 and January, February, and March 1970. All canid-like scats (Murie 1954) with a diameter exceeding 20 mm were collected except those of extreme age that displayed loss of form, complete dryness, and a chalky appearance. Scats between 20 and 25 mm in diameter were not considered to be deposited by other canids since coyotes and feral dogs were rare or absent in the study area. All visible scats, regardless of size or condition, were collected at several wolf rendezvous sites to assess the food habits of specific packs and their pups.

Scats were individually labelled, air dried, and autoclaved to kill ova of parasites. Hair, bone fragments, teeth, claws, seeds, and other food remains were washed free of amorphous fecal material, then degreased with carbon tetrachloride. Hair of prey species was identified by microscopic examination of cuticular scale patterns made visible by impressions of the hair (Williamson 1951) in a casein cement containing polyvinyl acetate. The manual of Adorjan and Kolenosky (1969) provided a source for comparison of scale impressions.

Definitions of several terms used throughout this paper closely follow the standard terminology of the canid literature. Murie (1944) used the term rendezvous to refer to specific areas used by a wolf pack during summer after the natal den was abandoned. Joslin (1967) referred to rendezvous sites and dens as summer homesites. The former were characterized by the trails, beds, and activity areas created by the adult and pup wolves that inhabited the site.

The term home range as used here follows the definition of Burt (1943). Scott (1947) and Sargeant (1972) found Etkin's (1964:21) definition of territoriality as "any behavior on the part of an animal which tends to confine . . . its movements to a particular locality" to be representative of territorial behavior in red fox *Vulpes fulva* populations. Noble's (1939) concept of territory as a defended area is not employed in this paper, but rather the broader definition of Etkin (1964) is adopted as being more applicable to wolf behavior, with the recognition that territories of wolf packs may tend to be mutually exclusive regardless of the mechanisms of territorial maintenance.

RESULTS AND DISCUSSION

Food Habits

From June 1969 through September 1971, 637 wolf scats containing remains of 757 prey items were collected. Most scats represented late spring and summer periods, but small samples were obtained in the winter and autumn of 1970 (Table 3). An additional 142 scats were obtained at 4 rendezvous sites occupied by 3 packs in summer 1970.

The principal prey items of wolves in the study area were deer, moose, and beaver (Table 3). Varying hare *Lepus americanus* (3%) and 5 genera of small rodents (3.6%) including *Tamiasciurus, Tamias, Synaptomys, Clethrionomys,* and *Microtus* contributed small fractions of the total occurrences. Remains of vegetation, principally the fruit and seeds of *Rubus* spp., *Vaccinium* spp., *Amelanchier* spp., and *Prunus virginiana,* and several mammal, bird, and fish species comprised nearly 14 percent of the food occurrences. Woodchuck *Marmota monax,* muskrat *Ondatra zibethicus,* porcupine *Erethizon dorsatum,* black bear *Ursus americanus,* wolf, and ruffed grouse *Bonasa umbellus* were among the various mammal and bird species represented.

Summer food habits were determined from those scats obtained from mid-May through late September. Deer (55.5%), moose (13.1%), and beaver (9.7%) comprised over three-fourths of the summer food occurrences (Fig. 3). Deer was the single most important food item.

The importance of deer in the summer diet of wolves was illustrated by a series of scats collected in the western portion of the study area during 1968–1971. Fifty-three percent of the prey occurrences in 54 scats collected in 1968 were deer (Halvorson 1969, unpublished honors thesis, Macalester College, St. Paul, Minnesota). Deer numbers declined substantially in this area following the severe winter of 1968–1969 (Mech and Frenzel 1971), but deer remained the most significant food in the diet of wolves in the summers of 1969 (51% occurrence) and 1971 (68%). By 1971, western portions of the study area were characterized by high moose densities, and deer densities that probably were less than 3/km², but wolves continued to heavily exploit deer as a food source. Similarly, Peterson (1955) found high use of deer by wolves in Ontario despite a ratio of prey biomass that favored moose.

These data indicate the importance of deer to wolves in northeastern Minnesota and illustrate the secondary contributions of moose and beaver. Other food items including vegetation, and several species of mammals and birds comprised the remainder of the summer diet. Wolves in this study relied more on miscellaneous food items than did wolves in other eastern boreal forest habitats (Table 4), but deer, moose, and beaver were clearly the mainstay of the summer diet.

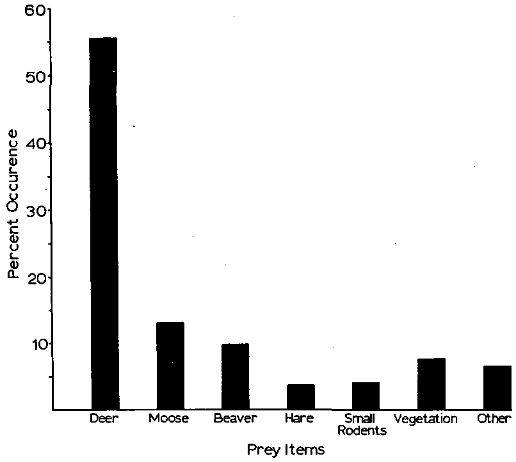

FIG. 3. Percentage occurrence of prey items in 532 wolf scats collected during the summers of 1969–1971.

Utilization of Deer Fawns

The analysis of 520 scats collected over a 3-year period, mid-May through late September, revealed the seasonal importance of deer fawns to wolves, and illustrated changes in the diversity of the wolves' diet during late summer. Prior to mid-June, few fawn remains occurred in the scats, but adult deer comprised about three-fourths of the total food items (Table

TABLE 3.—OCCURRENCES OF FOOD ITEMS IN WOLF SCATS COLLECTED IN NORTHEASTERN MINNESOTA, JUNE 1969–SEPTEMBER 1971

Year	Months Sampled	Number of Scats	Portion of Study Area	Deer	Moose	Beaver	Hare	Small Rodents	Vegetation	Other	Total Items
1969	Jun–Sep	164	Western ⅓	99	54	9	4	7	14	7	194
1970	Jan–Mar	69	Western ⅓	47	15	1	–	–	–	8	71
1970	Jun–Sep	124	Central–Eastern	76	11	23	17	12	14	17	170
1970	Oct–Nov	36	Western ⅓	25	3	7	–	2	1	1	39
1971	May–Sep	140	Central–Eastern	105	7	25	1	2	12	14	166
1971	Jun–Aug	104	Western ⅓	79	13	6	1	4	9	5	117
Totals		637		431	103	71	23	27	50	52	757
Percentage occurrence				56.9	13.6	9.4	3.0	3.6	6.6	6.9	100

TABLE 4.—SUMMER FOOD HABITS OF WOLVES IN EASTERN BOREAL FOREST HABITATS. DEER DO NOT OCCUR ON ISLE ROYALE, BUT ARE PRESENT IN VARYING DENSITIES IN ALL OTHER AREAS LISTED

Study Area Location	Number of Scats	Total Food Items	Percentage Occurrence, Deer, Moose, and Beaver	Percentage Occurrence, Other Food Items	Reference
Marten River, Ontario	226	225	97	3	Pimlott et al. 1969
Algonquin Park, Ontario	1,435	1,427	96	4	Pimlott et al. 1969
Pakesley, Ontario	206	216	88	12	Pimlott et al. 1969
Isle Royale, Michigan	205	253	85	15	Mech 1966
Northeastern Minnesota	532	647	78	22	This Study

5). From mid-June to mid-July, deer was still the primary species eaten but nearly half the deer remains in the scats represented fawns. After mid-July, the percentage occurrence of deer declined and only about one-third of the total deer occurrences in the scats consisted of fawns.

Deer fawns apparently became a significant food item for wolves immediately following the peak fawning period. Verme (1965) and Jackson and Hesselton (1973) found that most deer in latitudes approximating those of northeastern Minnesota gave birth during the third week of June. The abrupt decrease in both the proportion of fawns and the total number of deer taken after midsummer probably reflected decreased numbers or vulnerability of fawns, and exploitation of other, more readily available foods by the wolves.

Cook et al. (1971) and White et al. (1972) documented fawn–coyote *Canis latrans* relationships in Texas where predation related events accounted for 82 percent of the fawns that died, and deer comprised 70 percent occurrence in the coyote diet during June. These authors found that coyote predation on fawns decreased markedly by July as coyotes turned to ripening fruit, and fawns were able to escape if encountered. Although fawns apparently become less vulnerable after mid-July, wolf predation on them continued into autumn with fawns being taken about in proportion to their relative abundance (Pimlott et al. 1969). Thus, wolf predation, if wolves are abundant, can be a major mortality factor for fawns throughout the summer period. Pimlott (1967) suggested that such predation related mortality may not be compensatory with other mortality factors. White et al. (1972:904) recognized that: "Heavy predation on newborn ungulates apparently represents one of the most important loss factors and evolutionary forces in many populations."

Foods Consumed at Rendezvous Sites

The food habits of adult and pup wolves of specific packs were determined by analyzing scats collected at 4 rendezvous sites occupied during August and September 1970. Vegetation, consisting mainly of

TABLE 5.—OCCURRENCES OF ADULT AND FAWN DEER IN WOLF SCATS COLLECTED DURING SUMMER IN NORTHEASTERN MINNESOTA, 1969–1971

Time Period	Number of Scats	Percentage Occurrence of Deer	Number of Occurrences		Fawns/ Total Deer Occurrences
			Adult Deer	Fawns	
10 May–14 Jun	84	77	66	8	0.12
15 Jun–14 Jul	107	81	43	40	0.48
15 Jul–14 Aug	82	49	35	17	0.33
15 Aug–30 Sep	247	42	75	34	0.31
Totals	520	$\bar{x} = 55$	219	99	$\bar{x} = 0.31$

TABLE 6.—PERCENTAGE OCCURRENCE OF FOOD ITEMS IN WOLF SCATS COLLECTED AT 4 RENDEZVOUS SITES OCCUPIED BY 3 WOLF PACKS DURING AUGUST AND SEPTEMBER 1970

	Cross River, Site I (25 scats)	Cross River, Site II (60 scats)	Temperance River Site (32 scats)	Timber Lake Site (25 scats)
Deer	31.7	19.1	16.6	36.8
Moose	–	2.2	2.0	3.5
Beaver	12.4	45.4	7.4	22.8
Hare	4.8	–	–	1.7
Small Rodents	4.8	–	9.3	1.7
Vegetation	21.9	28.3	31.4	17.8
Other	24.4	5.0	33.3	15.7

fruit remains, constituted significant percentages of the total food items in each collection (Table 6). Deer comprised a significant but variable fraction of the diet of all 3 packs. Beaver were an important component of the diet of 2 packs, but moose were seldom utilized.

Adult and pup wolves apparently exploited the fruit-bearing shrubs common at all 4 rendezvous sites. Several wolf trails were observed leading to large patches of wild raspberries, and adult-sized scats containing nothing but raspberry remains were seen some distance from rendezvous site areas in the summers of 1970 and 1971.

Winter Food Habits

An adequate sample of scats to determine winter food habits was not obtained in this study, but 69 scats collected in winter contained percentages of deer and moose (66 and 21%, respectively) similar to those found in the summer scats. Stenlund (1955) found deer in 80 percent of 51 wolf stomachs collected in winter in northeastern Minnesota, and Pimlott et al. (1969) found that 90 percentage occurrence of the winter diet of wolves in Algonquin Park was deer.

Wolf Capture Data

Trapping effort during this study totaled 14,628 trap nights distributed over 3 field seasons (Table 7). Ninety-four wolves were captured 114 times. Trapping success averaged 128 trap nights per wolf capture, but varied from 57 to 219 during trapping periods of 10 to 119 days. Eighteen wolves including 13 adults and yearlings ultimately were recaptured, and 1 wolf was captured 3 times. The recapture rate for adults and pups was 20 percent. Additional recaptures probably would have occurred if intensive retrapping of areas previously trapped had been attempted. Limited trapping was conducted in areas trapped

TABLE 7.—DISTRIBUTION OF TRAPPING EFFORT, AND WOLF CAPTURES PER TRAP NIGHT OF EFFORT

Year	Field Season	Portion of Study Area Trapped	Area Trapped (km^2)	Total Trap Nights	Number of Wolf Captures[1]	Trap Nights per Wolf Capture
1969	1 Jun–27 Sep	Western	741	5,500	34	162
1970	14 Jun–24 Sep	Central	1,585	5,048	40	126
	25 Sep–11 Nov	Western	420	2,185	10	219
1971	1 May–24 Oct	Central	1,585	1,420	25	57
	25 Oct–3 Nov	Eastern	280	475	5	95
Totals				14,628	114	$\bar{x} = 128$

[1] 114 captures of 94 wolves.

TABLE 8.—TRAP NIGHT AND CAPTURE DATA OF WOLVES FOR THE SUMMER OF 1970 AND SPRING OF 1971. TRAPPING WAS CONDUCTED ON A 1,585-KM² AREA LOCATED IN THE CENTRAL PORTION OF THE STUDY AREA

Period Trapped	Number of Days Trapped	Trap Nights Employed	Number of Wolf Captures[1]	Trap Nights per Wolf Capture	Trap Nights per Other Carnivores Captured[2]
1970					
15 Jun–15 Jul	31	1,687	8	211	169
16 Jul–15 Aug	31	1,832	4	458	80
16 Aug–24 Sep	32	1,529	28	55	55
Totals	94	5,048	40	$\bar{x} = 126$	$\bar{x} = 83$
1971					
6 May–18 May	13	364	11	33	73

[1] 51 captures of 48 individual wolves.

[2] 66 other carnivores captured including 29 foxes.

in previous years, but of 21 wolves captured in such efforts in October–November 1970 and May 1971, 10 (48%) had been tagged previously.

The 1969 trapping data were not comparable to those of 1970 and 1971 since neck snares, and a variety of trapping scents were initially used. Trapping techniques were standardized after mid-July 1969.

The June–September 1970 trapping program represented the efforts of a single trapper tending 50–75 traps daily while attempting to sample a 1,585-km² area initially unfamiliar to him. Thirty-eight wolves were captured in 94 days; trapping success varied from 55 to 458 trap nights per wolf capture during 3 monthly periods (Table 8). One wolf was captured per 44 km² of area trapped. A success rate of 1 wolf per 33 trap nights was obtained when a portion of the area known to contain several packs was intensively retrapped for a 2-week period in spring 1971. Other carnivores including foxes, fishers *Martes penanti,* bobcats *Lynx rufus,* bears, raccoons *Procyon lotor,* and skunks *Mephitis mephitis* were incidentally trapped despite efforts to avoid such captures. Captures of carnivores other than wolves were most numerous in late summer when trapping efficiency for wolves was also greatest (Table 8).

Frequency distributions of recaptures for adult wolves tagged and recaptured in the same field season closely fit a constructed geometric series, but pup recaptures were best approximated by the Poisson distri-

TABLE 9.—OBSERVED AND EXPECTED FREQUENCY DISTRIBUTIONS FOR THE CAPTURES OF 106 WOLVES TRAPPED IN NORTHEASTERN MINNESOTA 1969–1971

ADULTS

Number of Captures	Observed Frequency	Expected Frequency (Geometric)	Expected Frequency (Poisson)
1	60	60.4	47.2
2	6	5.1	13.0
3 or more	0	0.5	5.8

PUPS

Number of Captures	Observed Frequency	Expected Frequency (Poisson)
1	30	28.6
2	8	7.9
3	2	1.4
4 or more	0	2.1

TABLE 10.—SEX, AGE, WEIGHT, AND CAPTURE DATA FOR 12 WOLVES RADIOTRACKED IN 1970 AND 1971 IN NORTHEASTERN MINNESOTA

Wolf Number	Sex	Age[1]	Weight (kg)	Pack Affiliation	Date Captured 1971	Location of Capture	Remarks
300	♀	A	25.4	Cross River	10 May	S10 T59N R5W	Lactating when captured
400	♂	A	35.4	Temperance River	6 May	S12 T59N R5W	Teeth worn but not excessively
550	♂	P	10.0	Temperance River	14 Aug	S29 T60N R4W	
175	♂	P	11.8	Temperance River	17 Aug[2]	S32 T60N R4W	
350	♀	A	28.2	None	6 May	S1 T59N R5W	Nonbreeding female captured 1970 & 1971
250	♀	Y	25.4	Onion River	14 May	S25 T60N R4W	Teeth unworn; teats undeveloped
450	♀	A	27.2	Lutsen	6 May	S14 T60N R3W	Lactating when captured
075	♂	A	34.0	Ward Lake	13 May	S6 T60N R2W	Captured in 1970
150	♂	Y	28.2	Ward Lake	12 May	S6 T60N R2W	Captured as a pup in 1970
700	♀	P	11.4	Ward Lake	17 Aug	S29 T61N R2W	
750	♀	P	12.7	Ward Lake	22 Aug	S7 T60N R2W	
850	♂	P	10.4	Dyer's Lake	12 Sep	S5 T58N R5W	

[1] A = adult, P = pup, Y = yearling.
[2] 1970.

bution (Table 9). This implied that pup recaptures were randomly distributed, but the probability of capture for adults did not remain constant. Tagged adults evidently learned to avoid traps after their initial captures.

Although trapping was not used as a census technique in this study, the results obtained here indicate that it might be used to census pups if trap set locations were randomized. Since the probability of successive captures of individual pups apparently remained constant (Table 9) the pup population could have been estimated by summing observed capture frequencies (Eberhardt 1969).

Radiotelemetric Studies

In 1969 and 1970, 26 radio collars were placed on wolves, but transmitter malfunctions reduced their effectiveness, and intermittent attempts at radiotracking produced little useful data on movements. In May 1971, 6 wolves from 5 packs were radiotagged with transmitters that functioned until at least late October. These wolves, plus 5 others radiotagged during the 1971 field season and 1 pup radiotracked in 1970 (Table 10), provided much of the data on movements, home range, and population density presented here. None of the radiotagged wolves experienced debilitating trap injuries that might have altered their movement patterns and none exhibited abnormal blood chemistry or disease signs when captured (Seal pers. comm.).

Two lactating females, 2 adult males, a yearling male, and a yearling female comprised the 6 wolves initially radiotagged in

TABLE 11.—DATA ON RADIOTRACKING FROM AIRPLANE, MAY 1971–FEBRUARY 1972

Month	Number of Flights	Number of Hours Flown
1971		
May	1	2
Jun	7	21
Jul	14	30
Aug	14	25
Sep	12	23
Oct	9	19
Nov–Dec	10	25
1972		
Jan–Feb	5	16
Totals	72	161

1971. These wolves and their associates were located at about 3-day intervals between 27 May and 22 October during 57 monitoring flights (Table 11). In addition, those wolves with functional radios were intermittently radiotracked from late November until late February 1972 when 15 additional flights were made. Radiotracking success was 99 percent from the air, and 629 fixes on radiotagged wolves were obtained in 1971–1972. Ground radiotracking attempts resulted in an additional 152 fixes. Untagged associates of the radiotagged wolves frequently were observed from the air after mid-September and efforts to visually locate radiotagged animals usually were successful if attempted when snow cover was present.

Movements and Home Ranges

The 6 adult and yearling wolves initially radiomarked during 1971 were relocated from 59 to 109 times each from early May to late October (Table 12). Their movements encompassed elongated home ranges of 49 to 135 km² with length:width ratios (Stumpf and Mohr 1962) ranging from 1.2 to 2.8. These 6 wolves were members of 5 breeding packs with adjacent territories linearly distributed along the north shore of Lake Superior (Fig. 4).

Home ranges of the radiotagged individuals approximated the territories of their packs. Two male wolves of the Ward Lake Pack (wolf No. 150 and No. 075) were radiotracked concurrently. On 20 (36%) of 56 occasions their radio locations were identical and their home ranges nearly coincided (Fig. 5A). Sargeant (1972) found that the home range of a red fox closely approximated its family group's territory, and Jordan et al. (1967) showed that a wolf pack maintains a common territory despite frequent separation of the pack into various subgroups. Radiotagged wolves in this study frequently were observed with untagged associates as well as with radiotagged pack members. Radiotagged adult and pup members of the Ward Lake Pack frequently were found together, but a yearling male pack member was often separated from his radiotagged associates

TABLE 12.—LOCATION DATA AND HOME RANGE DIMENSIONS OF 7 ADULT AND YEARLING WOLVES RADIOTRACKED MAY–OCTOBER 1971

						Home Range Dimensions		
Wolf Number	Age[1]	Sex	Pack	Dates Located	Number of Days Located	Greatest Length (km)	Greatest Width (km)	Total Area (km²)
300	A	♀	Cross River	27 May–22 Oct	71	15.0	11.5	135
400	A	♂	Temperance River	27 May–22 Oct	68	18.1	10.2	122
250	Y	♀	Onion River	27 May–22 Oct	70	13.6	7.4	80
450	A	♀	Lutsen	7 May–23 Oct	109	12.8	4.6	49
075	A	♂	Ward Lake	27 May–22 Oct	59	14.6	12.2	106
150	Y	♂	Ward Lake	27 May–22 Oct	63	14.6	10.2	93
350	A	♀	None	6 Jun–22 Oct	56	27.8	10.9	192

[1] A = adult, Y = yearling.

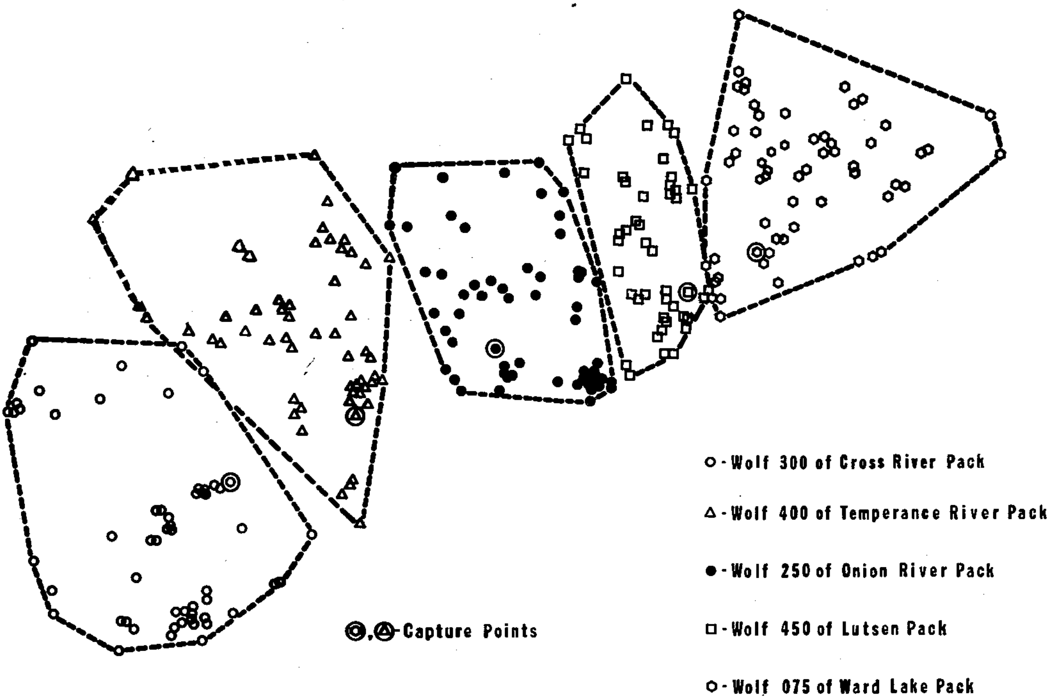

FIG. 4. Radiolocations and home range boundaries of 5 adult and yearling timber wolves radiotracked via aircraft, 27 May–22 October 1971.

(Table 13) by distances of 3 or more kilometers (Fig. 5B).

The home ranges of the radiotagged wolves of this study were not uniformly used, but rather the wolves appeared to frequently visit certain specific sites while avoiding others. High use areas included rendezvous sites and food resource areas; these acted as biological centers of activity (Ables 1969).

All 5 packs frequented dumps and refuse piles within their territories. From 1 August until mid-September, wolf No. 250 centered her movements around a dump site in the southeastern corner of her home range. She was radiolocated near the dump on 32 of 45 occasions during this period, and from mid-September until 22 October she made occasional forays back to the dump. Cursory observations of the distribution of wolf signs on the study area also suggested unequal use of the total area. Wolf signs were observed frequently on some roads and trails within the home ranges of the radiotagged wolves, but rarely observed on others.

Movements from Rendezvous Sites

Pups were present in all 5 packs in 1971, and movements of the radiotagged adults followed the pattern suggested by Murie (1944) in which individual adult wolves ranged widely during hunting forays but returned regularly to resting sites fre-

TABLE 13.—ASSOCIATION OF 4 RADIOMARKED WOLVES OF THE WARD LAKE PACK, 17 AUGUST–22 OCTOBER 1971

Wolf Number	Age	Number of Days Located With One or More Radioed Associates	Days Located when Independent of Associates
075	Adult	21	6
150	Yearling	19	13
700	Pup	25	4
750	Pup	22	7

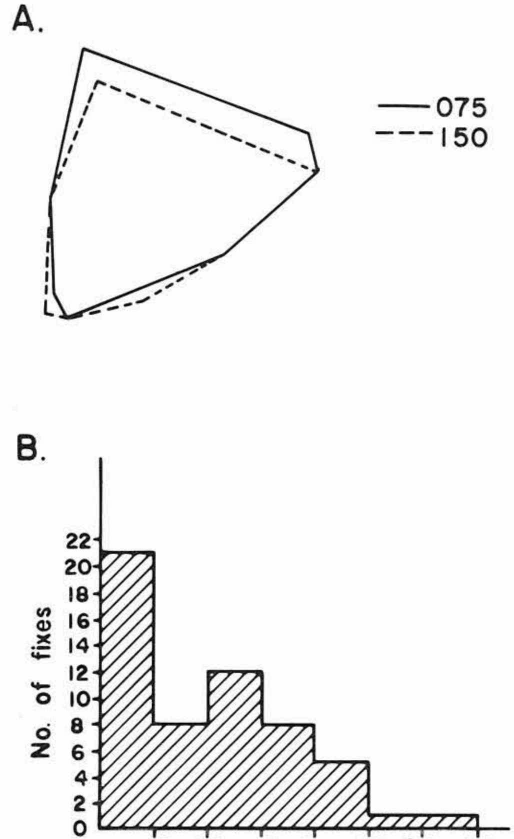

FIG. 5. A. Home range boundaries of male wolves No. 075 and No. 150, May 1971–February 1972. B. Distribution of distances observed between male wolves No. 075 and No. 150 on 56 days, 27 May–22 October 1971.

FIG. 6. A rendezvous site occupied by the Temperance River Pack in 1970. The rendezvous sites observed in this study were located on both upland and lowland sites sparsely vegetated with shrubs and trees.

quented by the pups (Fig. 6). The adult wolves in this study frequently were absent from the pack rendezvous sites during the daylight hours and were found to range up to 13 km from the site (Table 14). Histograms of activity radii around rendezvous sites of radiotagged wolves (Fig. 7) indicate that movements of adults away from the rendezvous sites often were in excess of 3.2 km except for wolf No. 450. The 49-km^2 territory of the Lutsen Pack was substantially smaller than the territories of the other 4 packs and this reduced the maximum linear movements possible for pack members.

Irregular attendance at homesites was characteristic of females with young as well as adult males; this contrasts with Murie's (1944) observation that female wolves seldom left their litters. Female wolves No. 450 and No. 300 were both absent from their dens when captured in early May, and No. 450 was regularly located away from her den after mid-May (Table 14). However, the 1.4-km mean distance she ventured from the den during this period was much less than the 3.2-km mean distance she traveled from a rendezvous site occupied by the pack later in the summer.

The activities of the wolves when they were absent from their homesites are unknown, but presumably they were hunting. Kolenosky and Johnston (1967) and Joslin (1966, unpublished master's thesis, University of Toronto, Toronto, Ontario) suggested that wolf family groups spent most of their inactive time at homesites, and Murie (1944) observed that wolves returned regularly to such sites to rest. Patterns of rendezvous site occupancy at night are poorly understood since radiotracking or direct observations then are difficult to conduct.

Movement data were obtained for 5 radiomarked pups including 3 members of

TABLE 14.—HOMESITE ATTENDANCE OF 5 ADULT WOLVES IN THE SUMMER AND AUTUMN OF 1971

							Location When Absent From Site		
Wolf Number	Sex	Name of Homesite	Dates Homesite Occupied	Number of Days Data Obtained	Occasions Present at Site[1]	Occasions Absent	Number of Days Located	Mean Distance From Site (km)	Max. Distance From Site (km)
300	♀	Cross R., Schroeder	19 Jul–3 Aug 14 Aug–13 Sep	47	28	34	11	6.4	10.6
400	♂	Blind Temperance	12 Aug–9 Oct	56	23	44	15	6.1	13.1
450	♀	Lutsen Den	8 May–30 Jun	33	19	25	7	1.4	2.4
450	♀	Poplar R.	16 Aug–26 Sep	34	22	13	11	3.2	5.4
075	♂	Murmur Creek	15 Aug–8 Sep	21	1	24	13	3.7	7.0
150	♂	Murmur Creek	15 Aug	22	2	28	14	5.1	7.7

[1] 1–2 locations per day determined.

the 5 packs intensively studied in 1971 (Table 15). Radiomarked pups usually were either regularly present at rendezvous sites during the daylight hours or were present as often as absent. Their forays from the sites extended as far as 6.9 km, but the mean distance they ventured was less than that of the adults (Tables 14, 15). During occupancy of the rendezvous sites, pup movements did not increase in magnitude as summer progressed; movements of 3 km or less from the sites were common over the entire observation period (Fig. 8). Pups were not radiotracked prior to mid-August, and their movements between birth and the time of capture were not determined. Their physical capabilities prior to mid-August, however, seemingly would preclude much individual movement despite their ability to move short distances as a group (Joslin 1967).

Litters did not always travel as a unit during forays from rendezvous sites. Pups of the Temperance River Pack were observed split into 2 groups separated by 4 km on 1 September 1971. Similarly, the 2 radiotagged pups of the Ward Lake Pack were frequently separated; on 14 September 1971 they were radiolocated 8.7 km apart.

Joslin (unpublished master's thesis) reported periods of rendezvous site occupancy that averaged 17 days in August and September in Algonquin Park, Ontario. The radiomarked pups in this study did not move between sites nearly as often; the minimum time spent at any site was 25 days, the maximum was 59 days (Table 15). Final abandonment of rendezvous sites by the pups occurred as early as 8 September, and pups of all 5 packs had begun to range widely by 10 October. The presence of a large food source in the form of a moose carcass, moose entrails, and a garbage dump initially attracted the pups of the Cross River, Temperance River, and Ward Lake packs, respectively, from their rendezvous sites. Movements of pups subsequent to utilization of these food sources were extensive and similar to those of the adult pack members. Following rendezvous site abandonment, the radiomarked members of all 5 wolf packs and their associates ranged widely throughout their territories,

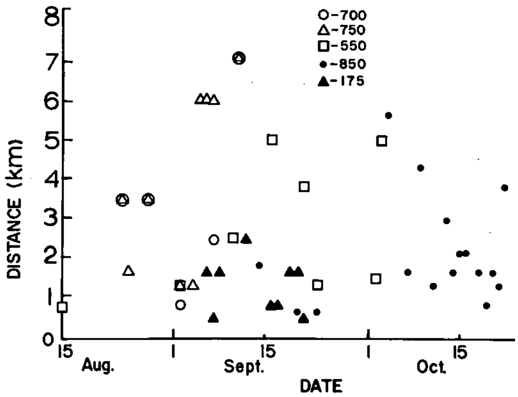

FIG. 8. Distances traveled from rendezvous sites by 5 radiotagged wolf pups, August–October 1971.

and all but the Onion River Pack ventured up to 2.4 km farther north than they had during the summer months.

Movements of 1 radiomarked pup including occupancy of the rendezvous site, initial forays from the site, and movements after site abandonment are illustrated in Fig. 9. Similar movements were typical of all radiomarked pups, but the dates of extended forays were somewhat earlier for wolf No. 750.

Variation in the dates of final rendezvous site abandonment may be a function of varying stages of physical development of the pups. The Ward Lake Pack which left its rendezvous site by mid-September was known to contain 4 precocious pups on 3 June; 3 of these weighed 11.3–12.7 kg when captured in mid-August. The Temperance River Pack, in contrast, contained 1 pup which weighed only 4.5 kg in mid-August and that pack did not abandon its last rendezvous site until the second week in October.

Extensive movements of packs following abandonment of their rendezvous sites appeared characteristic. These early autumn movements frequently found individuals and packs at the limits of their territories; the Cross River and Temperance River

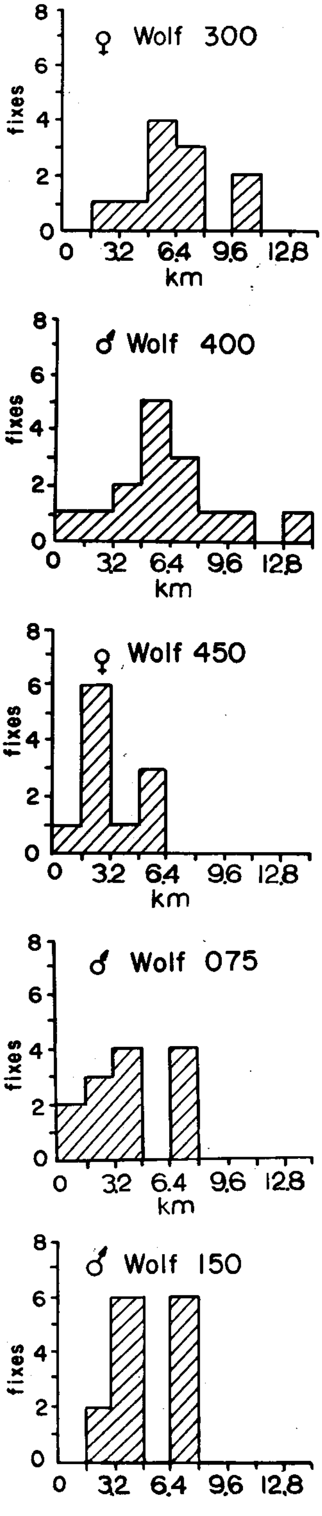

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FIG. 7. Frequency distributions of adult wolf activity radii around pack rendezvous sites.

TABLE 15.—HOMESITE ATTENDANCE OF 5 WOLF PUPS RADIOTRACKED IN 1970 AND 1971

							Location When Absent From Site		
Wolf Number	Sex	Name of Homesite	Dates Homesite Occupied	Number of Days Data Obtained	Occasions Present at Site[1]	Occasions Absent	Number of Days Located	Mean Distance From Site (km)	Max. Distance From Site (km)
700	♀	Murmur Creek	15 Aug–8 Sep	21	20	6	5	3.4	6.9
750	♀	Murmur Creek	15 Aug–8 Sep	18	9	12	9	3.8	6.9
550	♂	Blind Temperance	12 Aug–9 Oct	54	47	18	8	2.6	4.8
175	♂	600 Road (1970)	22 Aug–23 Sep[2]	18	8	10	9	1.4	2.4
850	♂	Dyer's Lake	13 Sep–22 Oct[2]	34	19	19	16	2.1	5.4

[1] 1–2 locations per day determined.
[2] Field work terminated 23 September 1970; 22 October 1971.

packs were observed at a moose carcass and a moose entrail pile, respectively, in areas unoccupied by either pack during the summer period. Significantly, a lone wolf radiotracked during autumn (No. 350) also moved extensively beginning in late September, and on 20 October she was 5.6 km west of any previously recorded location. Late winter, with movements characteristic of the breeding season (Mech and Frenzel 1971), and early autumn appear to be the 2 periods when wolves undertake their most extensive seasonal movements.

Movements of a Lone Wolf

The movements of 1 additional wolf were monitored during the period of study of the 5 packs. This wolf, an adult nonbreeding female, was radiotagged in May 1971 within the territory of the Temperance River Pack. The 56 radiolocations subsequently obtained for her indicated a total home range of 192 km^2 including portions of the territories of 4 different packs. However, 79 percent of her locations were within a 70-km^2 area of intensive use that was essentially triangular in shape with the base parallel to the shore of Lake Superior and the apex between the ranges of the Temperance River and Onion River packs (Fig. 10).

From 6 June to 9 July, wolf No. 350 was located on 9 days. All locations were in the central and western portions of the area of intensive use. On 11, 13, and 15 July she was located in the extreme northeastern corner of her range, but by 17 July she had returned to the area of intensive use where she remained until 23 August. After 23 August, this wolf ranged widely from the northwestern to the eastern to the southeastern and southwestern corners of her range. On 23 September and 20 October, she traveled to within 0.8 km of occupied rendezvous sites of 2 different packs. Although this wolf was captured well within the territory of the Temperance River Pack, her total home range nearly overlapped the territory of the Onion River Pack and she was never detected near the Temperance River rendezvous site, nor was she ever observed with associates. Apparently, this wolf was not associated with a pack and existed as a solitary individual occasionally traveling into the territories of adjacent packs but living primarily in a pack-free area. Mech and Frenzel (1971) postulated a similar pattern of movement for lone wolves and Jordan et al. (1967) reported that unassociated wolves on Isle Royale behaved in a like manner.

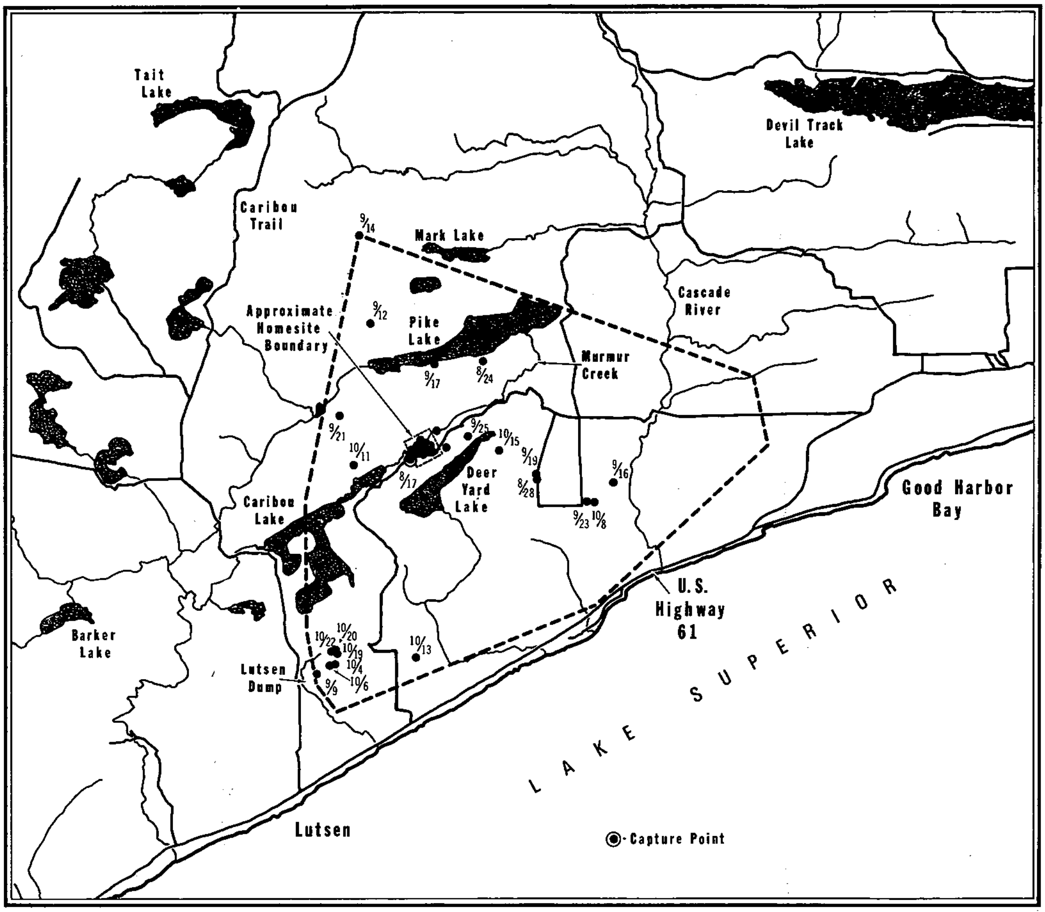

FIG. 9. Radiolocations of wolf pup No. 750, 17 August–22 October 1971. The dashed line delineates the home range of an adult male member of the pack, wolf No. 075.

Winter Movements

Radiotracking flights designed to monitor the winter movements and activities of the 5 wolf packs were begun on 30 November 1971. Radio signals from 2 of the 6 initially tagged wolves (wolves No. 400 and No. 075) were not received during the winter period, but radio contact with 1 or more members of each pack was maintained until at least mid-December since additional wolves had been radiotagged in late summer. Transmitter malfunctions and wolf mortality reduced the number of functioning radios to 3 when flights were terminated on 26 February 1972.

Movements of radiotagged wolves were not extensive during the winter and were concentrated in the southern portions of the packs' summer and autumn territories (Table 16). No shift from a summer to a winter range was observed as reported by Pimlott et al. (1969) and Kolenosky (1972), but rather a portion of the summer territory was utilized intensively during winter. Cowan (1947), Kuyt (1972), and Parker (1973) observed similar compression of wolf territories during winter in Canada and attributed them to concentration of prey. Slight extension of territories to the shore of Lake Superior including areas of up to 18 km^2 occurred for the Onion River, Temperance River, and Ward Lake packs

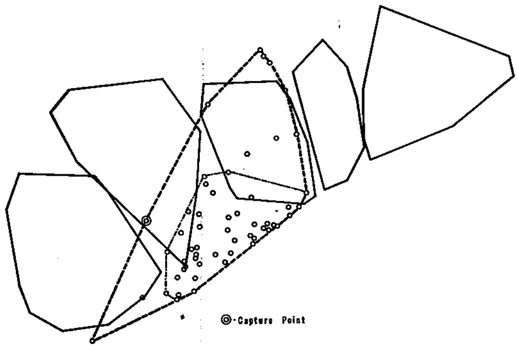

FIG. 10. Radiolocations of an adult nonbreeding female wolf in relation to the territories of 5 resident wolf packs. The lighter dashed line represents an area used intensively by this wolf.

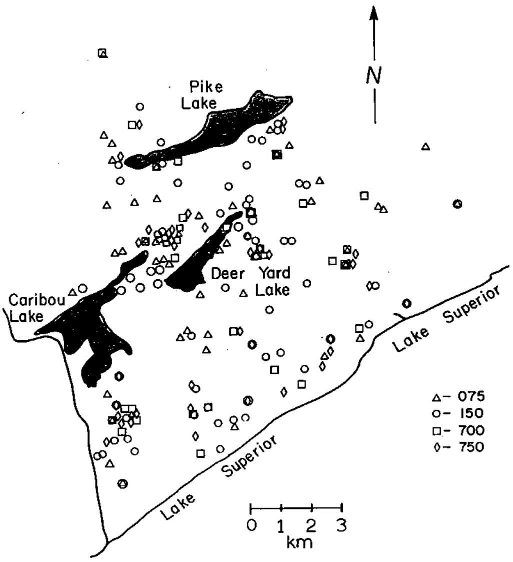

FIG. 11. Radiolocations of 4 wolves of the Ward Lake Pack, May 1971–February 1972.

(Table 16). During winter, none of the radiomarked wolves was located farther than 9 km inland from Lake Superior; movements were confined to elongated areas parallel to the shore.

Integrity of pack territories was maintained during winter since radiotagged wolves were not located within areas occupied by adjacent packs. Three radiotagged wolves of the Ward Lake Pack were tracked for varying periods until late February 1972. The resulting 39 winter relocations coincided with the summer–autumn fixes and provided additional evidence that the home range of a wolf approximated the territory of its pack (Fig. 11).

Movements of Eartagged Wolves

Eighteen wolves eartagged during this study were recaptured or killed at intervals of 8 to 31 months after their initial captures. Straight-line distances between initial and final captures ranged from 1 to 15 km for 14 of these wolves (Table 17). One female was recovered 110 km from the point of her original capture. Pimlott et al. (1969) reported that movements of tagged wolves in Ontario ranged from 5 to 137 km over recovery intervals of 1 to 7 years.

Significantly, 3 of 4 wolves tagged as yearlings evidently did not disperse from the area of their original capture. Of 30 wolves of all ages tagged and released in 1969 in the western portion of the study area, only 1 was recaptured in 1970 when the central portion of the study area was

TABLE 16.—RADIOLOCATION DATA OF 5 WOLVES RADIOTRACKED IN THE WINTER OF 1971–1972

Wolf Number	Number of Days Located	Extreme Dates of Locations	Maximum Distance Between Locations (km)	Maximum Distance From Lake Superior (km)	Area Utilized Adjacent to Summer–Autumn Range (km^2)
250	15	30 Nov–26 Feb	8.3	2.2	13
700	14	30 Nov–26 Feb	13.0	8.8	–
750	15	30 Nov–26 Feb	10.2	3.4	–
150	10	30 Nov–30 Dec	10.4	3.4	16
550	9	30 Nov–29 Dec	6.9	8.0	18

TABLE 17.—RECAPTURE INTERVAL AND STRAIGHT-LINE DISTANCE TRAVELED BY 18 WOLVES TAGGED AND RELEASED IN NORTHEASTERN MINNESOTA 1969–1972. A = ADULTS, P = PUPS, Y = YEARLINGS

Wolf Number	Sex	Age at Initial Capture	Interval Between Captures (Months)	Distance Between Captures (km)
815	♀	A	31	20
117	♂	A	23	19
			12	42
393	♂	P	20	9
615	♀	Y	19	14
619	♂	A	18	9
			9	8
601	♀	Y	16	14
158	♀	A	14	9
167	♂	P	14	5
105	♀	Y	14	110
813	♂	A	14	26
109	♀	P	13	15
129	♂	A	13	7
171	♂	A	11	10
644	♀	Y	10	14
677	♀	A	9	1
641	♂	P	9	2
686	♂	P	9	7
660	♀	A	8	2

trapped. Apparently, little interchange of wolves occurred between the 2 adjacent areas and the resident wolves occupied restricted home ranges. However, 2 wolves, a male pup and an adult female known to be members of packs with territories that did not border on the north shore of Lake Superior were killed within 0.8 km of Lake Superior during winter.

Five wolves eartagged in 1970 were recaptured and radiotagged in 1971. A comparison of individual home range length (as revealed by radiotelemetry) with the distance between captures in successive years indicated no discernible relationship (Table 18). Home range length:recapture distance ratios ranged from 1.9 to 8.5 for the 5 wolves. Estimates of the home range dimensions of noninstrumented wolves based on recapture distances were not made in this study since only crude approximations could result.

Discussion of Data on Movements

Joslin (1967) and Kolenosky and Johnston (1967) have reported summer wolf movements in Ontario in habitats similar to those of northeastern Minnesota. Joslin (1967) relied on howling responses as an index to movements. He reported pack territories of up to 65 km^2 and pack movements that averaged 3.0 km between rendezvous sites, but he was unable to determine the extent of daily movements of individual adults. Kolenosky and Johnston (1967) monitored radiomarked adult and yearling wolves and found summer home ranges of 18 to 70 km^2 and daily movements of up to 5.6 km straight-line distance. These movements and home ranges were similar in magnitude to those observed in northeastern Minnesota during the present study.

The studies of Murie (1944), Stenlund (1955), Burkholder (1959), and Mech (1966) have demonstrated that during winter wolf packs are capable of moving 56 to 72 km in a 24-hour period and may occupy territories of up to 12,950 km^2. The

TABLE 18.—HOME RANGE LENGTH AND DISTANCE BETWEEN SUCCESSIVE CAPTURES OF 5 WOLVES TRAPPED IN 1970 AND RECAPTURED IN 1971

Wolf Number	Recapture Interval (Months)	Distance Between Captures (km)	Telemetry-Revealed Home Range Length (km)	Home Range Length/ Recapture Distance
350	10	14.4	27.8	1.9
075	9	7.7	14.6	1.9
175	9	2.2	18.1[1]	8.1
150	9	6.6	14.6	2.2
300	8	1.8	15.0	8.5

[1] Based on pack territory as indicated by Wolf No. 400.

inherent desire of wolves to travel (Stenlund 1955) has been interpreted by Mech (1966) as necessary for wolves to locate vulnerable prey. Although some wolf packs travel extensively and occupy large territories, Cowan (1947), Stenlund (1955), Pimlott et al. (1969), and Mech and Frenzel (1971) have shown that other packs apparently confine their annual activities to areas of 130 km^2 or less. The radiotagged wolves we studied occupied territories as small or smaller than the minimum territories previously reported in the literature.

The presence of large numbers of deer wintering along the shore of Lake Superior probably influenced the winter movements of wolf packs with territories bordering the lake. The data on winter movements presented here, although incomplete, suggest prolonged periods of occupancy of small areas near the shore of Lake Superior. Cursory observations showed few deer wintering farther than 3.2 km from the shore, and wolf signs on the interior lakes were notably scarce. Deer were very numerous near the shore; a portion of the territory of the Ward Lake Pack contained 45 deer per km^2 in the winter of 1973 (Peterson pers. comm.). Young and Goldman (1944) and Banfield (1951) suggested that wolf movements may be reduced when prey is abundant, and Kelsall (1968) indicated that wolves utilize the trail system of prey species to facilitate movements in deep snow. If these observations apply to Minnesota wolves, they may explain the reduced winter movements of wolf packs with territories bordering Lake Superior.

If the shore area draws deer from well within the interior, wolf packs with territories not bordering the shore could lose a substantial number of potential prey animals otherwise available during the snow-free months. That some of the interior wolves moved with the deer is substantiated by 2 observations of interior pack members killed by humans on the shore during winter. Similarly, the Cross River Pack was observed feeding on a kill in January 1972 within the territory of the Temperance River Pack. Such movements, however, probably were of short duration due to the apparent saturation of available space near the shore by resident wolf packs. Mech (1972) reported increased incidents of territorial trespass by wolves following a decline in prey density in northeastern Minnesota.

The spatial organization of the wolf packs in the study area (Fig. 4) indicated exclusive occupancy of discrete, nonoverlapping territories by separate packs during summer and autumn. The only radiotagged wolf known to venture into the territory of a strange pack was a solitary adult female (No. 350). The mechanisms responsible for pack spacing are unknown, but mutual avoidance through howling and scent marking (Joslin 1967) as well as active territorial defense (Murie 1944, Jordan et al. 1967) probably are involved. Opportunities to observe wolves at their territory boundaries were rare, but in September 1971 the Cross River and Dyer's Lake packs occupied rendezvous sites 1.6 km apart near their common boundary. Both packs utilized a refuse dump on the common boundary, but the radiotagged members of each pack were always on their own side of the dump. Howling responses from both packs could readily be elicited even at midday. Identical behavior by members of the Ward Lake and Lutsen packs was also observed. On 25 occasions, 1 or more of the 4 radiotagged Ward Lake wolves visited a dump on their western boundary but never were detected in the territory of the Lutsen Pack.

Year-to-year stability of wolf pack territories was indicated by some of the trapping and telemetric data presented here as well as by observations of local residents in the study area. Proposed locations of pack territories based on the 1970 trapping results proved substantially correct when the territories were defined by radiotelemetry in 1971. Most of the tagged wolves recaptured at intervals of 8 months or more were taken near their original capture points (Table 17) thus suggesting con-

TABLE 19.—SEX AND AGE DISTRIBUTION OF 121 WOLVES CAPTURED OR KILLED IN THE STUDY AREA 1969–1971

Year	Wolves Examined	Percent Pups	Number of Adults and Yearlings		Number of Pups	
			Males	Females	Males	Females
1969	33	42	8	11	7	7
1970	62	37	19	20	16	7
1971	26	46	9	5	6	6
Totals	121	$\bar{x} = 40$	36	36	29	20

tinued use of familiar areas. Four of 5 wolves tagged in 1970 and radiotracked in 1971 (Table 18) were also radiotracked for brief periods in 1970; all 1970 relocations were within the home range areas defined in 1971.

Mr. Lloyd Scherer, Lutsen, Minnesota, has kept detailed observations on wolves and wolf signs within the range of the Lutsen Pack since 1965. Two to 5 wolves have been present there during each of 9 years; his observations and the results of the present study indicated that reproduction occurred during at least 5 years. A similar but less detailed history is available for the Ward Lake Pack through reports of local trappers. Wolves have been present within the territory of that pack since at least the early 1960's.

Population Characteristics

Sex and Age Ratios

A sample of 121 wolves captured or killed in the study area from June 1969 to April 1972 was examined to determine the approximate sex and age structure of the wolf population. Included were 94 wolves live-trapped and released, and 27 additional wolves killed by local residents or captured by other researchers operating concurrently in the study area. Thirty-six adult and yearling males, an equal number of adult and yearling females, 29 male pups, and 20 female pups comprised the sample (Table 19). No significant shift in sex ratios or age groups was detected among the 3 yearly subsamples ($P < 0.01, \chi^2 = 2.23$).

Males and females were equally represented in the adult (19♂♂, 18♀♀) and yearling (17♂♂, 18♀♀) age groups, and the sex ratio among pups did not differ significantly from 50:50 ($P < 0.05$, $t = 1.27$) despite an apparent excess of males (29♂♂, 20♀♀). The even sex ratio among the adults and yearlings contrasted with Stenlund's (1955) observation that 64 percent of a sample of 156 Minnesota wolves were males.

The pooled sample of wolves contained 40 percent pups; each of the yearly subsamples also approximated this percentage (Table 19). Of the 72 nonpups examined, 35 were yearlings and 37 were classified as 2 years of age or older. Of these, few were judged to be "old" on the basis of extreme tooth wear. The calculated autumn age structure of the wolf population was 40 percent pups, 29 percent yearlings, and 31 percent adults; 69 percent of the population consisted of immature animals less than 19 months of age. The calculated percentages are approximate indicators of the actual percentages since some males may have been incorrectly aged. Female yearlings were aged by 2 criteria (tooth wear and teat development), whereas yearling males were aged only by tooth wear. Pups of both sexes, however, were readily distinguished from adults and yearlings on the basis of weight.

Eighty-three percent of 18 adult females displayed signs of lactation during the spring and summer of capture. Adult, lactating females captured in May and June bore unmistakable evidence of reproductive success, while those captured later in the summer retained elongated, pigmented, and slightly enlarged mammae.

The effects of capture technique biases on sex and age ratios observed among trapped wolves have not been evaluated in the literature. Pimlott et al. (1969), Stenlund (1955), and Rausch (1967) apparently assumed the various sex and age groups of wolves were trapped or shot in proportion to their relative abundance in the population. Stenlund (1955) found similar sex

Table 20.—Probable Sex and Age Composition of 5 Radiomarked Wolf Packs

Pack	Size of Territory (km²)	Total Members	Number Captured (1971)	Adults			Yearlings			Pups		
				Males	Females	Sex Unknown	Males	Females	Sex Unknown	Males	Females	Sex Unknown
Cross River	145	9	2	1	1	1	1	1[1]	–	–	–	4
Temperance River	140	8	3	1	1	–	2	–	–	2	–	2
Onion River	93	8	4	1	1	–	1	2	–	–	1	2
Lutsen	52	5	1	1	1	–	–	1	–	–	–	2
Ward Lake	122	10	4	1	2	–	1	–	2[1]	–	3	1

[1] Probable survivors of 1970 litters known to contain at least three pups each in September 1970.

ratios among samples of trapped wolves compared to those shot from airplanes. However, the results of this study indicated that adult wolves learned to avoid traps encountered after their initial captures. This suggests that pup:adult ratios calculated from trapping data may not be accurate in wolf populations subject to heavy trapping pressure.

Trapping pressure in northeastern Minnesota immediately prior to the initiation of this study was not heavy. From 1969 to 1971 only 8–12 wolves per year were known to be killed in the study area due to sport trapping activities. Since most of the 121 wolves used to determine the sex and age compositions presented here were obtained in discrete areas during the first 2 years of the study, and since adult wolves were not excessively trapshy prior to the research effort, no attempt was made to correct the data for possible biases.

Population Density

Forty wolves were identified as members of the 5 packs intensively studied through radiotelemetry in 1971. Pack sizes in December based on aerial observations of the packs ranged from 5 to 10 (Table 20); 4 of the 5 packs contained 8 or more members. The presence of these large packs in close proximity is unique among pack size reports in the literature (Mech 1970).

In 1971, 17 pups were identified in the 5 packs on the basis of howling responses obtained in August, September, and October. Ten of the 23 adults and yearlings present were captured in 1971; the known presence of these wolves along with observations of the packs in 1970 and 1971 were used to construct a probable sex and age structure of the packs (Table 20). The presence of a mated pair of adults in each pack was assumed when constructing the probable pack compositions. These adults, known to be present due to the occurrence of pups in each pack, were assumed to survive into early autumn 1971; 4 were captured during the previous spring and summer.

The probable age distribution and sex ratio of the pack members closely resembled the corresponding values calculated for the population in the entire study area. Pup, yearling, and adult percentages were 43, 28, and 30, respectively, and the sex ratio of adults and yearlings approximated 50:50. Nonbreeding adults were rare, and no evidence of more than 1 breeding female per pack was obtained during the trapping efforts.

In addition to the 5 intensively studied core packs, the presence of 6 peripheral packs was suggested by the presence and distribution of wolf signs in the study area and the capture of lactating females or pups in discrete and distant areas (Table 21). Two wolves in each of 2 peripheral packs were radiotracked during summer and autumn 1971. Their movements indicated the approximate territory boundaries of the Dyer's Lake and Clara Lake packs; the territory boundaries of the other peripheral packs were estimated after examin-

TABLE 21.—LACTATING FEMALES, PUPS, AND TOTAL WOLVES CAPTURED IN 1970 AND 1971 FROM 6 WOLF PACKS. THESE PACKS HAD RANGES LOCATED PERIPHERALLY TO THE RANGES OF 5 RADIOMARKED PACKS (SEE FIG. 12)

	Wolves Captured						
	Total		Lactating Females		Pups		
Pack Name	1970	1971	1970	1971	1970	1971	Remarks
Dyer's Lake	–	4	–	–	–	2	Territory not trapped in 1970
Manitou River	4	2	1	1	1	–	1971 trapping in June only, one yearling caught June 1971
Houghtaling Creek	3	–	–	–	3	–	Adults trapshy; territory not trapped in 1971
Timber Lake	6	–	–	–	1	–	Signs of large pack observed in area June–August 1971
Clara Lake	4	2	1	–	–	–	Abundant signs throughout summers 1970–71, 3 adults escaped from traps
Devil's Track	1	2	–	–	–	1	Abundant signs of large pack in area Sep–Oct 1971; 7 wolves observed in December 1971

ing the distribution of signs and the location pattern of captured wolves.

The known territories of the 5 core packs in relation to the approximate territory boundaries of 6 peripheral packs are shown in Fig. 12. Estimated autumn numbers of wolves in each of the peripheral packs (Table 22) were based on animals captured or observed from the air within the respective boundaries of each pack territory. Peripheral packs with territories in the interior apparently occupied larger areas ($\bar{x} = 192$ km^2) than the core packs ($\bar{x} = 111$ km^2) with territories bordering Lake Superior. Interior packs apparently also contained fewer members, but estimates of their pack sizes probably were conservative.

If the summer and autumn territories of the 5 core packs are enlarged to include observed winter movements, the 40 members of those packs occupied approximately 552 km^2 during the year with a density of 13.7 km^2 per wolf. Density figures expressed as square kilometers per wolf within each pack territory ranged from 10.4 to 17.6. The 79 members of the 11 core and peripheral packs occupied 23.6 km^2 per

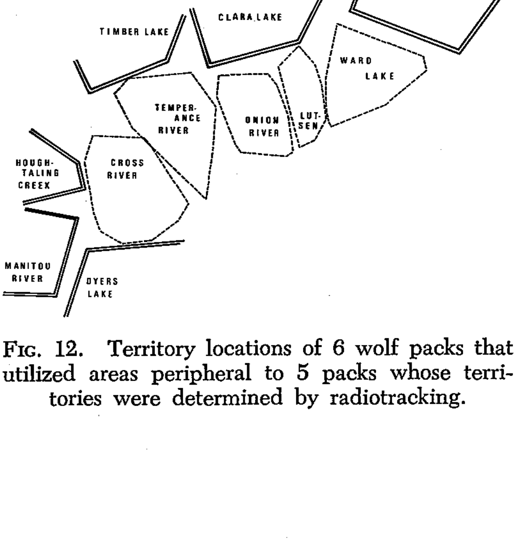

FIG. 12. Territory locations of 6 wolf packs that utilized areas peripheral to 5 packs whose territories were determined by radiotracking.

TABLE 22.—ESTIMATED 1971 PACK SIZE AND TERRITORY AREA OF THE 6 WOLF PACKS DESCRIBED IN TABLE 21

Pack Name	Total Members	Estimated Size of Territory (km^2)
Dyer's Lake	8	88
Manitou River	6	148
Houghtaling Creek	5	153
Timber Lake	8	194
Clara Lake	5	225
Devil's Track	7	244

TABLE 23.—REPORTED POPULATION DENSITIES OF TIMBER WOLVES IN EASTERN BOREAL FOREST HABITATS

Location	Intrapack Densities (km^2/wolf)	Population Density (km^2/wolf)	Authority
Isle Royale	26–36, 91, 135	18–26	Mech 1966 Jordan et al. 1967
Ontario	16, 16	26	Pimlott et al. 1969
Minnesota	26, 47, 47, 54–73	44	Stenlund 1955
Minnesota	23	44 or less	Mech and Frenzel 1971
Minnesota	10, 12, 12, 6, 18	24	Present Study

wolf in 1,865 km^2 comprising both occupied pack territories and interspersed areas between territory boundaries.

Pimlott (1967), Pimlott et al. (1969), and Mech (1970) reviewed the literature on wolf population densities and noted that winter densities of about 1 wolf per 25.9 km^2 represented the maximum values reported. Pimlott et al. (1969) and Jordan et al. (1967) observed densities of this magnitude in Algonquin Park, Ontario, and Isle Royale, Michigan, respectively. By contrast, densities in western Canada and the Northwest Territories have been reported at about 1 wolf per 259 km^2 (Cowan 1947, Kelsall 1957), except for local populations subject to winter compression. The population density observed in northeastern Minnesota during the present study, when expressed either in terms of intrapack density or total area density is as high as or higher than values reported in previous wolf studies in areas of eastern boreal forest habitats (Table 23). This may reflect a more accurate estimate due to the techniques employed in this study, but probably indicates the actual presence of a population of higher density. The census techniques used here depend upon accurate delineation of pack territories and careful enumeration of pack composition. This results in an absolute population estimate, the weakest component being enumeration of those packs observed infrequently or not radiotracked. Estimates of numbers in such packs are conservative since they can only be based on wolves captured.

The number of wolves verified as present in the 5 core packs represents a minimum figure since additional, undetected wolves could have existed in the area as loosely associated pack members. The 10 members of the Ward Lake Pack were never observed as a single group, and wolves which seldom associated with the 4 radiomarked members of the pack probably would not have been tallied. Lack of dense overstory vegetation allowed aerial observations of pups at some summer rendezvous sites, but a total count was rarely possible. Censusing of pups by eliciting howling responses tends to underestimate the number of pups due to the difficulty of identifying individuals when 5 or more pups howl simultaneously.

The presence of unknown numbers of wolves not associated with packs and therefore undetected in this study, would act to increase the calculated wolf density. Pimlott et al. (1969) estimated that up to 20 percent of the wolf population in some areas may consist of lone individuals, and Mech and Frenzel (1971) postulated that lone wolves shift about in areas unoccupied by packs. Such areas were present in the study area, but they were not extensive.

Mortality

Mortalities stemming from disease, injury, or starvation were undetected during the study period, but 1 instance of mortality as a result of intraspecific strife was recorded (Van Ballenberghe and Erickson 1973). There were 51 known instances of wolf mortality caused by humans in the study area involving both tagged and untagged wolves from June 1969 to April 1972

TABLE 24.—SEX AND AGE DISTRIBUTION OF 51 TAGGED AND UNTAGGED WOLVES KILLED IN THE STUDY AREA, JUNE 1969–APRIL 1972

	Adults and Yearlings			Pups		
Time Period	Males	Females	Sex Unknown	Males	Females	Sex Unknown
Jun–Dec 1969	3	–	4	1	–	–
Jan–Dec 1970	6	3	4	2	6	2
Jan 1971–Apr 1972	4	7	4	2	1	2
Totals	13	10	12	5	7	4

(Table 24). Mortality data for 1969 were incomplete and included only those wolves killed in the western third of the study area. Undoubtedly, some wolves killed in the study area were not reported, particularly after November 1970 when the Superior National Forest was closed to the legal taking of wolves. Three wolves with functional radio collars were shot by deer hunters in 1970 and 1971 and escaped to die or were intentionally left where they fell.

Thirty-seven (73%) of the 51 wolves killed were trapped or shot and 11 (22%) were killed by motor vehicles. All but 6 of the observed mortalities occurred from October to April; those killed during the summer months were either run over by vehicles or shot in close proximity to human dwellings. Pups comprised 31 percent of the identified mortalities. Mortality factors were not selective for males or females among either adults or pups, but sample sizes of each age group were small. Those wolves reported as being of unknown sex (Table 24) represented reliable reports of mortality by cooperating field personnel of the U. S. Forest Service and Minnesota Department of Natural Resources. Some might have been incorrectly aged, since pups cannot be reliably separated from adults by size after November (Stenlund 1955).

From 1969 through 1972, 106 wolves of all ages were tagged and released in the study area. All seemed capable of survival after release. Fifteen (14%) of the tagged wolves were eventually recovered including 6 of 66 adults and yearlings released (Table 25). The reported deaths of 11 wolves during the first year following their release indicated a minimum annual mortality of 10 percent.

Of 40 wolves in 5 radiomarked packs, at least 7 (18%), including 4 members of the Ward Lake Pack, were killed by humans in the winter of 1971–1972. Three of these were trapped and 1 was killed by a car. The Dyer's Lake Pack also lost 4 of an estimated 8 pack members present in late autumn 1971. In contrast, no members of the Cross River Pack were known to be killed in 1970 and 1971, perhaps due to the relative inaccessibility of their range. The observed mortalities in the radiomarked packs did not exceed the annual recruitment of the packs.

The mortality data for 1970 and 1971 indicated that an average of 21.5 wolves per year were killed in the 2,606-km^2 study

TABLE 25.—KNOWN MORTALITIES OF EAR TAGGED WOLVES IN NORTHEASTERN MINNESOTA, 1969–1971

Age When Tagged	No. Tagged and Released	No. of Tag Returns	Mortality Factors			Mortalities Within 1 Year After Capture (%)	Mean Survival after Release (days)
			Shot	Trapped	Hit by Auto		
Pup	40	9	3	4	2	89	121
Yearling–Adult	66	6	4	2	0	50	251

area. If the calculated population density of 1 wolf per 24 km^2 applied to the entire study area, the total population of 109 wolves experienced a minimum annual mortality of 20 percent. This rate probably was a better estimate of the true mortality caused by humans in the population than was the lower rate (10%) indicated by tag returns. Mortality rates based on tag returns probably are underestimated due to the avoidance of traps by adult wolves following their initial captures. Population turnover, however, as shown by the percentage of pups in the autumn population (40%), indicated that mortality rates determined both from tagged and untagged wolves were probably conservative.

The calculated kill on the study area was 1 wolf per 121 km^2. Since hunting and trapping appear to be the major mortality factors, mortality rates might fluctuate with hunting and trapping pressure. Significantly, nearly as many wolves were killed in 1971–1972 as in 1970–1971 despite closure of the 1971 Minnesota deer season and a federal ban on wolf trapping on the Superior National Forest.

Highway mortalities occurred regularly in the study area as a result of a dense wolf population in an area subject to considerable motor vehicle traffic both near the shore of Lake Superior and on inland gravel roads. DeVos (1949) reported a similar pattern of highway mortality for wolves in Ontario.

Pup Survival

Mech (1970:354) outlined a method of computing pup survival in a wolf population given: (1) the autumn age structure of the population, (2) adult sex ratio, (3) average litter size, and (4) percentage of adult females bearing litters. The assumptions involved included similar autumn and prewhelping proportions of adults and yearlings, a stable population, and accurate measurement of all "given" population parameters. Despite the questionable accuracy of the first assumption, this method can give a reasonable approximation of pup survival if accurate data on other aspects of the population have been gathered.

If this method is applied to the data of this study (assuming an average litter size of 6), it yields a pup survival rate of 44 percent to the age of 6 months. In the 5 core packs, a known 17 (57%) of a probable total of 30 pups survived until early winter. Three of the 5 packs each contained 4 pups in early autumn; 1 of these also contained 4 on 3 June indicating 100 percent pup survival for that pack during summer. This contrasted with the Lutsen Pack which lost 3 of 5 pups known to be present in May 1971.

Additional indicators of good pup survival in the study area were present including information on pack size. Rausch (1967) reasoned that large packs are due in part to high pup survival rates, and Mech (1970) reported that packs of 8 or more wolves were rare. Six packs of 8 or more wolves were identified in the study area and numerous pups were known to be pack members. No losses of pups were detected among those radiotracked in 1970 and 1971. The 1970 data suggested about the same number of pups in the autumn population of the 5 packs, therefore indicating similar survival rates over a 2-year period.

Effects of Hunting and Trapping

Although Pimlott et al. (1969) stated that losses of pups in Algonquin Park may have been as high as 75 percent during the first summer, Mech (1970) calculated a pup survival rate in the Algonquin Park population of 43 percent to the age of 8 months, assuming that an even sex ratio existed among breeding adults. Adjusting Mech's calculations to conform with the adult sex ratio actually obtained (24♂♂:15♀♀) indicates that pup survival was probably even higher. The Algonquin Park wolf population was not subject to mortality by humans during the study period.

Mech (1970:61), when discussing the effects of human exploitation on wolf populations, stated that "Exploitation . . . seems to stimulate both reproduction and pup

TABLE 26.—REPORTED POPULATION PARAMETERS OF EXPLOITED AND UNEXPLOITED WOLF POPULATIONS IN ONTARIO, ALASKA, AND MINNESOTA

Study Area	Exploitation Regime	Pups and Yearlings in Population (%)	Percentage Adult Females That Bred	Pup Mortality[1] 0–7 Months (%)	Yearling Mortality[1] 8–19 Months (%)	Authority
Ontario	Unexploited	48	59 (17)[2]	57	45	Pimlott et al. 1969
Alaska	Exploited	70	89 (89)	55[3]	31	Rausch 1967
Minnesota	Exploited	69	83 (18)	56	29	Present Study

[1] Based on calculations outlined by Mech (1970:354).
[2] Sample size in parentheses.
[3] Determined by aging 593 female wolf carcasses, then applying Mech's calculations.

survival. . . ." Rausch (1967) stated that mortality of pups rather than lack of their initial production accounted for the varying percentages of pups seen in diverse wolf populations. However, the data from Alaska, Ontario, and the present study (Table 26) suggest similar pup survival rates under varying regimes of exploitation. In addition, extensive observations of individual litters in unexploited populations (Murie 1944; Haber 1968, unpublished master's thesis, Northern Michigan University, Marquette, Michigan; Pimlott et al. 1969; Joslin unpublished master's thesis) suggested little or no detectable mortality during the period of observation.

There is evidence that prenatal and neonatal losses due to genetic and environmental factors account for a large proportion of the total mortality of dog pups (Anderson and Wooten 1959, Scott 1967). In wolves, as with many mammals, a pup's chances for survival to 6 months probably are good if it survives its first few weeks. If early mortality caused by genetic and environmental factors constitutes a major portion of the total pup mortality, pup survival during summer probably would not be affected by the degree of exploitation of the population. Possible mechanisms that might cause differential pup survival in exploited and unexploited wolf populations have not been suggested in the literature, but a direct relationship between food supply and pup survival has been proposed (Van Ballenberghe and Mech in press).

The population characteristics of northeastern Minnesota wolves presented in this study suggest that human exploitation has stimulated wolf productivity and produced an age structure considerably different from that of an unexploited population. Most population parameters and mortality rates of the Minnesota population approximated those of Alaskan wolves which were also subject to exploitation, but contrasted with the Algonquin Park, Ontario, population which was protected (Table 26). Yearling mortality, the proportion of juveniles, and the percentage of adult females that bred all appear substantially different in the Ontario population compared to the Alaska or Minnesota populations. Differences in litter size also exist in exploited and unexploited wolf populations (Mech 1970). Rausch (1967) reported an average litter size of 6, while Pimlott et al. (1969) found that Ontario litters averaged only 4.9. Stenlund (1955) reported an average litter size of 6.4 for Minnesota wolves subject to intensive hunting and trapping pressure.

Proposed population parameters of the exploited northeastern Minnesota wolf population are contrasted with those of a protected population in Algonquin Park, Ontario, in Table 27. Proposed values were based on available data of the present study and those of Pimlott et al. (1969). Stability of both populations was assumed. We believe the proposed values closely approximate actual parameters, and seasonal trends in both populations are accurately portrayed.

Autumn samples of 100 wolves included markedly different age structures in each population (Table 27). The Minnesota

TABLE 27.—PROPOSED POPULATION PARAMETERS OF EXPLOITED AND UNEXPLOITED WOLF POPULATIONS IN NORTHEASTERN MINNESOTA AND ALGONQUIN PARK ONTARIO

	Autumn Population	Wolves Harvested	Winter Mortality	Dispersal Losses	Postwinter Population	Postwhelping Population	Summer Mortality
Northeastern Minnesota[1]							
Pups (6–10 months)	40	8	1	0	–	80	40
Yearlings (11–22 months)	30	10	1	9	31	31	1
Adults (23 months +)	30	8	1	0	31	31	1
Totals	100	26	3	9	62	142	42
Algonquin Park[2]							
Pups	31	–	13	0	–	62	31
Yearlings	17	–	1	5	18	18	1
Adults	52	–	6	0	57	57	5
Totals	100	–	20	5	75	137	37

[1] Exploited population; based on data of the present study.
[2] Unexploited population; based on data of Pimlott et al. (1969).

population was reduced by 38 percent by late winter due to harvest losses, natural mortality, and dispersal. The Algonquin Park population, not subject to harvest, lost 25 percent of its autumn numbers to natural mortality and dispersal. About 80 and 62 pups, respectively, were born into each population; approximately 50 percent of those died, along with varying numbers of adults and yearlings by autumn.

If this model accurately represents seasonal population changes, as we believe it does, several differences in the dynamics of the 2 wolf populations are illustrated. Despite the presence of nearly twice as many adults in the Algonquin Park population in spring, fewer pups were born due to an adult sex ratio favoring males, fewer adult females that bred, and a smaller average litter size. Pup mortality rates in summer were identical in both populations but effective reproduction (percentage of pups born that survive to 1 year) was considerably greater in the exploited population (39 vs. 29%). Evidently, compensatory mechanisms (Errington 1946) act to reduce natural mortality of pups during their first winter in wolf populations subject to harvest. Apparently, natural losses among adults are also light in such populations, probably due to the presence of relatively few wolves of extreme age.

Pimlott et al. (1969) reported that dispersal was probably not an important factor in stabilization of the Algonquin Park wolf population density. Exploited and unexploited wolf populations may contain approximately equal numbers of 22-month-old wolves that could disperse (Table 27). Unharvested wolf populations, therefore, may not supply significantly greater numbers of potentially harvestable animals to peripheral areas than moderately exploited populations of comparable density.

Population Regulation

The proximate and ultimate factors acting to regulate wolf populations are poorly understood despite several studies designed to investigate them (Jordan et al. 1967, Pimlott et al. 1969) and much speculation based on scanty data (Mech 1970:316–325). The relative contributions that stress, food supply, territoriality, and human exploitation make to wolf population mechanics appears to be unique for each population. Pack density, mean pack size, prey abundance, and degree of exploitation vary considerably among wolf populations; those factors regulating 1 population might be relatively unimportant to the dynamics of another. Additionally, temporal changes likely affect the factors operating on a specific population. Fox (1971) inferred size stability of individual wolf packs over many years. He probably based his thoughts on the initial reports of the Isle Royale studies (Mech 1966), but the long-term history of the Isle Royale wolf population has been characterized by dynamic change rather than marked stability (Wolfe and Allen 1973).

Various environmental, behavioral, and physiological mechanisms might act to regulate the number of individuals per pack or the number of packs per area, or both, in any given wolf population. Limited data on territoriality, stress, and food supply exist for several wolf populations in Canada, Alaska, and the lower 48 States. Comparisons of a general nature may be drawn among these populations.

Territoriality.—Territoriality in timber wolves, as for animals in general, is one of the most important and complex factors regulating population performance. Its effects, however, are not always obvious. Brown (1969), in an extensive review of the regulating effects of territoriality in bird populations, described 3 hypothetical levels of population density in which territoriality would have varying regulatory effects. These ranged from low-density populations with widely spaced, noncontiguous territories, to dense populations in which territory owners occupied all optimum as well as marginal habitats. Only in the latter populations would some individuals be prevented from breeding and thus form a breeding surplus existing in and around occupied territories. Territoriality might regulate such a population if a significant surplus existed or through high emigration or mortality rates of individuals unsuccessful in establishing territories. Brown (1969: 304) concluded that many authors had considered territorial behavior to limit the breeding density of various bird populations, but critical evidence concerning surpluses was often lacking.

Sargeant (1972:229–230) discussed the spatial characteristics of red fox family territories and concluded: "The findings of this and other studies suggested that red foxes have an innate minimum and maximum spatial requirement that was manifested in their territoriality. Within these limits, territory size was a reflection of population density, which in turn was dependent on overall environmental conditions. As densities of red fox populations diminished, the size of territory of the remaining animals increased. Only when population densities fell below the level at which maximum territory size occurred did uninhabited areas appear in suitable habitat."

We believe that Brown's and Sargeant's concepts of territoriality have application to timber wolf population ecology, despite the paucity of data on wolf populations. It is clear that wolf territories resemble elastic discs (Huxley 1934) that are shaped primarily by population pressures and environmental resources. It is likely that such territories are entirely discrete only when minimum territory size is approached, probably due to the increased efficiency of patrolling small territories. Wolf populations exist over a wide range of densities with respect to occupancy of available habitat. In northeastern Minnesota, virtually no suitable wolf habitat was unoccupied. The presence of a significant surplus of potential breeders in addition to territorial occupants has, however, never been demonstrated in a dense wolf population. Extraterritorial wolves on Isle Royale are thought to be low-order social subordinates or senile individuals (Jordan et al. 1967). Thus, the role of territoriality, of itself, in regulating wolf populations appears minimal, despite contrary speculations by Murie (1944) and Stenlund (1955).

Stress.—The regulatory effects of social stress on a wolf population might be manifested at 3 distinct levels including the individual, the pack, and the population. Possible mechanisms at each level might function through physiological involvement of the endocrine system (Selye 1950, Christian 1959), behavioral factors resulting from social interactions (Schenkel 1947, Rabb et al. 1967), or epideictic displays (Mech 1970:322–323). Such mechanisms acting singly or in combination apparently act to reduce the potential productivity of dense wolf populations. Rausch (1967) observed a natality rate of 2.67 pups per adult in an Alaskan wolf population of low density. In contrast, the dense Algonquin Park population (Pimlott et al. 1969) produced only 1.11 pups per adult; stress factors evidently reduced the potential productivity of this population by 42 percent through proximate factors including an excess of adult males, a reduction in mean litter size, and failure of many adult females to breed (Mech 1970). Significantly, the summer survival rate of pups born in the Algonquin Park population was apparently unaffected by these stress factors (Table 26).

Studies of captive wolves (Rabb et al. 1967) have demonstrated that intrapack social stress during the breeding season prevented courtship fulfillment among social subordinates in large packs containing several potentially fertile females. Similar behavior has been suggested but not conclusively demonstrated on Isle Royale (Mech 1966). In natural populations, large packs frequently are split, thus allowing social subordinates to breed, but records of more than 2 litters being born into large, socially stable packs are rare.

The effects of interpack stress on a wolf population have been demonstrated in a unique natural experiment on Isle Royale. From 1959 to 1966, this island population varied from 20 to 28 wolves, a maximum variation of 21 percent from the 8-year average of 23 animals (Jordan et al. 1967). The social organization of the population was dominated by a single pack of 15–22 wolves during this period, but in late winter 1966 the pack disintegrated following the death of the alpha male. In 1967, the maximum population was 30 including a pack that immigrated to the island, and several instances of severe strife were recorded (Wolfe and Allen 1973). By 1969, the population had declined to 17 individuals, a 43 percent reduction in 2 years, presumably as a result of interpack strife and possibly emigration. The population built to only 18 wolves in 1970 (Wolfe and Allen 1973), and the pack stability characteristic of earlier years was not maintained, since 2 separate packs had partitioned the island.

Food supply.—A close relationship between population density and food supply has been suggested for several diverse carnivore species including the great horned owl *Bubo virginianus* (Rusch et al. 1972), lynx *Lynx canadensis* (Nellis et al. 1972), coyote (Clark 1972), and wolf (Jordan et al. 1967). Food supply might influence wolf population dynamics through the direct links of reproduction, mortality, and behavior, or it might interact with other regulating mechanisms including territoriality and social stress.

Pimlott (1967) suggested that 3.9 deer per km^2 with an annual productivity of 37 percent would be required to support a population of 1 wolf per 25.9 km^2 assuming wolf food habits similar to those in Algonquin Park, Ontario. Pimlott may have overestimated the minimum daily food requirements of wolves, but his calculations imply that declining deer densities in the presence of a dense wolf population may reduce wolf numbers to a level compatible with available prey.

Although several authors (Pimlott 1967: 276, Mech 1970:320) have indicated that stability of the Isle Royale wolf population occurred in the presence of abundant food, Jordan et al. (1967) inferred that pup starvation during years of poor moose calf production limited growth of the wolf population. However, no direct measurements of productivity or sex and age ratios have been made of that wolf population. If summer starvation occurred, pup mortality patterns on Isle Royale differed markedly from those in a similarly dense wolf population in Algonquin Park, Ontario (Table 26). The characteristics of the different prey species available to each population might account for these differences.

A direct relationship between richness of food supply and population density has been established for numerous bird species (Brown 1969) and several mammalian carnivores including the red fox (Ables 1969) and coyote (Clark 1972). For territorial species, this implies reduction of territory size in environments rich in food (Ables 1969), probably due to increased population pressures (Sanderson 1966). Minimum territory sizes are related to satisfaction of energy needs (McNab 1963), but may never be reached in socially intolerant species (Armstrong 1965). The literature available on wolves suggests that the interactions between food supply, movements, territory dimensions, and population density described for other species apply equally well to wolf ecology. Kuyt (1972) and Parker (1973) found that wolf densities could reach 1 per 18–21 km^2 in the presence of concentrated caribou populations of 176 per km^2. These wolf densities are about 24 to 44 percent higher than the density of 1 per 25.9 km^2 suggested by Pimlott (1967) as maximum for the species.

We suggest that the available data on the wolves of Isle Royale, Michigan, Algonquin Park, Ontario, and northeastern Minnesota indicate that food supply has been a primary determinant of the ultimate densities reached by these populations. Similar densities of major prey species and similar wolf food habits have produced similar wolf population densities in Algonquin Park and northeastern Minnesota despite marked differences in population age structures. Minimum territory sizes in both populations were less than 75 km^2. This suggests that reduced social stress resulting from exploitation, a disrupted social structure or the abnormally low average age of individuals in the Minnesota population was not the primary factor determining territory size or pack density. Large packs occupying small territories, reduced winter movements, and close association with wintering deer indicated that those Minnesota wolf packs with territories bordering Lake Superior were able to meet their energy requirements without the necessity of large territories and extensive movements. Interpack stress, if it occurred, did not block reproduction in the smaller packs nor did it prevent packs from existing in territories as small as 50 km^2.

It is significant that 40 wolves comprising the 5 radiomarked packs of this study occupied an area similar in size to Isle Royale where, despite a ratio of 30 moose per wolf, only 17 to 30 wolves dominated by a single pack have existed from 1959 to 1970. A lack of adequate numbers of vulnerable moose distributed uniformly over the island might be the most plausible reason why Isle Royale was not apportioned into several wolf pack territories.

Pimlott (1967) emphasized that contemporary biologists studying disturbed forest ecosystems often have a distorted view of wolf–ungulate relationships. He reasoned that adaptations between ungulates and their predators evolved in stable environments incapable of supporting high prey densities. An obvious exception to this was the American prairie which supported the densest prey populations on the continent. The accounts of early explorers, naturalists, and hunters (Young and Goldman 1944) indicated that wolves were exceedingly numerous on the prairie. A direct measure of their abundance is provided by the records of poisoning kills between 1855 and 1880 (Young and Goldman 1944:329–332). Strychnine treated baits set in restricted areas and tended by 2–3 men accounted for up to 1,000 wolves during a single winter.

Few, if any, of the North American wolf populations studied since 1940 have existed on a food base comparable to that of wolves on the American prairies prior to 1850. We suggest that biologists studying these populations have had distorted perspectives concerning the role of food supply in the population dynamics of wolf populations. Despite the documented existence of evolved mechanisms designed to lower the productivity of dense wolf populations, we believe that the available evidence indicates that environments rich in food lower the threshold of such mechanisms and are the ultimate factor accounting for the existence of dense wolf populations. The ultimate density that wolves might reach in environments containing truly an abundance of food remains unknown.

MANAGEMENT

Biological Input

Since the early 1940's, northern Minnesota has had the largest population of timber wolves remaining in the lower 48 states. Stenlund (1955) reviewed the population trends of wolves in Minnesota and concluded that the population in the Superior National Forest reached a peak in the period 1925–1940, then declined gradually until 1946. In 1947 and 1948, the population dropped sharply, probably due to widespread aerial hunting, then remained stable from 1949 to 1953. No data exist for 1954–1966, but Mech and Frenzel (1971) found that average pack sizes were significantly larger during 1967–1969 than during 1948–1953. This indicated an increase in the population some time during that period. The apparent increase may have occurred after bounty payments ceased on 30 June 1965.

The data of Mech and Frenzel (1971), Van Ballenberghe (1972, unpublished doctoral dissertation, University of Minnesota, St. Paul, Minnesota), and Mech (1973) enabled Mech (1973) to calculate the first objective population estimate of wolves in the Superior National Forest. Forest-wide wolf populations of 405 ± 20, and 388 ± 14 for the winters of 1971–1972 and 1972–1973, respectively, were calculated from data on 21 wolf packs occupying territories that comprised 39 percent of the Forest. These data indicated the presence of about 45 breeding wolf packs residing in one-sixth of the total wolf range of the state. The wolf population in the Forest during the early 1970's was 40 percent higher than the population estimated there by Stenlund (1955) 20 years earlier.

The number of wolves present in the entire state of Minnesota has never been accurately established. Early estimates as high as 800 wolves were proposed for the 10,620-km^2 Superior National Forest by Forest Service officials (Stenlund 1955). Olson (1938) estimated a wolf population of about 1 per 26 km^2 in a study area of 6,475 km^2, and Stenlund (1955) estimated that 300 to 400 wolves inhabited 18,130 of the 31,000 km^2 of primary wolf range in the state. Mech (1966) erroneously interpreted Stenlund's 300–400 estimate as applying to the entire state. The estimate of 300–400 appeared again as the wolf population estimate for Minnesota in the Bureau of Sport Fisheries and Wildlife Red Book of Endangered Species (U. S. Dept. of the Interior 1966). The Minnesota Department of Natural Resources has recently estimated the number of wolves inhabiting both the primary and secondary wolf ranges in the state at 750 (Leirfallom 1970).

The continued maintenance of the present high wolf density is closely linked with the future of the deer population in northeastern Minnesota. Deer numbers have declined throughout northern Minnesota in recent years due to deteriorating habitat and a series of severe winters (Gunvalson 1971). Significantly, this decline occurred both within the major wolf range and in areas of low wolf density (Mooty 1971). Although alternate prey species are available, their density is not high enough to support the present wolf population in the near absence of deer. The wolf population on Isle Royale did not exceed the population density observed in this study despite moose populations of up to 1.5 per km^2 on the island (Jordan et al. 1967). The Isle Royale moose population density greatly exceeds that of northeastern Minnesota, and the moose population on the island contains sufficient numbers of vulnerable prey to support a relatively dense wolf population.

A decline in wolf numbers is imminent in some areas of northeastern Minnesota and its signs already are apparent. The level of nutrition of the wolves captured in this study appeared less than optimal based on interpretations of blood parameters (Seal pers. comm.). Growth, condition, and survival of some pups have been affected by poor food supplies (Van Ballenberghe and Mech in press) and some packs in the interior of the Superior National Forest have declined in size since 1971 (Mech 1973). The level to which the present wolf population will fall is unknown, but it may approach the densities characteristic of the early 1950's when both deer and wolves were relatively rare in remote areas of the Superior National Forest (Stenlund 1955). Such ecological relationships are clearly more characteristic of the region than are the dense wolf populations of recent years.

Habitat improvement measures designed to increase deer densities might be employed to maintain dense wolf populations in northeastern Minnesota. However, unless they occurred as by-products of other land use practices, e.g., logging, such measures probably would not be economically feasible, nor would they affect large enough areas to have a significant effect on wolf numbers. It is unlikely that deer habitat on the Superior National Forest will increase substantially as a result of Forest Service timber sales since such sales comprise a relatively small proportion of the forest (Peek unpublished doctoral dissertation). Additionally, reforestation of conifers on timber sale sites reduces their long-term value as high quality deer habitat. Therefore, natural or prescribed fires probably represent the best land treatment tool for creating extensive areas of deer habitat, particularly in remote portions of the Superior National Forest.

The effects of wolf predation on moose and deer populations in northeastern Minnesota have not been fully evaluated. Peek (unpublished doctoral dissertation) concluded that wolf predation could be a major mortality factor for moose calves, but that wolf predation did not limit the growth of the moose population on the Superior National Forest. Limited data on deer populations are available for the forest, and it is apparent that deer are now absent there in many areas that supported moderate deer populations during the late 1960's (Mech 1973). We suggest that increased rates of winter predation (Mech and Frenzel 1971) during several severe winters since 1965, heavy predation on fawns during summer, the presence of many lightly used areas of winter deer habitat on the Forest (Wetzel 1972, unpublished master's thesis, University of Minnesota, St. Paul, Minnesota), and the rapidity of the deer decline circumstantially indicate that wolf predation accelerated the decline of deer in portions of northeastern Minnesota. The effects of wolf predation probably were greatest in those areas where deer wintered in small, scattered yards.

Contacts Between Humans and Wolves

Those wolf packs with ranges bordering Lake Superior had maximum opportunity for wolf–human contact due to concentration of human activity within their ranges. These contacts occurred during the snow-free seasons as well as in winter when wolves were more visible and their activities were more obvious. Several habits of the wolves increased their potential for observation and exploitation by humans; these included frequent foraging at dumps and refuse piles, feeding on roadkilled deer, and interactions with domestic dogs in close proximity to human dwellings. The occurrence of substantial human activity within their territories habituated some wolf packs to the presence of humans. Numerous instances of wolves passing within 50 m of occupied houses were recorded in this study including 4 cases where wolves were shot as a result.

Despite the relatively high potential for wolf–human contact and the lack of wolf protection on nonfederal land, wolf mortality did not appear excessive and the wolf population density was high. Many of the wolves shot were taken incidental to other human activities such as deer hunting.

TABLE 28.—NUMBER OF WOLVES BOUNTIED ANNUALLY IN COOK COUNTY, MINNESOTA, 1960–64, AND MEAN NUMBER BOUNTIED 1950–1952 AND 1960–1064

Year	Number Bountied	Harvest (km^2/wolf)
1960	71	65
1961	35	130
1962	46	98
1963	56	83
1964	51	91
1950–52	$\bar{x} = 39$	117
1960–64	$\bar{x} = 52$	88

Similarly, the bulk of the trapping pressure was not exerted by professional trappers.

The vital statistics of the study area population and its degree of exploitation indicated that the rate of exploitation was not excessive. It did not approach that rate in effect during the bounty years when the wolf population was less dense (Stenlund 1955). A review of the wolf harvests in Cook County during the last 5 years of the statewide bounty system (Table 28) indicated a stable harvest trend during that period. The mean number of wolves bountied per year, 1960–1964, was significantly greater than the mean number bountied during 1950–1952. This suggested either an increase in the population or more efficient exploitation; if the efficiency of exploitation did increase, it evidently was still insufficient to reduce the wolf population. The exact number of wolves harvested per year in Cook County at present is unknown, but it probably is less than during the bounty years. The calculated kill on the study area of 1 wolf per 121 km^2 probably was greater than the kill rate for the entire county since much of the county is inaccessible to hunters and trappers.

Political Input

Political decisions involving a minimum of ecological input have historically determined wolf management policies in Minnesota. Supression of wolf numbers through bounty incentives was the primary management strategy endorsed by the state legislature from statehood through 1965. Following termination of the statewide wolf bounty, no management plan was adopted and wolves retained their unprotected, nongame status on state, county, and private lands.

National concern for Minnesota's wolves did not materialize until the late 1960's when, ironically, the state's wolf population was apparently approaching its highest level in recent times. In 1967, the Secretary of the Interior classified the eastern timber wolf as an endangered species despite its essentially secure continental population. The endangered classification of wolves, along with publication of several ecological studies on wolves in the late 1960's, and an increasing ecological awareness by the public all served to focus attention on Minnesota's wolves. Organizations such as the Fund for Animals, the Defenders of Wildlife, Help Our Wolves Live, and the National Audubon Society publicized the plight of the wolf and urged public efforts toward protection. They emphasized that wolves in Minnesota were in immediate jeopardy of extinction due to overharvest (Van Ballenberghe 1974).

These efforts contributed to the decision to close the Superior National Forest to the harvest of wolves in November 1970. This forced the drafting of a statewide wolf management plan based on available ecological data and endorsed by the U. S. Forest Service, U. S. Bureau of Sport Fisheries and Wildlife, and the Minnesota Department of Natural Resources. Although the plan contained provisions for a 6,100-km^2 sanctuary area, a closed season, yearly bag limits, and a harvest goal of 150–200 wolves per year, it was opposed by protectionist groups. Public pressures led to withdrawal of support by the Department of the Interior, ostensibly because the plan would have allowed harvest of an endangered species. The management plan was not implemented by the 1973 Minnesota legislature, and the Commissioner of Natural Resources lacked the authority to manage wolves or regulate their harvest.

The Endangered Species Act of 1973 granted federal protection to all endangered species and allowed the states to enter into cooperative agreements with the Secretary of the Interior for management of such species. The 1974 Minnesota legislature granted the Department of Natural Resources authority to formulate a management plan for the wolf and if the plan is acceptable to Interior, Minnesota would retain management authority over the wolf. Under provisions of the federal act, the wolf could be delisted as an endangered species and reclassified as threatened. Such reclassification could permit broader latitude in management strategies including control of depredating wolves and regulated sport harvest.

We feel that total protection of Minnesota's wolves is ecologically unnecessary and could increase local resentment so that massive wolf poisoning campaigns would occur throughout the major wolf range. Many northern Minnesota residents inherently dislike wolves and in recent years have had to tolerate the problems associated with a dense wolf population. These include depredations on domestic livestock including dogs and cats, and competition with wolves for wild game. A reduction of wolf numbers through sport hunting and trapping in the problem areas probably is the most practical way to reduce these conflicts.

The wolves of Minnesota are a unique natural resource. They and their habitat deserve to be managed so as to maximize the recreational, aesthetic, and scientific components of their consumptive and nonconsumptive values. These values are not mutually exclusive and can be compatibly realized without jeopardizing the continued presence of the wolf as a viable member of the state's fauna. We suggest that the ecological information gathered on Minnesota's wolf population since 1968 by this and other studies is now adequate to manage the population intelligently. The initiative to undertake such management, however, must come through the political process.

SUMMARY

Parameters and food habits of the timber wolf population were studied on a 2,600-km^2 portion of the primary wolf range in northeastern Minnesota from June 1969 to February 1972. Scat analysis, livetrapping, and radiotracking techniques were employed.

Deer, moose, and beaver comprised 77 percent of the food items in 532 scats collected during summer. White-tailed deer was the most important prey species throughout the year; deer comprised over half of the occurrences of prey species. Deer remained the most significant food item for wolves over the study period despite a declining deer population and moose densities of up to 0.8 per km^2.

Deer fawns became a significant food item for wolves during the peak fawning period. Approximately half of the deer occurrences in wolf scats collected mid-June to mid-July consisted of fawns; significant wolf predation on fawns continued into early autumn. During late summer, wolves consumed fewer deer and utilized wild fruits, small rodents, and several species of mammals and birds.

Live trapping efforts totaled 14,628 trap nights; 94 wolves were captured 114 times. Of 121 wolves captured or killed in the study area, 69 percent were pups or yearlings. The calculated survival rate of the pups was 44 percent from birth to the age of 6 months.

Hunting and trapping accounted for 73 percent of the observed wolf mortalities. The known minimum annual mortality rate of the population was 20 percent, but the population age structure suggested that the true mortality rate was about 40 percent per year.

Nine members of 5 wolf packs with linearly adjacent territories bordering Lake Superior were radiotracked in 1971–1972. Pack territories were discrete and varied in size from 52 to 145 km^2. Pack sizes ranged

from 5 to 10. Winter movements of 5 radiomarked wolves of these packs were limited and concentrated near the shore of Lake Superior, probably in response to the presence of deer yards.

Six wolf packs with territories adjacent to the radiomarked packs were identified and their territory sizes and pack compositions estimated. The population density of the 11 packs was 1 wolf per 23.6 km^2.

Despite a high potential for wolf–human contact along the shore of Lake Superior, mortality of wolves by humans was not excessive, although it did act to maintain a high percentage of juveniles in the population. The presence of a concentrated source of prey during winter is thought to have facilitated the maintenance of large packs that occupied small territories throughout the year.

Maintenance of the wolf in Minnesota as a viable member of the state's fauna does not necessarily depend on total protection as a management strategy. As deer numbers decline in northern Minnesota due to maturation of forest communities, the wolf density will also decline to a level more typical of northern ecosystems. Management of wolves in northeastern Minnesota is ultimately linked to the political process.

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