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POPULATION CHARACTERISTICS, ECOLOGY, AND MANAGEMENT OF WOLVERINES IN NORTHWESTERN ALASKA

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POPULATION CHARACTERISTICS, ECOLOGY, AND MANAGEMENT OF WOLVERINES IN NORTHWESTERN ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

Audrey J. Magoun, M.S.

Fairbanks, Alaska

September 1985

POPULATION CHARACTERISTICS, ECOLOGY, AND MANAGEMENT

OF WOLVERINES IN NORTHWESTERN ALASKA

RECOMMENDED:

Frederick C. Dean

R. Dale Guthrie

Roger W. Pearson

Samuel J. Harbo

Philip A. Gipson

Chairman, Advisory Committee

S.F. MacLean Jr.

Head, Department of Biology, Fisheries and Wildlife

APPROVED:

Dean, College of Natural Sciences

D.B. Hawkins

Director of Graduate Programs

9/8/85

Date

ABSTRACT

A radiotelemetry study of wolverines was initiated in 1978 as part of a larger research program sponsored by the U.S. Fish and Wildlife Service in northwestern Alaska. The primary goal of this research was to determine aspects of wolverine behavior and ecology that are important to the management of wolverines in northwestern Alaska. Between April 1978 and May 1981, 26 wolverines were captured, 12 males and 14 females; 23 were radiocollared. Nine wolverine kits in five litters were produced by three of the radiocollared females between March 1978 and May 1982. The average rate of reproduction for the study population was 0.6 kits/female/year. Birth of kits occurred in early March. Kits grew rapidly, reaching adult size by November. Resident female wolverines maintained home ranges that were exclusive of other females except their offspring; average summer home range size was 94 km^2. Data were insufficient to determine if adult male home ranges overlapped; overlap did occur between adult and juvenile males. Summer home range size for adult males averaged 626 km^2. Data were insufficient to determine annual home range size. Denning and raising young had a major influence on the movement patterns of adult females. Movements of males were influenced by breeding behavior from late winter through summer. Wolverine social structure appeared to be typical of the intrasexual territoriality of solitary carnivores. Wolverines scentmarked frequently using urine and secretions from the ventral gland and anal sacs. Caribou and ground squirrels were the most important foods. Food was apparently limited during the winter months and influenced wolverine movements and productivity. The presence of caribou and moose may be the most important factor influencing wolverine populations in northwestern Alaska. Wolverines do not appear to be overexploited at this time, but an attempt should be made to obtain more accurate harvest statistics and baseline data to establish wolverine population size and structure in northwestern Alaska.

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ACKNOWLEDGMENTS

Funding for this study was provided by the Alaska Department of Fish and Game, Alaska Trappers Association, National Geographic Society, National Rifle Association, National Wildlife Federation and the American Petroleum Institute, Pope & Young Club, Sigma Xi, U.S. Fish and Wildlife Service, and the Wildlife Management Institute. I sincerely appreciate Dr. Maurice G. Hornocker's help in procuring funding for the final phase of the field work and his continual interest in the project.

I would like to thank my graduate committee chairman, Dr. Philip S. Gipson, for his encouragement to begin this study and his support throughout its duration, and my committee members, Drs. John W. Coady, Frederick C. Dean, R. Dale Guthrie, Samuel J. Harbo, and Roger W. Pearson, for their interest and helpful discussions. I would also like to thank my field assistants Bill Busher, Craig George, Ruth Gronquist, Debaran Kelso, Kip Kermoian, and Robin O'Connor for their time and companionship, much of which was without monetary reward. I would like to express my sincere appreciation to Harry Reynolds, who provided much logistical support and entertainment. Many others helped with various phases of my study: pilots, secretaries, co-workers, and friends. I would like them to know that their contribution is not forgotten. To Anders Bjärvall of Sweden, I would like to say thanks for many stimulating discussions about wolverines and for a wonderful visit to your study area. Finally, many thanks to my husband, Patrick Valkenburg, for being there whenever he was needed as pilot, field assistant, and friend.

INTRODUCTION

This wolverine (Gulo gulo) study was part of a larger research program on selected wildlife species in the National Petroleum Reserve in Alaska (NPR-A) conducted by the U.S. Fish and Wildlife Service and the Alaska Department of Fish and Game (ADF&G) in response to oil and gas exploration and development activities in NPR-A (National Petroleum Reserve in Alaska Task Force 1978). Of major concern were the possible effects of oil and gas development on the Western Arctic Herd (WAH) caribou (Rangifer tarandus) and, consequently, on the predators and scavengers which subsist on caribou in NPR-A. When the wolverine research was initiated in 1978, research on the biology and movements of the WAH caribou had been underway for many years, and studies had recently begun on wolves (Canis lupus) and grizzly bears (Ursus arctos) in NPR-A. Nothing was known about wolverines in the area.

Very few detailed studies of wolverine ecology have been conducted. Until the late 1970's, tracking wolverines in snow was the primary method of obtaining information on movements and behavior (Quick 1953, Haglund 1966, Myrberget et al. 1969, and others). Krott (1959) published some information on wolverine behavior from observations of semi-tame wolverines. Information on wolverine reproductive biology was obtained through examination of carcasses collected from hunters and trappers (Wright and Rausch 1955, Pulliainen 1968, Rausch and Pearson 1972, Liskop et al. 1981, and others). In Montana in 1977, Hornocker and Hash (1980) initiated the first radiotelemetry study on wolverines.

In 1979, a year after my study was initiated, Whitman and Ballard (1984) and Gardner (1985) began using radiotelemetry techniques to study wolverines in southcentral Alaska.

Several aspects of the study in NPR-A were unique in terms of wolverine research to date and make the results particularly important as a complement to other wolverine studies. Direct observations of wolverine behavior were routinely possible due to the lack of forested habitat. The work provided the first documentation of breeding behavior in free-ranging wolverines (Magoun and Valkenburg 1983) and the most complete information on the interrelationships of female wolverines and their offspring. Unlike most wolverine populations, this population had no large herbivores available as winter food. Finally, the study population was unaffected by human exploitation.

Though wolverines have been essentially unharvested in the study area due to its remote location, the area is open to wolverine hunting and trapping; wolverines are harvested in areas adjacent to the study area, usually in the vicinity of villages. The study area lies within ADF&G's Game Management Unit 26 (GMU 26). Most of the wolverine harvest from this unit is reported from Subunit 26A, that portion of GMU 26 west of the Itkillik River (Figure 1-1).

The methods used to take wolverines in GMU 26 include trapping and shooting from the ground; both are legal methods for a licensed trapper. An unlimited number can be taken by a trapper from 1 November to 15 April. In addition, the 1983 harvest regulations specify that one wolverine may be shot on a hunting license (1 Sep-31 Mar). Shooting is

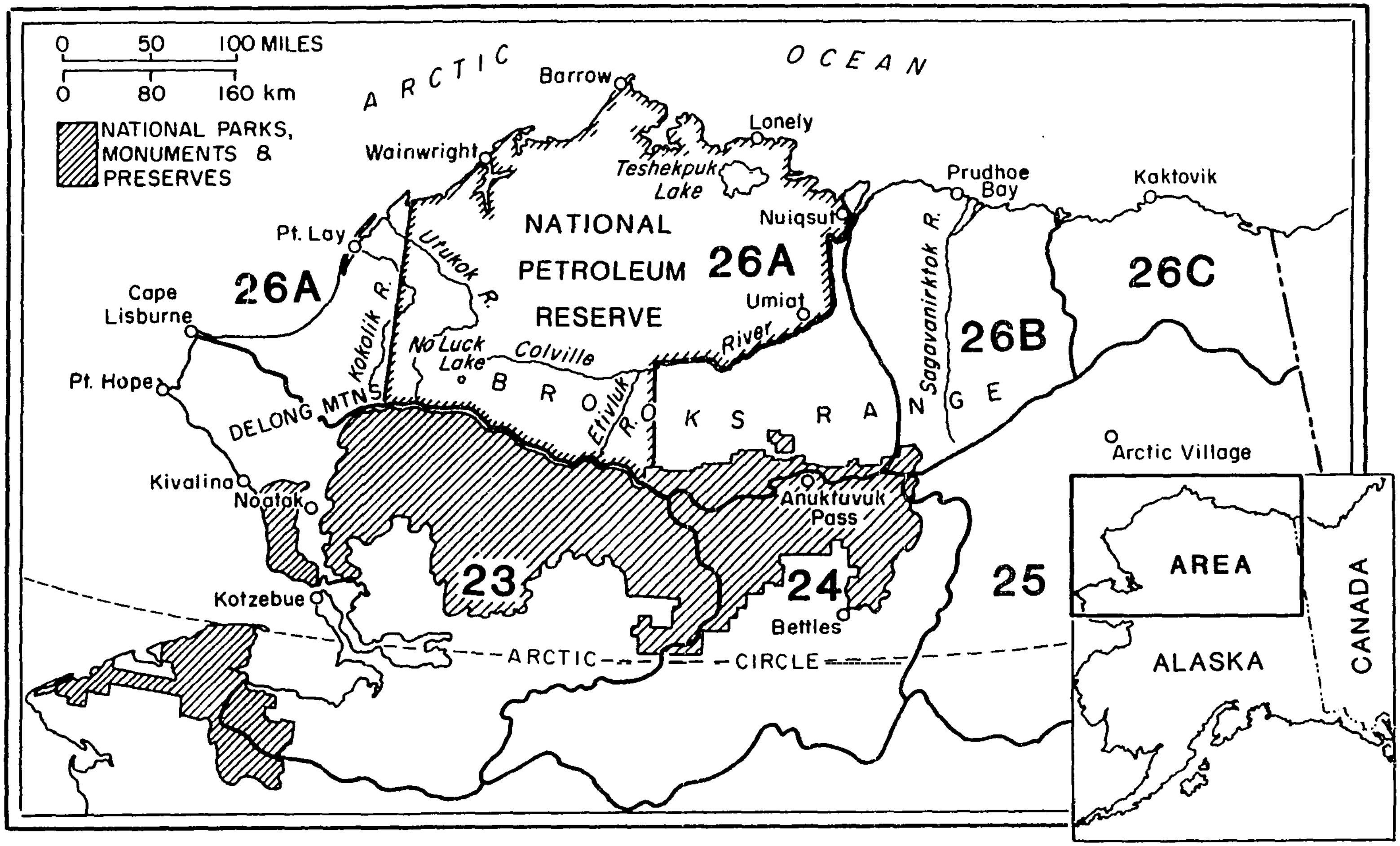


Figure 1-1. Location of National Petroleum Reserve in Alaska and Game Management Unit 26.

a very effective method for harvesting wolverines when they can be tracked using snowmobiles or airplanes. However, wolverines cannot be shot legally while the vehicles are in operation.

Documentation of wolverine harvests in GMU 26 is primarily by means of an ADF&G sealing program requiring a metal locking tag be attached to the hide; the tag must remain in place until the hide is processed (tanned or made into garments). The sex, capture date, harvest location, and method of harvest are recorded by a Department agent at the time of sealing.

The purpose of gathering harvest data is to monitor harvest levels and evaluate the effectiveness of current harvest regulations in preventing overharvesting. Monitoring harvests and instituting harvest regulations implies that managers are knowledgeable concerning both the size of the wolverine population and the appropriate harvest level. At this time, an estimate of wolverine population size has been made for only one area in Alaska (Whitman and Ballard 1983). No technique for estimating wolverine density and productivity over large areas has been developed, and it is unlikely that the resources for developing and implementing such a technique will be available in the near future. The wolverine sealing program, therefore, offers the only feasible vehicle for monitoring wolverine harvests and managing wolverine populations, but deducing wolverine population dynamics from sealing statistics is difficult. The age structure of the harvested segment of the population is unknown and factors which affect harvest levels and sex and age ratios are little understood. The primary goal of my research was to investigate those aspects of wolverine behavior and ecology that are important in the management of wolverines in northwestern Alaska. The specific objectives of the research were:

1. to determine the population characteristics of wolverines in the study area,
2. to determine the home range and movements of wolverines in the study area in order to estimate wolverine density in northwestern Alaska,
3. to investigate wolverine social behavior and define the relationship of social structure to density and movements of wolverines,
4. to determine the food habits of wolverines in the study area, particularly in relation to the WAH caribou, and examine the impact of food availability on reproduction, population density, and movements of wolverines,
5. to examine wolverine management considerations in northwestern Alaska.

STUDY AREA

The National Petroleum Reserve in Alaska (NPR-A) is a 95,000-km^2 area in northwestern Alaska (Figure 1-1) under the jurisdiction of the U.S. Department of the Interior (National Petroleum Reserve in Alaska Task Force 1978). The study area lies between 68°30' and 69°N, and 160°30' and 162°30'W in the southwestern corner of NPR-A along the upper portions of the Utukok and Kokolik River drainages (Figure 1-2). Field operations were concentrated in the "Driftwood area" near the junction of the Utukok River and Driftwood Creek (Figure 1-2).

The study area spans two major physiographic provinces described by Wahrhaftig (1965). The Brooks Range Province in the southern portion of the study area ranges in altitude from 1100 m to 1500 m. The Arctic Foothills Province ranges from 360 m to 1100 m in the south and 180 m to 360 m in the north. The Brooks Range Province is characterized by "steep, knife-like ridges, aretes, cirques, and U-shaped valleys" and the Arctic Foothills Province by "tundra-covered rolling hills, plateaus, and low, east-west oriented ridges and sporadic conical ice mounds (National Petroleum Reserve in Alaska Task Force 1978).

The study area is treeless, the vegetation characterized by tussock tundra, dry upland meadows, cutbank and floodplain vegetation, and talus and outcrop vegetation. Spetzman (1959) presented detailed descriptions of vegetation in NPR-A.

The nearest weather station is located at Umiat 370 km east of the study area at 69°22'N, 152°10'W. Weather patterns in the study area are

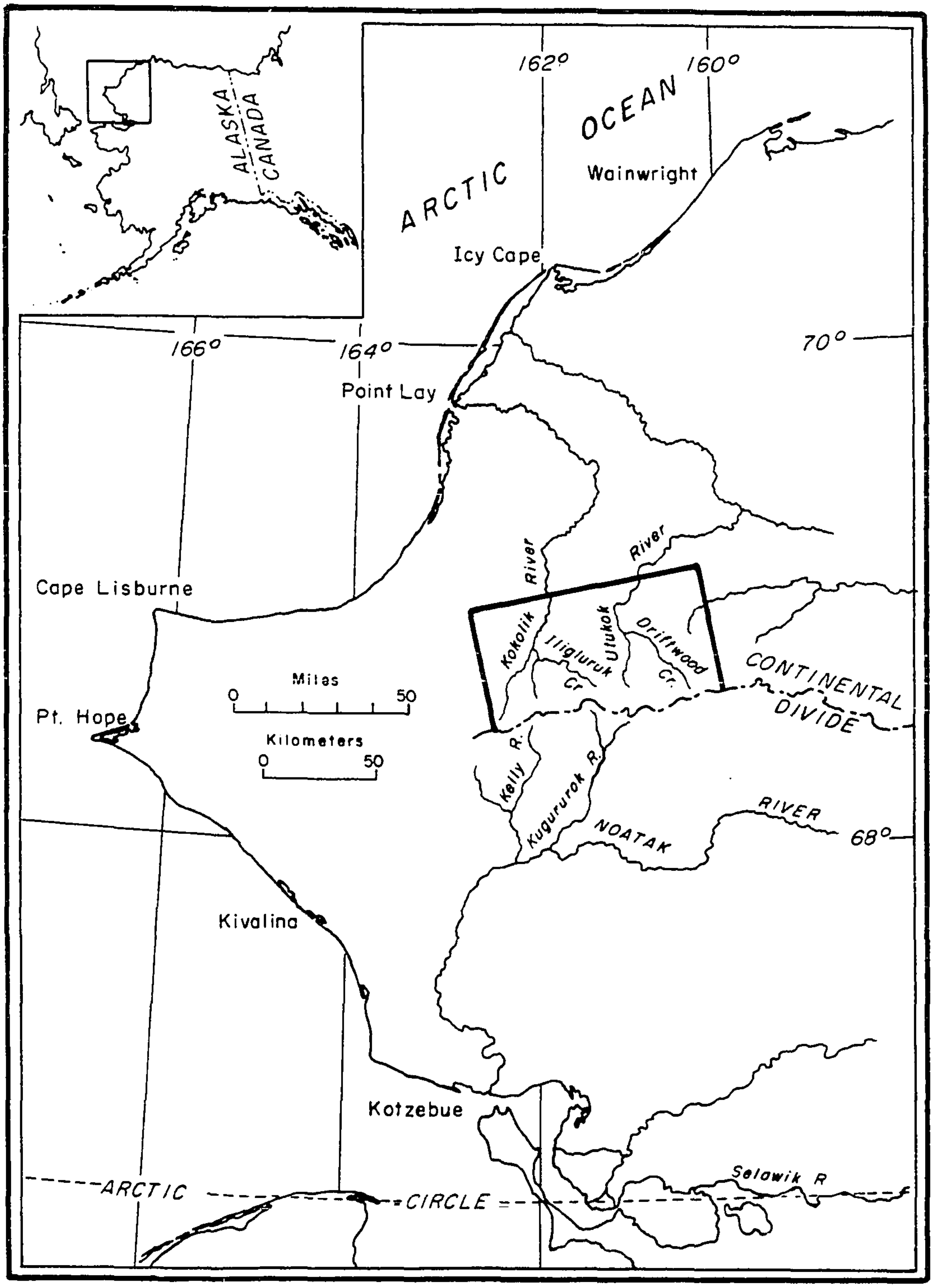


Figure 1-2. Location of the study area.

not consistent with patterns at Umiat; however, yearly averages are probably similar. The average maximum temperature (Jul) at Umiat was approximately 15 C; the average minimum temperature (Feb) was approximately -37 C. The average annual precipitation at Umiat was <150 mm, with precipitation occurring most frequently in November and December. The annual mean wind speed at Umiat was 6 knots with a maximum of 60 knots, usually from the west or east. The winds were calm 17% of the time. From December through February, a wind chill lower than -31 C occurred 50% of the time. During February, the coldest month, a wind chill factor of -43 C occurred 50% of the time (National Petroleum Reserve in Alaska Task Force 1978).

Caribou are seasonally abundant in the study area, which lies within the spring and summer range of the WAH, estimated to number 106,365 animals in 1978 (Davis et al. 1979) and approximately 160,000 in 1981 (Davis et al. 1982). Caribou are numerous during late May and early June when major portions of the herd are migrating through the study area to reach the core calving ground approximately 100 km to the northwest. Some calving may occur in the Driftwood area. The peak of calving is between 2 and 10 June. Yearlings and adult male caribou, migrating somewhat behind the pregnant cows, move north and west through the Driftwood area in June to join the cows and newborn calves during the postcalving movement. During late June and early July, most of the herd has aggregated west of the study area, but an eastward shift in July brings large numbers of caribou back into the study area. Caribou numbers increase during August and remain relatively high in September until the beginning of the fall migration. Caribou are scarce by late October and virtually absent during winter.

Moose (*Alces alces*) occur infrequently in the study area. Numbers are higher in summer than in winter. Coady (1979) counted only 2 moose in the Utukok and Kokolik River drainages in April 1977, but he noted that over 15 different moose were observed in these drainages in summer 1977.

Besides wolverines, mammalian carnivores in the study area include grizzly bears, wolves, red foxes (*Vulpes vulpes*), arctic foxes (*Alopex lagopus*), and short-tailed and least weasels (*Mustela erminea* and *Mustela nivalis*, respectively). The density of bears in the study area is approximately 1 bear/42 km^2 (Reynolds 1980). Bears are in hibernation from October to May. Only one wolf pack lived in the study area; its summer home range roughly coincided with the wolverine study area (James 1983). During summer 1978, the pack consisted of two adults, five yearlings, and four pups. The pack did not winter in the study area but followed the WAH caribou south of the Brooks Range. Red foxes were much more common than arctic foxes during the study. Both species undergo periodic fluctuations in numbers, but arctic foxes probably do not occur in significant numbers except in years when lemming populations are high (see p. 134). Foxes are the only larger mammalian carnivores besides the wolverine that are active in the study area during winter.

Smaller mammals that occur in the study area include marmots (*Marmota broweri*), arctic ground squirrels (*Spermophilus parryii*), lemmings (*Lemmus sibiricus*, *Dicrostonyx rubricatus*), voles (*Microtus oeconomus*, *Microtus miurus*, *Clethrionomys rutilus*), and shrews (*Sorex arcticus*). Marmots occur only in areas of extensive talus and outcrops. Arctic ground squirrels occur throughout the study area and are particularly abundant in dry upland meadows. Both marmots and ground squirrels hibernate from October until April. While these two species are fairly stable in numbers, lemmings, voles, and shrews undergo population fluctuations (see p. 134).

Depending on habitat type, from 20 to 50 species of birds have been reported to breed in areas adjacent to the study area (Irving and Paneak 1954, Kessel and Cade 1958, Maher 1959). The willow ptarmigan (*Lagopus lagopus*) is one of the few species which remain year-round in the Driftwood area. Fluctuations in ptarmigan numbers can be dramatic; winter flocks of 300 or more birds were common in 1978 when ptarmigan were abundant.

METHODS

Capture Techniques

The six capture techniques that were used during the study are listed in descending order by the number of different wolverines captured with each technique (see Table 1-1):

1. Immobilizing with Cap-Chur equipment (Palmer Chemical and Equipment Co., Douglasville, Ga.) from a helicopter.
2. Livetrapping and immobilizing.
3. Immobilizing (with a Cap-Chur gun or jab-stick) wolverines cornered in shallow rock caves or snow tunnels.
4. Running juvenile wolverines down on foot and capturing by hand without immobilization.
5. Digging a litter from a natal den.
6. Immobilizing with Cap-Chur equipment from a snowmobile.

Immobilization

Ketamine hydrochloride (Vetalar, Parke-Davis and Co., Detroit, Mich.) was the most effective drug when used at a dosage of approximately 22 mg/kg of body weight. A mixture of phencyclidine hydrochloride (2 mg/kg) (Sernylan, Bio-ceutics Laboratories, Inc., St. Joseph, Mo.) and xylazine (4 mg/kg) (Rompun, Haver-Lockhart Bayvet Div., Cutter Laboratories, Shawnee, Kans.) also produced suitable results, having a response time similar to that of ketamine hydrochloride. Phencyclidine hydrochloride when used alone caused repeated convulsions. The wolverines usually responded to the immobilization drug within 5 minutes after the intramuscular injection. Recovery began 45-60 minutes later.

Tagging

The captured wolverines were eartagged with plastic rototags (Nasco West, Modesto, Calif.) and tattooed on the inside of the upper lip. Body measurements and weights were recorded. Two of the first premolars (from an upper and lower jaw) were pulled when possible for age determination. Photographs of throat coloration patterns were taken. Wounds, scars, and missing toes and teeth were noted.

Wolverines over 4 months old were outfitted with radio collars (Telonics, Inc., Mesa, Ariz.). Two sizes of radio collars were used, the larger (260 g) on adult males and some adult females and the smaller (130 g) on juveniles and some adult females. The radio collars were equipped with either a whip antenna or an internal antenna. Some transmitters had a variable pulse signal that allowed me to determine if the wolverine had been inactive for more than 2 minutes. When the wolverine remained motionless for 2 minutes, the pulse rate dropped to 60 pulses per minute, but with movement, the pulse increased to 80 per minute.

Age Determination

Estimates of the ages of captured wolverines were made using several criteria: tooth cementum annuli, general condition of the teeth, length of teats for females and length of testes for males, extent of scars and wounds, and observations of breeding. Taking into consideration the time of year that the wolverines were captured, these criteria were used to categorize a wolverine as an adult, subadult, or juvenile. A limited amount of known-age material I have collected suggests that one cementum annulus is present by the time a wolverine is 1 year old and an additional annulus is laid down each year. A wolverine was considered an adult if there were at least three cementum annuli, based on Rausch and Pearson's (1972) results that indicated some wolverines may not breed for the first time until their third summer. Wolverines with two cementum annuli could have been sexually mature, but none of the extracted premolars had two cementum lines. If a premolar had not been extracted, a wolverine was considered an adult if there was evidence of sexual maturity (i.e., breeding behavior, presence of kits, teat development >10 mm, testes length >25 mm). A wolverine was classified as a subadult if it had one cementum annulus and showed no evidence of sexual maturity. If a premolar had not been extracted, a wolverine was considered a subadult if tooth wear was slight and average teat length was <5 mm or average testis length was <20 mm after 1 April (see pp. 24-26). A wolverine was classified as a juvenile if it was known to be <12 months old. The age of a wolverine that could not be placed in one of these categories was considered undetermined. The term "yearling" refers to subadults from 13 to 24 months of age and is used when I wish to emphasize the animal's age class. A juvenile was considered a yearling on 1 March after its first summer.

Radiotracking

Most radio locations of wolverines were made from the air using PA-18 aircraft equipped with a receiver (Telonics, Inc.) and a 3-element Yagi antenna (Telonics, Inc.) on each wing, mounted perpendicular to the fuselage. Radio signals were in the 150-151 MHz range. The wolverines were visually located whenever possible to pinpoint their locations and observe activity and the type of habitat being used. Radio locations were recorded on 1:250,000 U.S. Geological Survey maps or 1:60,000 aerial photographs.

The radiotracking schedule varied seasonally. The majority of locations (68%) were made in the summer (May-Aug). Midwinter (Dec-Feb) locations were difficult to obtain because of inclement weather and darkness. Often, an aircraft was not available during this period. Most radiotracking in winter (Sep-Apr) was done in March and April (63%). Tracking intensity varied among different wolverines (see Appendix A).

The difficulties of maintaining visual and radio contact with the wolverines, due to their speed of travel and to terrain features, limited radiotracking from the ground as an efficient means of obtaining data.

Home Range Estimation

Mohr's (1947) method of home range determination (minimum polygon method) was used so that home range data from my study area could be conveniently compared to those from other wolverine studies. Home ranges were calculated separately for the summer period (May-Aug) and for the entire year (Jan-Dec). Radio locations were generally evenly distributed during the summer period but were poorly distributed during the remainder of the year (see Appendix A). Therefore, "summer home range" is treated separately from "yearly home range"; the term "yearly home range" is used primarily for convenience in expressing home range size based on all radio locations and does not necessarily approximate actual yearly home range size. An average summer home range and an average yearly home range were calculated for males and for females by summing the sizes of each wolverine's home range for each year and dividing by the total number of wolverine-years for each sex. Only those home ranges with at least 10 locations for the summer or at least 20 for the entire year were used in the calculations.

Food Habits Analysis

Food habits during summer were determined primarily through direct observation of radiocollared wolverines either from aircraft or from the ground. If a wolverine was observed eating, carrying, caching, or capturing a food item, an attempt was made to identify the item either by visual identification or indirectly by the method of capture such as mousing. Additional information on food habits was gathered at sites where a female left her kits while she hunted (rendezvous sites). Food remnants were noted and scats were collected at these sites.

Scat analysis was the main method of determining winter food habits. Scats were collected along wolverine trails from January through March, from natal den sites used in March and April, and from rendezvous sites used in May and June. Scats were dried and broken apart, sorted into categories, and the material in each category weighed. The following categories were analyzed separately: caribou, red fox, arctic ground squirrel, other small mammals (as a group), bird (including feathers and eggshells), and soil. No attempt was made to sort lemmings, microtines, or shrews into separate categories or to identify them by species because of their low prevalence in the scats. Scats containing soil were broken into sieves so that the food remains could be separated from soil, a major component of some scats.

Scats collected along winter trails were analyzed individually for each of three winter periods (early-Sep, Oct, Nov; mid-Dec, Jan, Feb; late-Mar, Apr). The number of scats containing a particular food category was expressed as a proportion of the total number of scats containing food remains (frequency of occurrence). The weight of food material in each category was expressed as a proportion of the total weight of all food remains (percent dry weight). Scats collected at dens or rendezvous sites were analyzed as a group due to the difficulty of differentiating between individual scats and of determining the date of deposition. Therefore, only percent dry weight was calculated for these scats. Though the percent dry weight does not necessarily measure the relative importance of each food category at the collection site, it does allow for a comparison between collection sites and between years.

For soil, frequency of occurrence was determined by dividing the number of scats containing soil by the total number of scats collected along winter trails for each winter period. The percent dry weight was determined by dividing the total weight of the soil by the total weight of all scat material collected during each winter period.

CHAPTER 1

CHARACTERISTICS OF THE STUDY POPULATION

Results and Discussion

Between April 1978 and May 1981, 26 wolverines were captured, 10 more than once (Table 1-1). Twenty-three wolverines were radiocollared; three that were too young to carry collars (M16, M24, F25) were eartagged and released. Radio locations were obtained 864 times (Appendix A). Most of the radio locations were made from aircraft. Visual contact with the wolverines occurred during 75% of the aerial radio locations.

Sex and Age Ratios.--Of 26 wolverines captured during the study, 12 (46%) were males and 14 (50%) were females, which does not differ significantly from a 50:50 ratio. At the time of initial capture, 50% of the wolverines were adults (7 males, 6 females), 27% were juveniles (4 males, 3 females), and 15% were subadults (1 male, 3 females); two were of undetermined age.

Residency Status.--A wolverine was classified as a "resident" (R) of the study area if it was (a) a juvenile captured in the study area before the middle of November, because no juvenile was known to leave its natal area before 16 November, or (b) a subadult or adult radiocollared in the study area that was tracked during three of the

Table 1-1. Characteristics of wolverines captured in northwestern Alaska, 1978-1984 (see notes below the table).

	Status	Age	Capture Dates	Method of Capture	Body Length (cm)	Hind Foot Length (cm)	Neck Circ (cm)	Chest Circ (cm)	Shoulder Height (cm)	Weight (kg)	Testes Length (mm)	Condition
Males												
M2	U	S	15 Apr 78	1	84/106	18	--	52	-----	13.2	20	1
M3	R	A	15 Apr 78	1	84/106	20	--	52	-----	15.9	32	2
M5	R	A	17 Apr 78	1	81/103	16	--	46	-----	12.9	26	2
M6	PR	A	17 Apr 78	1	84/106	18	--	46	-----	12.5	25	2
M8	R	J	29 Jun 78	1	43/63	17	27	36	-----	9.1	0	0
M12	R	A(5)	7 May 79	1	85/110	19	35	48	34/47	14.5	--	2
M13	R	J	12 May 79	4	51/62	15	22	33	--/30	3.6	0	0
			30 Jun 79	1	71/89	18	28	37	25/36	7.7	0	
			19 Aug 79	2	90/111	19	33	44	32/44	10.9	0	
			19 Nov 79	2	96/120	18	31	45	35/48	12.5	0	
M14	R	J	12 May 79	4	49/57	14	23	32	--/31	3.6	0	0
			27 Jun 79	1	67/88	17	28	36	29/39	7.7	0	
			4 Nov 79	2	95/114	19	34	48	37/48	15.4	0	
			9 Nov 79	2								
M17	PR	A(3)	29 Jun 79	1	82/104	19	36	45	-----	----	--	-
M20	R	A	21 Feb 80	2	93/109	18	36	46	36/48	13.6	21	1
M21	PR	A	28 Feb 80	2	87/96	20	37	48	33/49	15.4	20	4
M25	R	J	8 Apr 81	5	41/47	8	--	20	15/19	----	0	0
Females											Teat Length (mm)	
F1	PR	U	15 Apr 79	1	72/94	16	--	47	-----	9.5	--	-
F4	R	A	17 Apr 78	1	79/83	15	--	43	-----	8.6	--	4
		A(4)	29 Jun 79	3	80/99	16	32	38	30/42	9.3	5	

Table 1-1. Continued.

	Status	Age	Capture Dates	Method of Capture	Body Length (cm)	Hind Foot Length (cm)	Neck Circ (cm)	Chest Circ (cm)	Shoulder Height (cm)	Weight (kg)	Teat Length (mm)	Condition
F7	R	A(4)	29 Jun 78	1	------					10.9	12 (8-18)	3
			21 Apr 79	2	85/104	18	29	40	----	10.4	17 (15-17)	
			23 Mar 80	2	82/100	18	30	38	31/42	9.5	8 (6-11)	
F9	R	J	16 Oct 78	1	78/101	17	30	42	--/42	10.7	0	1
		A(6)	15 Sep 84	1	76/100	17	30	41	--/--	10.9	--	--
F10	R	A	16 Oct 78	1	74/94	16	30	39	--/38	9.5	2	2
			4 Nov 79	2	78/96	18	31	42	28/42	9.5	5 (4-7)	
			24 Feb 80	2	76/92	18	29	42	29/40	10.2	6 (4-8)	
F11	PR	A(4)	7 May 79	3	70/93	16	30	37	30/40	----	5 (4-7)	2
F15	R	J	29 May 79	4	47/57	13	24	33	23/31	3.8	0	0
			2 Jul 79	4	61/81	17	27	36	27/35	6.4	0	
			14 Feb 80	2	79/94	17	30	42	30/41	9.5	0	
F16	R	J	29 May 79	4	48/58	13	24	33	22/28	3.6	0	0
F18	U	U	2 Nov 79	2	84/106	17	33	44	31/44	10.4	3	
			22 Nov 79	2	83/106	18	30	38	-----	9.5		
F19	PR	A	13 Nov 79	2	89/108	16	30	46	32/42	10.0	5 (3-7)	3
			26 Feb 80	2	------	--	--	--	-----	----	-	
			29 Feb 80	2	------	--	--	--	-----	----	-	
			29 Mar 80	2	76/96	17	29	39	30/43	10.0	7 (5-7)	
			9 Apr 80	2	-----	--	--	--	-----	----	-	
			10 Apr 80	2	-----	--	--	--	-----	----	-	
F22	U	S	18 Mar 80	2	75/92	18	30	40	27/40	8.8	0	1
			19 Mar 80	2	-----	--	--	--	-----	---	-	
			20 Mar 80	2	-----	--	--	--	-----	---	-	
F23	U	S(1)	26 Apr 80	6	83/104	18	32	41	31/42	9.5	0	1
F24	R	A(4)	21 Mar 81	2	78/98	18	31	40	-----	10.0	12 (8-16)	3
F26	R	J	8 Apr 81	5	42/48	8	14	23	15/20	----	0	0

Table 1-1. Continued.

Explanation of Characteristics:

Wolverines were numbered sequentially in order of their capture; the numbers are prefixed by "M" or "F" to indicate male or female, respectively; dashed lines indicate no measurement was taken.

Status:
R = Resident
PR = Probable resident
U = Undetermined
(see pp. 18, 22-23)

Age:
J = Juvenile; all juveniles were less than 4 months old except for F9 who was approximately 9 months old
S = Subadult
A = Adult
U = Undetermined
(see pp. 13-14)
Cementum age is given in parentheses when available

Method of Capture:
1 = Darted from helicopter
2 = Livetrapped
3 = Darted in a rock cave or snow tunnel
4 = Caught by hand without immobilization drugs
5 = Dug from a den
6 = Darted from a snowmobile

Body Length: Head to base of tail/Head to tip of tail

Shoulder Height: Top of scapula to wrist/Top of scapula to tip of claws

Weight: Weighed to the nearest 0.5 pounds, then converted to kilograms

Testes Length: The average length of the testes measured with calipers; a "0" measurement indicates the testes had not yet descended

Teat Length: Average length of teats measured with a metric rule; teats that were underdeveloped were not included in the average; the smallest and largest measured teats are in parentheses; the highest number of teats measured per female was 8 (F10)

Condition:
0 = Juveniles still with some deciduous teeth; no scars
1 = Teeth in good condition with essentially no wear; only minor scars
2 = Teeth chipped and/or slightly worn; some incisors may be missing; some scars or healed broken bones
3 = Teeth noticeably worn; a number of teeth including canines broken; several incisors may be missing; scars and/or healed broken bones
4 = Teeth very worn; broken teeth including canines; some teeth missing; many scars; missing toes and/or healed broken bones

summer months (May-Aug) and not located outside the area during summer unless the locations were within a portion of its summer home range that extended beyond the borders of the study area. Sometimes a wolverine radiocollared in the study area dropped its collar, or the radio transmitter failed before the wolverine could be tracked for 3 months in summer; the wolverine was classified as a "probable resident" (PR) if (a) it was seen in the study area at least twice, separated by an interval >50 days, and at least one of the locations was within the summer period, and (b) any location outside the study area during the summer period could have been part of a summer home range that extended beyond the border of the study area. A wolverine would have been considered a nonresident (i.e., transient) if it had been radiocollared in the study area in winter and then moved out of the study area and no part of its summer home range fell within the study area; however, no captured wolverine was identified as a nonresident. The residency status of a wolverine was considered "undetermined" (U) if none of the above conditions were applicable. For the purposes of the following discussion, all "probable residents" were considered residents.

The residency status of four of the radiocollared wolverines (M2, F18, F22, F23) could not be established. All four of these wolverines could have been born in the study area. M2 and F22 were subadults when they were captured in April 1978 and 1980, respectively. The possibility that they dispersed, perhaps as yearlings, is discussed in Chapter 2. The other two questionable females (F18, F23) dropped their radio collars shortly after their captures so that information on their residency status could not be obtained. F18 could have been a resident; she was captured on 2 November 1979 and again on 22 November 1979, an interval of 20 days. She could have been born in the study area or have been a transient recently entering the study area. Her capture was near the junction of several resident female home ranges. F23 was approximately 1 year old (Table 1-1) and was most likely born in the study area, though the possibility that she recently moved into the area cannot be refuted.

Physical Characteristics.—Weights and measurements for wolverines captured in the study area are presented in Table 1-1. The average weight for adult male wolverines ($\bar{x}$=14.1 kg) was significantly higher (t=6.86, $P<0.001$, df=10) than the average weight for adult females ($\bar{x}$=9.9 kg). By late June or early July when wolverine kits were approximately 4 months old, juvenile males M13 and M14 both weighed 55% of the average adult male weight and juvenile female F15 weighed 65% of the average adult female weight. The weights of subadult male M2 and juvenile males M13 and M14 at approximately 8.5 months of age were within the adult male weight range (the $\bar{x}\pm$SD and the range equals 14.1±1.36 kg and 12.5-15.9 kg, respectively); the weights of two subadult females (F9, F22) and the juvenile female F15 at approximately 11.5 months of age were within the adult female weight range (9.9±0.61 kg, 8.9-10.7 kg).

Sibling males M13 and M14, offspring of F7, weighed the same amount at approximately 14 weeks of age, but by November, M14 outweighed his brother by 2.9 kg. Juvenile male M8, raised alone by F7 in 1978, weighed 1.4 kg more than M13 and M14 at the same time of year. Male kit M13 grew at an average rate of 4 mm/day in length and 74 g/day in weight during the period 12 May to 19 August.

Testes development was used as one indicator of age in male wolverines. Testes were not descended in juvenile males at least through the age of 8 months. For males older than 12 months, average testis length ranged from 20 mm to 32 mm (Table 1-1). The average length of M2's testes (20 mm) was noticeably less than the average length of testes for M5 and M6 (25.5 mm) and considerably less than the average length for M3 (32 mm); all four males were captured within a 3-day period in the middle of April 1978. M2 was judged to be a subadult based on the length of his testes and on his general condition (Table 1-1). The greater length of M3's testes relative to those of M5 and M6 may have been influenced by dominance status. Both M5 and M6 had fresh wounds on their heads at the time of their capture, probably as a result of fighting, and were captured within a few kilometers of each other on the same day. Ralls (1971) suggested that aggression is more likely to occur between animals of near equal dominance.

Time of year is known to affect testis size. Average testis length for adults M20 and M21 (20.5 mm) in February 1980 was less than the average for adults M3, M5, and M6 (27.6 mm) in April 1978, but both M20 and M21 were observed breeding in June 1980 so they were known to be mature adults. This observation suggests that testis size in mature males increases between February and April as the breeding season approaches. Results from Rausch and Pearson's (1972) study of wolverine testis weights showed reduced testis weight in December-February, a nearly 2-fold increase in weight by late May and June, and a reduced weight in fall.

There appeared to be a relationship between the average length of a female wolverine's teats and her reproductive history, and for this reason, average teat length was used as an aid in determining age of females. Two juvenile females (F15, F16) and a subadult about 13 months old (F23) showed essentially no teat development (i.e., <1 mm). Two females whose average teat lengths were 2 and 3 mm (F10, F18, respectively) may have been sexually mature females that had not yet suckled young. For instance, when F10 was first captured on 18 October 1978, the average length of her teats was 2 mm. She was pregnant at the time and produced two kits in spring 1979. On 4 November 1979, about 1 year later, she was recaptured and her teat length averaged 5 mm. She may have been pregnant at that time as well, but her average teat length was only 6 mm by late February 1980 near parturition time. She was not observed with young in summer 1980 though she had demonstrated denning behavior in March 1980 (see Chapter 4). In any case, her average teat length had increased between 1978 and 1979 and was the result either of suckling young in 1979 or of her increased age. Females that were suckling young at the time of their capture had an average teat length of over 10 mm; the average varied considerably, perhaps depending on the month or on the number of young suckled. For instance, F7's teats averaged 17 mm in length when she was suckling two juveniles on 21 April

1979 but only 12 mm on 29 June 1978 when she had only one young. Also, F7 may no longer have been suckling her kit by 29 June. F24 raised no young in summer 1981, yet her average teat length was 12 mm on 21 March 1981 and a drop of milk was extruded from one teat, suggesting that kits had been born but did not survive.

Reproduction.--The number of known wolverine kits produced during the study was determined by sighting kits with radiocollared females during the summer and, in one case, by digging kits from a den (Table 1-2). A reproductive rate for the captured females (kits/female/year) was calculated by dividing the number of known offspring by the number of female-years; only radiocollared females >1 year old were considered. A "female-year" was included in the calculation if, in a given year, a radiocollared female was seen with young during summer or if young were dug from her den. A "female-year" was also included if data were sufficient to determine that the female was nonreproductive that year (i.e., raising no offspring). For a female to be considered nonreproductive, two or more of the criteria listed at the end of Table 1-2 were necessary. The only exception to the strict adherence to these criteria was the case of F19 in 1980. F19 did not demonstrate typical denning behavior in March and April 1980. She dropped her radio collar in early May, so that the remaining criteria could not be examined. However, the number of times she was recaptured in live traps that spring and her poor physical condition (see pp. 64-65) indicated she was

Table 1-2. Kits produced by radiocollared female wolverines in northwestern Alaska, 1978-1982. The number of kits was determined by seeing them with the reproductive female or digging them from her den. The identification code for each kit is in parentheses. The criteria for "nonreproductive" status are at the end of the table.

	Adult Females						Subadult Females	
	F4	F7	F10	F11	F19	F24	F9	F15
1978	0(c,d)	1(M8)	--	--	--	--	--	--
1979	0(a,d)	2(M13,M14)	2(F15,F16)	0(b,c)	--	--	0(a,b,c,d)	--
1980	0(a,d)	0(a,b,c,d)	0(a,c,d)	--	0(a)	--	--	0(a,b,c,d)
1981	--	2(M25,F26)	--	--	--	0(a,c)	--	(*)
1982	--	--	--	--	--	2(**)	--	--
Total	0	5	2	0	0	2	0	0

Criteria used to define a nonreproductive female:

a) Movements of the radiocollared female in March and April were not typical of denning females (see pp. 47, 49).

b) Movements of the radiocollared female in early May were not typical of females using rendezvous sites (see p. 49).

c) From 13 May to 9 July, the radiocollared female was not seen with kits though she was sighted at least five times during this period. This criterion was based on the fact that the earliest date kits were seen with their mother was 13 May and kits were seen with their mother regularly until at least 9 July (see Table 3-1). No female raising kits was sighted more than five times in this period before the kits were also sighted.

d) From 13 May until 9 July, the radiocollared female was observed resting at least once in an area with no concealing vegetation or snowdrifts nearby and kits were not present. This criterion was based on the fact that no female raising kits was observed resting away from her kits during this period.

* F15 was sighted five times from 4 June to 9 July and no kits were observed with her, but no other criteria could be applied.
**Two kits of undertermined sex.

unlikely to have produced kits, particularly since none of the other four radiocollared females reproduced that year.

Three radiocollared females produced a total of nine wolverine kits in five litters between March 1978 and May 1982 (Table 1-2). Litter size averaged 1.75 kits. If only the adult females are considered (Table 1-2), the average reproductive rate over the period of the study was 0.69 kits/adult female/year. If subadult females are included in the calculation, the average reproductive rate is 0.60 kits/female/year. Adult female F7 had an average reproductive rate of 1.25 kits/year over 4 years, but adult female F4 had a reproductive rate of 0.00 kits/year over the 3 years that she was observed.

Methods used to determine productivity (i.e., pregnancy rate, neonate survival rate, or average litter size) may account for some of the differences in productivity between this study and others reported in the literature. Average litter size for wolverines has been determined by counting corpora lutea, unimplanted blastocysts, fetuses, placental scars, or kits dug from dens (Table 1-3). In this study, average litter size was based primarily on the number of kits seen with their mother after natal den abandonment. Two litters were observed in May just after den abandonment, and two were observed in late June at rendezvous sites. In one case, the litter size was determined by digging the kits from a den in April. Litter size averaged 1.80 kits for all litters and 1.75 kits for litters after den abandonment. The kits were 1-4 months old by the time I observed them so any early mortality would have gone unnoticed. Most kits dug from dens are

Table 1-3. Indicators of average litter size for Old World and New World wolverines.

Source	Corpora Lutea	Fetuses	Placental Scars	Litters Dug from Dens
Rausch and Pearson (1972)	3.4 (N=121)	3.5 (N=54)	3.4 (N=99)	
Liskop et al. (1981)	2.8 (N=14)	2.6 (N=18)		
Hornocker and Hash (1981)	2.9 (N=15)	2.2 (N=6)		
Siivonen (1956)*				2.6 (N=45)
Krott (1959)*				2.2 (N=13)
Pulliainen (1963)*				2.6 (N=37)
Pulliainen (1968)				2.4 (N=21)
Zetterburg (1945)*				2.5 (N=38)
Nasimovich (1948)*				3.0 (N=1)
Parovchcikov (1960)*				2.2 (N=6)

*From Pulliainen (1968).

probably <2 months old (Pulliainen 1968). The average number of kits (1.75) seen with their mother in my study was significantly lower ($t=3.63$, $0.01<P<0.02$, $df=5$) than the average number of kits (2.57) dug from dens in a study by Pulliainen (1963) (cited from Pulliainen 1968), but the difference was not significant in a later study by Pulliainen (1968) when the average litter size was 2.38 kits. The mean number of kits in 161 litters in northern Europe was 2.5 (Pulliainen 1968). It is not possible to determine from these data whether average litter size in my study area was lower than that of other areas (Table 1-3).

The proportion of females producing litters may be lower in my study area than in Alaska in general, though verification of this was not possible. In a carcass study of trapped wolverines, Rausch and Pearson (1972) found that 50% of Alaskan wolverine females 16 to 28 months old were pregnant (N=40) while 92% of those 29 months old or older were pregnant (N=98). In my study, neither of the two subadult females (F9, F15) were seen with young. The pregnancy rate for adult females based on kits seen with their mother was only 40% (5 females with offspring in 13 female-years). However, the pregnancy rate calculated by Rausch and Pearson was based on in utero indicators, whereas pregnancy rate in my study was based largely on observations after natal den abandonment; therefore, the two rates cannot be compared. There is evidence that pregnancy rates in the study area may have been higher than that indicated by data in Table 1-2. In March 1980 both female F7 and F10 displayed behavior typical of denning females (pp. 47, 49), yet kits were not observed with the females in summer 1980. In 1981 female F24 was captured on 21 March, at which time her average teat length was 12 mm and I extruded a drop of milk from one teat, indicating that she had been pregnant; however, she also raised no kits the following summer. Other adult females may also have had unsuccessful pregnancies during the study period. Pregnancies would have had to occur in 10 of 13 female-years in order for the pregnancy rate in the study area to show no statistical difference from that observed by Rausch and Pearson (χ^2=3.87; $0.025<P<0.05$); this would have been the case if F7, F10, and F24 had been pregnant as suggested above and adult female F4 had lost kits in each of the 3 years that she was studied.

As noted in Chapter 4, food availability for wolverines may have been low during the study period, particularly in winter 1979-1980. None of the five radiocollared females produced kits in 1980; 1980 accounted for 30% of the female-years used in the calculation of reproductive rate. Therefore, the calculated reproductive rate of 0.69 kits/adult female/year may underestimate productivity over the long run. However, the reproductive rate in the study area is probably not often high; none of the five litters observed during the study had more than two kits. Four fetuses near term were found in one carcass taken in NPR-A north of the study area in 1977-78 (Appendix C). Wolverines in this area, which is often used by caribou as a wintering ground, may have a higher reproductive rate than wolverines in the study area.

Mortality.—Wolverines in the study area were essentially unharvested. One adult male (M17) was shot by a nonresident, guided hunter in spring 1981, but it was the only wolverine known to be taken within the study area. Adult male M21 was also shot by a hunter (Apr 1984), but the wolverine was south of the Brooks Range, outside of the study area near the confluence of Kagvik Creek and the Kugururok River. Another radiocollared male (M8) was trapped in March 1979, but this juvenile male had dispersed from the study area before his capture. Two adult wolverines radiocollared in the study area had toes missing (M21, F4) at the time of their capture. These injuries probably resulted from their being trapped prior to moving into the study area because no trapping is known to occur in the study area. No natural mortality was documented during the study.

CHAPTER 2

HOME RANGE AND MOVEMENTS

Results

Female Home Range Size.—The average summer home range for female wolverines was 94 km^2 (N=11 female-years; 8 individuals); the smallest was 38 km^2 and the largest 318 km^2 (Table 2-1). The average yearly range (see p. 15) was somewhat larger, 103 km^2 (N=10 female-years; 7 individuals), with the smallest being 53 km^2 and the largest 232 km^2.

Average home range size varied from year to year. Average summer home range was 152 km^2 (F1, F4, F7) in 1978, only 60 km^2 (F7, F9, F10, F11) in 1979, and 95 km^2 (F7, F10, F15) in 1980. The varying average home range size was influenced by small sample sizes, by the particular wolverines whose home ranges were used in the calculations, and by actual changes in home range size.

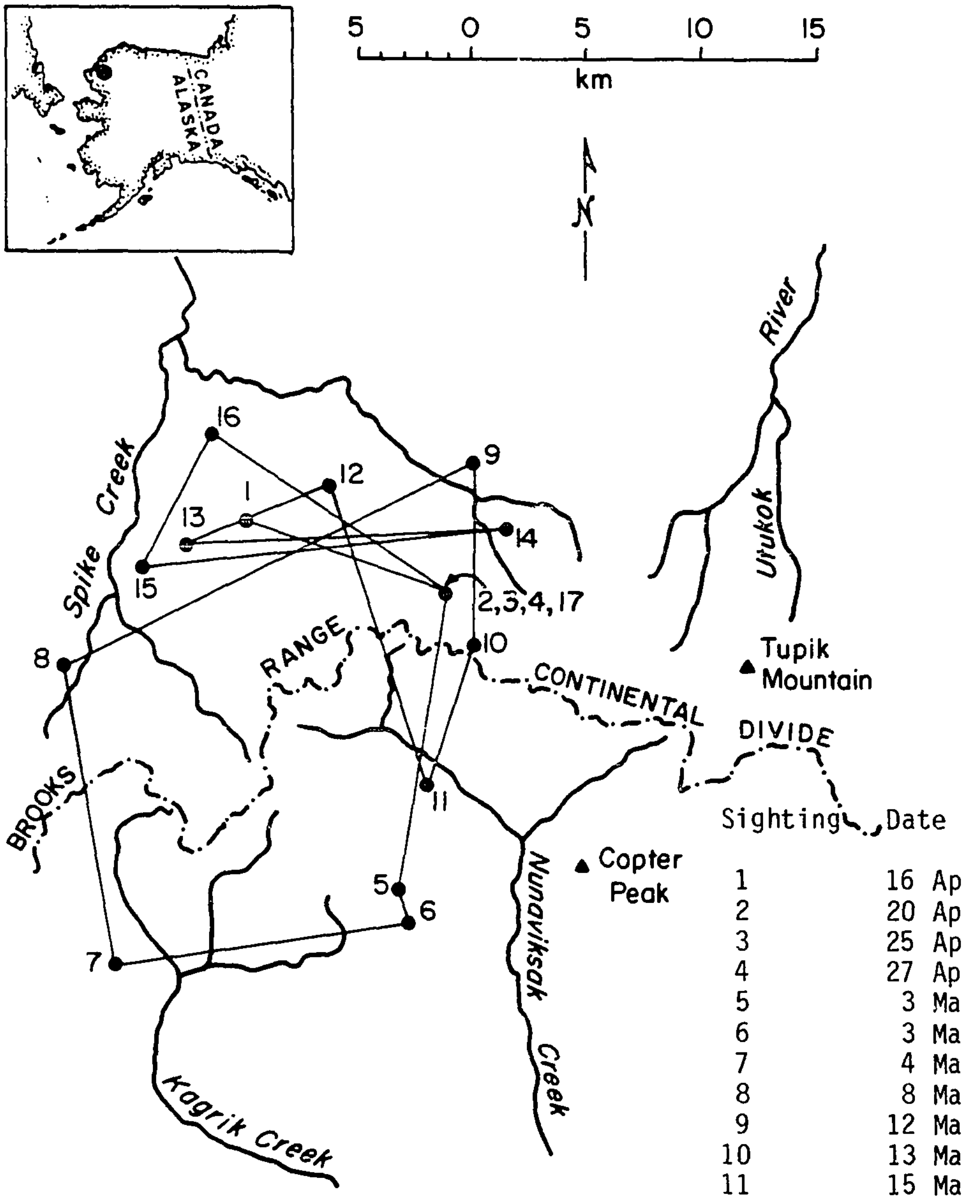
F1's summer home range was 142 km^2 larger than the next largest female summer home range. Approximately 144 km^2 was added to her home range during a 2-day period in early May when she made an extensive movement to the south (Figure 2-1). Movement data could not be collected after 20 June because F1 dropped her radio collar. An explanation of F1's exceptionally large home range is not apparent. Data on age criteria were not recorded at the time of F1's capture. She could have been a yearling undergoing predispersal movements (see

Table 2-1. Home range size (km^2) and number of locations for radiocollared female wolverines in northwestern Alaska, 1978-1982. Only radiocollared females with sufficient data to determine home range size in at least 1 year are included (a minimum of 10 locations for summer and 20 for the year). Note that "yearly" home range refers to home range size based on locations collected in a given year and does not necessarily represent an annual home range since the locations were not equally distributed throughout the year.

		Est Age*	Summer Home Range** (Number of Locations)	Yearly Home Range** (Number of Locations)
F1	1978	U	318 (13)	(17)
F4	1978	A	82 (26)	100 (34)
	1979	A		(11)
	1980	A		(14)
F7	1978	A	56 (16)	64 (31)
	1979	A	99 (69)	99 (90)
	1980	A	176 (70)	178 (92)
	1981	A		(4)
F9	1978	S		(4)
	1979	A	49 (38)	79 (58)
	1980	A		(5)
F10	1978	A		(2)
	1979	A	52 (27)	55 (45)
	1980	A	57 (60)	100 (82)
F11	1979	A	38 (15)	
F15	1979	J	(4)	(4)
	1980	S	53 (57)	53 (74)
	1981	U	(7)	(9)
F19	1979	A		(2)
	1980	A		232 (22)
F24	1981	A	56 (13)	68 (21)
	1982	A	(3)	(3)

* A = Adult; S = Subadult; J = Juvenile; U = undetermined (see pp. 13-14).

**Summer = May-August; Yearly = January-December.



Sighting	Date
1	16 April
2	20 April
3	25 April
4	27 April
5	3 May
6	3 May
7	4 May
8	8 May
9	12 May
10	13 May
11	15 May
12	19 May
13	28 May
14	2 June
15	7 June
16	10 June
17	20 June

Figure 2-1. Radio locations of female wolverine F1 showing an extensive movement into the Brooks Range during a 2-day period in May 1978.

p. 55) or a transient living temporarily in the study area. She could have been a resident making an excursion into a neighboring area even though it was within the summer period. On the other hand, her summer home range size may be within the variability of female summer home range sizes. The average summer home range size for female wolverines excluding F1 would be 72 km^2.

The average home range size for lactating females that raised young was 70 km^2 during March–August. Females which did not raise young but were known to be resident adults had an average home range of 97 km^2 during the same period (Table 2-2).

Male Home Range Size.--The average summer home range for adult male wolverines was 626 km^2 (N=4 male-years; 4 individuals); the smallest was 488 km^2 and the largest 898 km^2. The average yearly range was 666 km^2 (N=4 male-years; 4 individuals), with the smallest being 488 km^2 and the largest 917 km^2. The yearly range of M5 was larger than his summer range by 141 km^2 due to four locations (in late April) southeast of his summer home range. The summer home range of male M20 was 41% larger than the average for the other three adults.

Accurate calculations of average home range sizes were limited by sample size. For example, adult male M20's summer home range was 33% larger than that of adult male M5; however, locations for M20 were gathered into August while those for M5 ended after 13 July. If only M20's summer locations up to 13 July are considered, his home range would have measured 726 km^2, only 15% larger than that of M5. Data

Table 2-2. Home range size for radiocollared, resident female wolverines with and without young during all or part of the denning and summer periods in northwestern Alaska, 1978-1981.

	With Young	km^2		Without Young	km^2
F7	Jul-Aug 78	56	F4	Apr-Aug 78	100
F7	Mar-Aug 79	99	F7	Mar-Aug 80	178
F10	Mar-Aug 79	55	F9	Mar-Aug 79	68
			F10	Mar-Aug 80	72
			F24	Mar-Aug 81	68

collection also ended in the middle of July for adult male M3 but extended into August for adult male M12. A different problem affected home range calculations for M12. This male could not be located consistently when attempts were made to radiotrack him. Either inclement weather in the mountains or limitations on flight time prevented a thorough search for his signal on at least 4 days. This suggests that at least four of the outlying locations of his home range could have been missed, resulting in a calculated home range perhaps considerably smaller than his actual home range. Similarly, M5 was not always located because of a weak radio signal and flight time limitations.

Due to loss of collar or radio signal, no adult male was tracked for more than a year, though at least three adult males (M5, M17, M20) were seen in the study area for more than a year and the 2-toed track of another male (M21) was found regularly, 14 months after his capture, along the Utukok River in late winter 1981.

Home ranges were also calculated for three juvenile males (Table 2-3). The summer home range averaged 49 km^2; the average yearly range was 53 km^2. The movements of M13 just prior to his dispersal (see p. 55) were not considered in the calculations of his home range.

Home Range Overlap.—Most resident female wolverines maintained home ranges essentially exclusive of other females, and home ranges in summer never overlapped among females except for females and their offspring (Figures 2-2 through 5). Sightings of adult female F19 from

Table 2-3. Home range size (km^2) and number of locations for radiocollared male wolverines in northwestern Alaska, 1978-1982. Only radiocollared males with sufficient data to determine home range size in at least 1 year are included (a minimum of 10 locations for summer and 20 for the year). Note that "yearly" home range refers to home range size based on locations collected in a given year and does not necessarily represent an annual home range since the locations were not equally distributed throughout the year.

		Est Age*	Summer Home Range** (Number of Locations)	Yearly Home Range** (Number of Locations)
M3	1978	A	488 (28)	488 (32)
M5	1978	A	588 (19)	729 (24)
M8	1978	J	41 (15)	46 (35)
M12	1979	A	528 (25)	528 (28)
M13	1979	J	55 (23)	55 (31)
	1980	S		(13)
M14	1979	J	51 (36)	58 (41)
M20	1980	A	898 (42)	917 (53)
	1981	A		(2)

* A = Adult; S = Subadult; J = Juvenile (see pp. 13-14).
**Summer = May-August; Yearly = January-December.

Figure 2-2. The 1978 summer home ranges of radiocollared wolverines in northwestern Alaska (dashed lines used for male home ranges) and the 1978 winter locations that were outside the summer home range boundaries (designated by numerals corresponding to a wolverine's identification number).

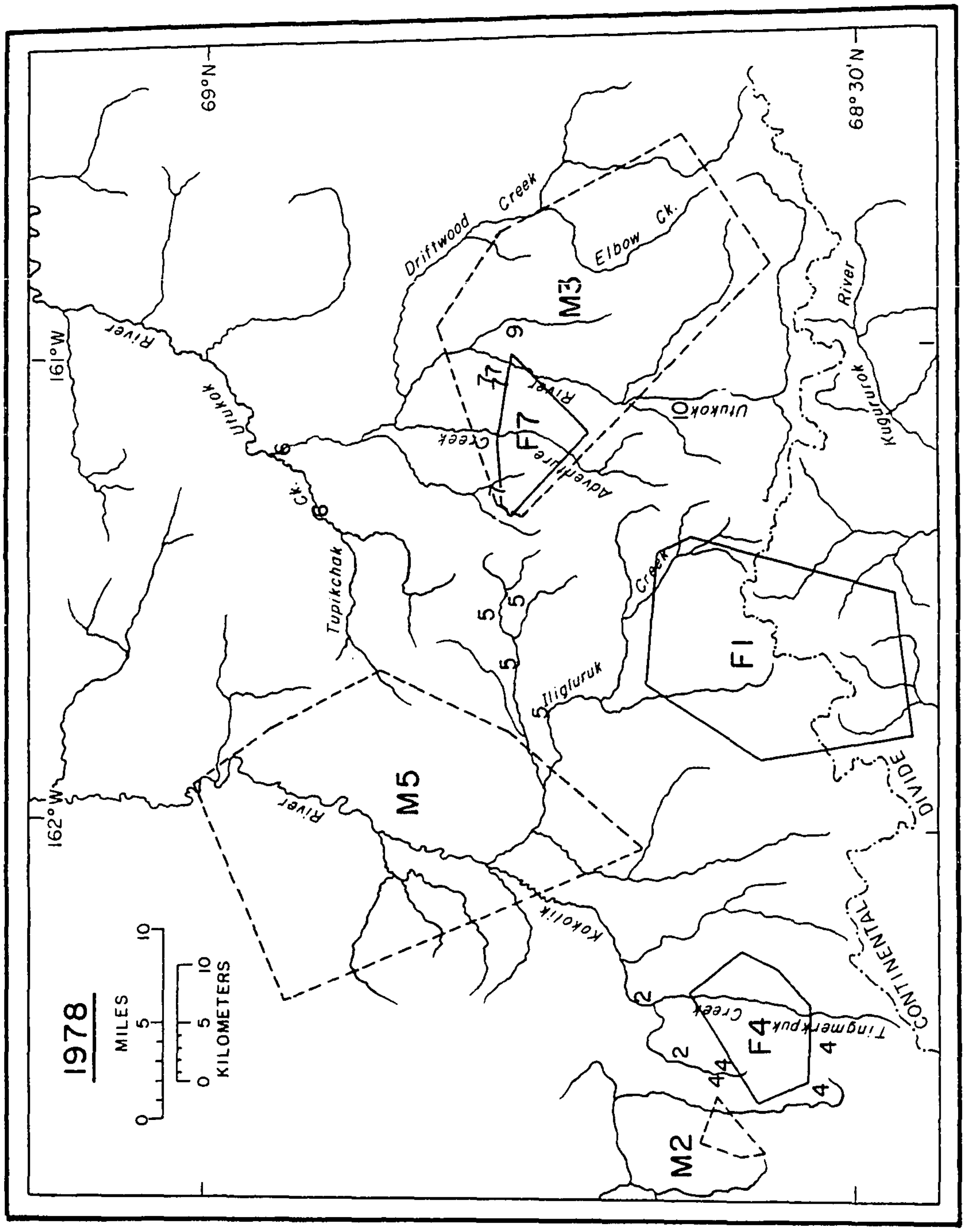

1978
MILES
0 5 10
0 5 10
KILOMETERS
69°N
68°30'N
161°W
162°W
Driftwood Creek
Elbow Ck.
M3
9
7
F7
Utukok River
Creek
Adventure
10
Utukok
Kugururok
River
6
8
Ck.
Tupikchak
5
5
5
5
Iligluruk
Creek
F1
M5
River
Kokolik
2
2
F4
Creek
Tingmerkpuk
4
4
4
4
M2
CONTINENTAL DIVIDE

Figure 2-3. The 1979 summer home ranges of radiocollared wolverines in northwestern Alaska (dashed lines used for male home ranges) and the 1979 winter locations that were outside the summer home range boundaries (designated by numerals corresponding to the wolverine's identification number).

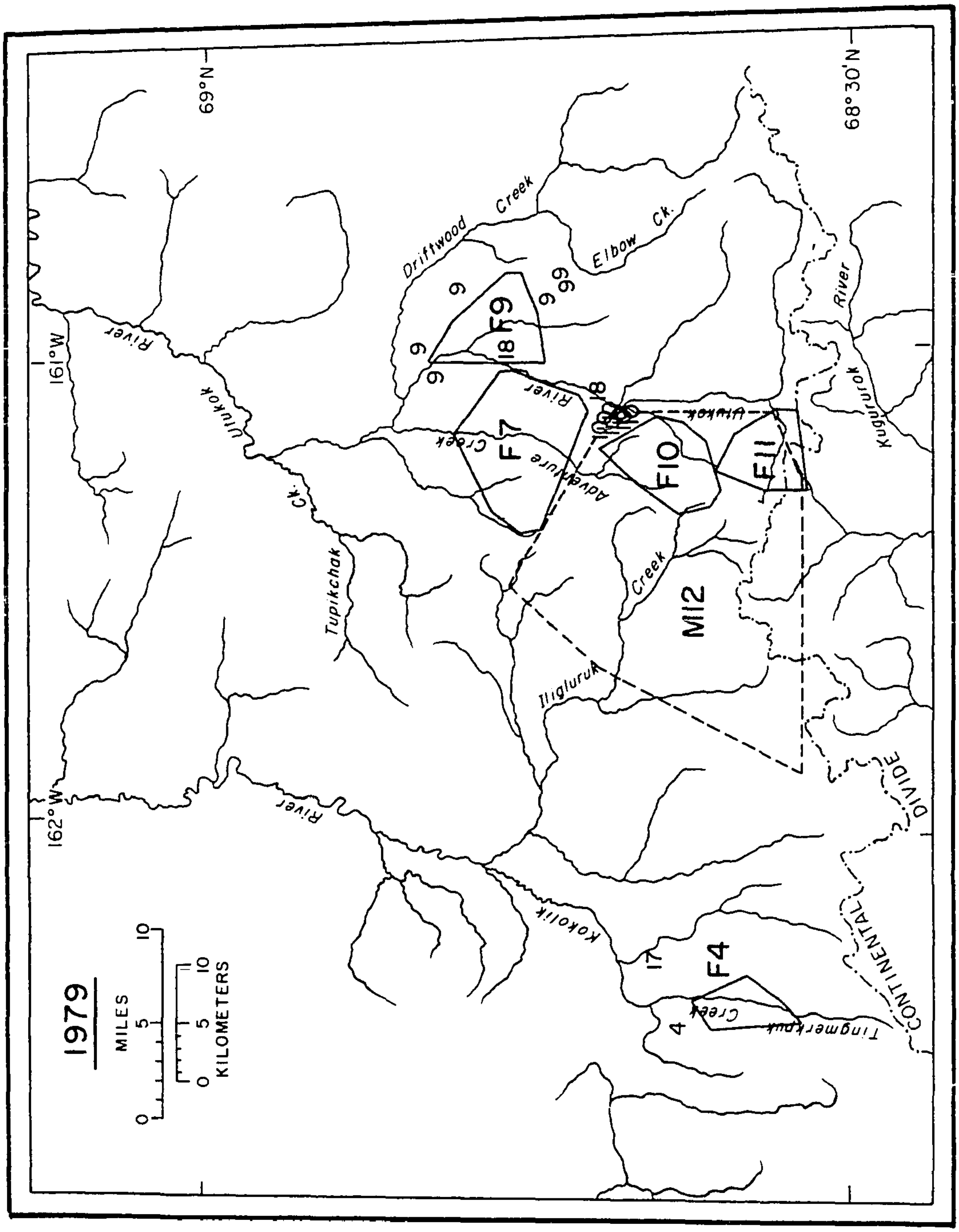

1979
MILES
0
5
10
KILOMETERS
0
5
10
69°N
68°30'N
161°W
162°W
Utukok
River
Driftwood
Creek
Elbow Ck.
Adventure
Creek
River
Tupikchak
Ck.
Iligluruk
Creek
Kokolik
River
Tingmerkpuk
Creek
Utukok
Kugururok
River
CONTINENTAL
DIVIDE
F9
F7
F10
F11
M12
F4
9
18
8
17
4

Figure 2-4. The 1980 summer home ranges of radiocollared wolverines in northwestern Alaska (dashed lines used for male home ranges) and the 1980 winter locations that were outside the summer home range boundaries (designated by numerals corresponding to the wolverine's identification number).

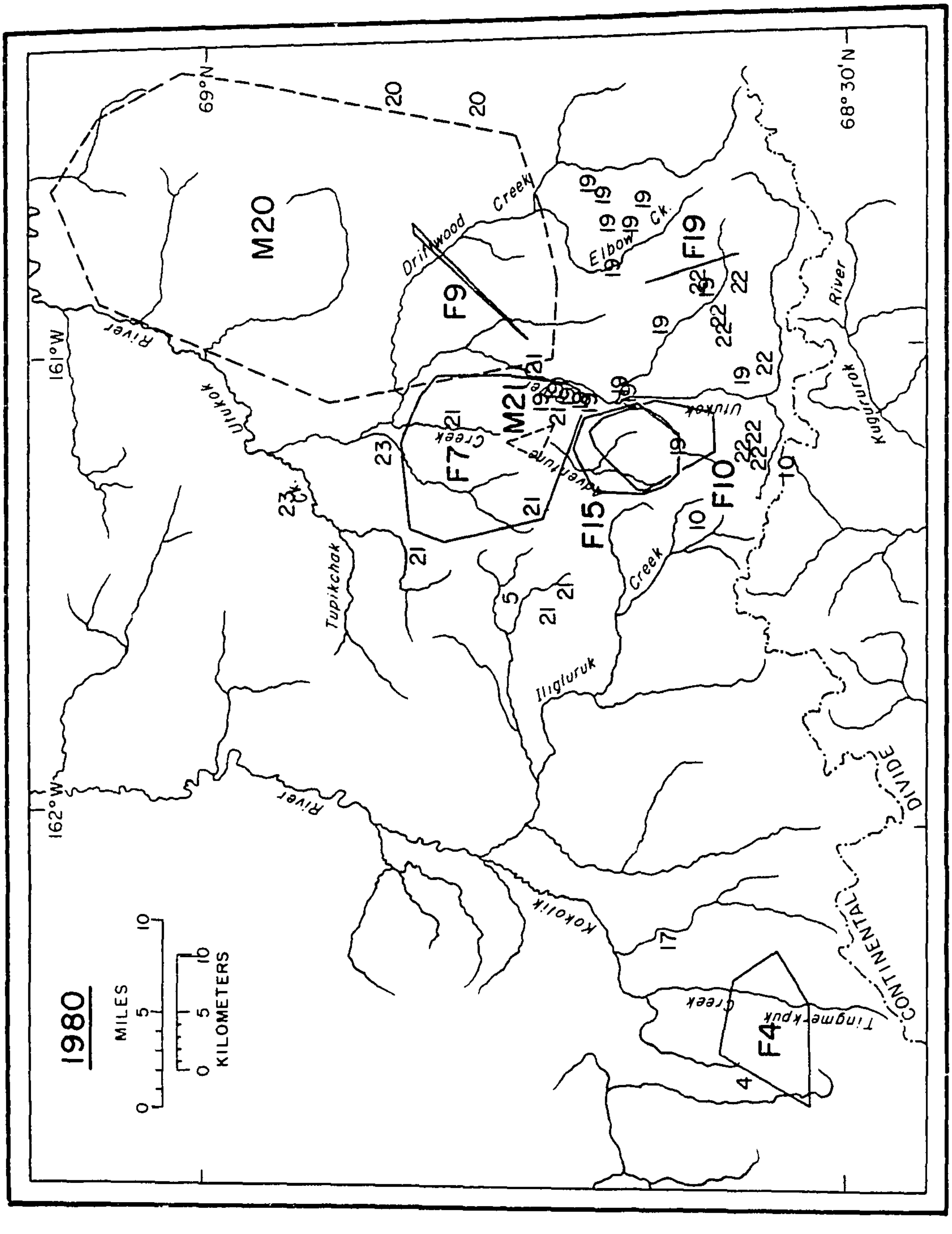
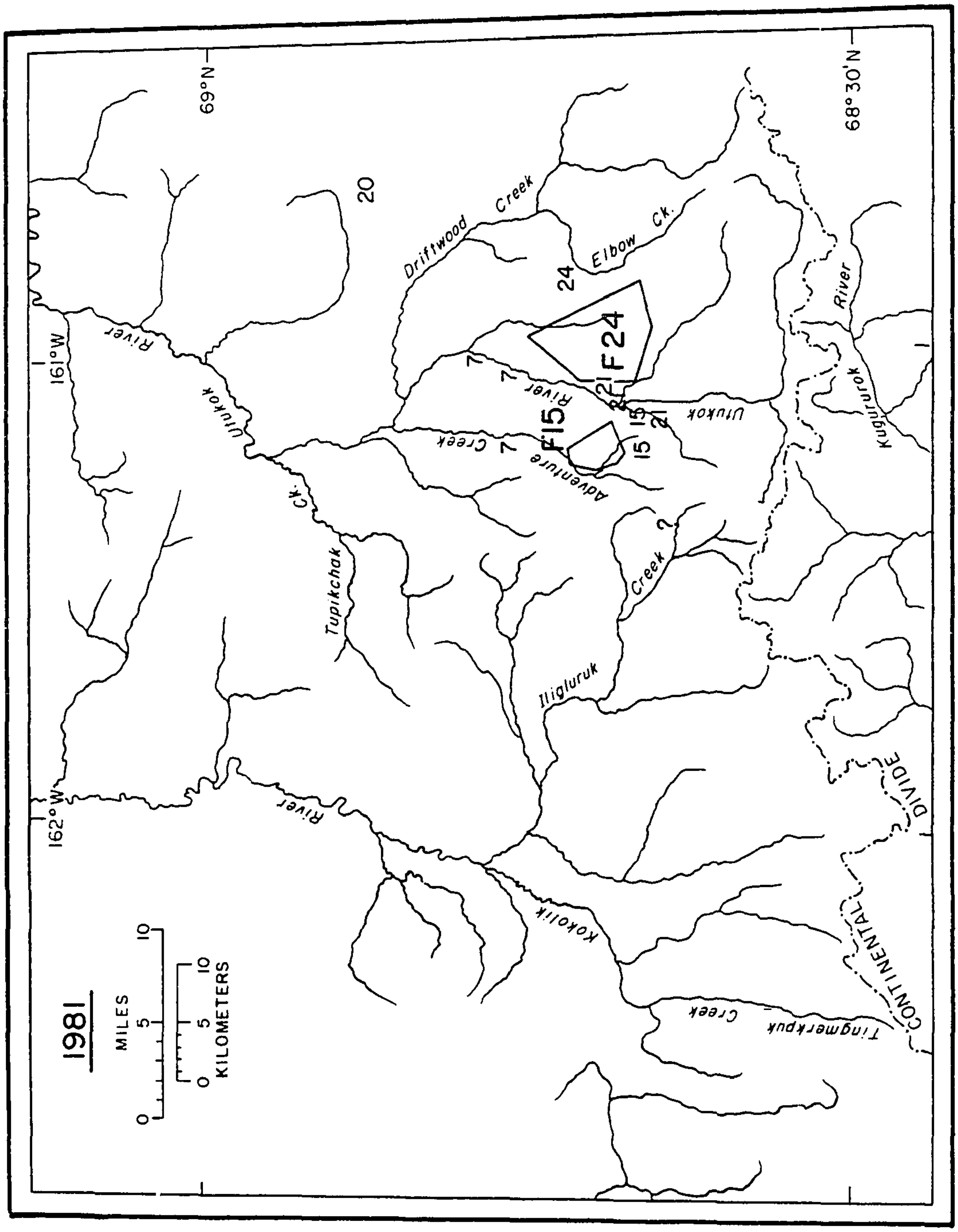

1980
MILES
0 5 10
KILOMETERS
0 5 10
162°W
161°W
69°N
68°30'N
M20
M21
F9
F7
F15
F10
F19
F4
Utukok River
Kokolik
River
Tupikchak
Ck.
Iligluruk
Creek
Driftwood Creek
Elbow Ck.
Adventure
Creek
Utukok
Kugururok
River
Tingmerkpuk Creek
CONTINENTAL DIVIDE
20
20
19
19
19
19
19
19
19
22
22
22
22
21
21
21
21
21
21
23
23
10
10
5
17
4

Figure 2-5. The 1981 summer home ranges of radiocollared wolverines in northwestern Alaska and the 1981 winter locations that were outside the summer home range boundaries (designated by numerals corresponding to the wolverine's identification number).


1981
MILES
0
5
10
0
5
10
KILOMETERS
162°W
161°W
69°N
68°30'N
Utukok River
Driftwood Creek
Elbow Ck.
Adventure Creek
Tupikchak Ck.
Iligluruk Creek
Kokolik River
Tingmerkpuk Creek
Kugururok River
CONTINENTAL DIVIDE
F15
F24
20
24
7
7
7
15
15
21
21
2

9 February to 8 May 1980 were scattered over 232 km^2 and fell within the home range boundaries of at least three other radiocollared females (Figure 2-4). Of 23 locations for this female, 21 were from the winter period (see Appendix A). Only two locations occurred in May before she dropped her collar, so there are essentially no data to establish whether her home range would have remained as large during the summer.

Female F24 probably ranged across other female ranges in winter 1982-83. F24 was radiocollared in March 1981. All her locations except one were recorded within her 1981 home range boundary depicted in Figure 2-5, including locations for her and two kits in May 1982. On 4 May 1983, her radio signal was received 25 km south of her 1981 home range near a moose carcass on the south side of the Brooks Range. The female was evidently alive at that time because the transmitter pulse rate changed at the approach of the tracking aircraft. She was not visually located but was probably in one of several snow tunnels in the area; fresh wolverine tracks were numerous. No attempt to locate her again was made until July 1983. At this time, the radio was still transmitting but was buried beneath river gravel about 0.5 km downstream from where the moose carcass had been. Apparently, F24 had either died or dropped her collar. There was no evidence to indicate whether she had returned to the study area.

F10 and her yearling daughter F15 were the only two resident females known to have overlapping summer home ranges (not including females with juveniles). F15 was born in March 1979 and her home range that summer probably approximated that of her mother since other juveniles (M8, M13, M14) were known to remain in their mother's (F7) home range during their first summer and fall. Both F15 and F10 had dropped their collars and could not be tracked in summer 1979. F15 and her female sibling F16 were visually located with their mother on 13 November 1979, indicating that they were still using their mother's home range in the middle of November during their first year. Both F10 and F15 were recollared during the winter and tracked during summer 1980. As a yearling, F15 ranged over 62% of her mother's home range with 50% of her locations within the overlap area (Figure 2-6). Sixty-one percent of F10's home range overlapped her daughter's with 40% of her locations in the overlap area. However, only about half of the overlap area was used intensively by each wolverine, F15 remaining largely to the north and F10 to the south. Only 20% of F15's locations fell within the area intensively used by her mother and less than 10% of F10's locations fell within the intensively used area of her daughter.

Unfortunately, data were insufficient to determine if summer home ranges of adult males were mutually exclusive. Only two males (M3, M5) were radiotracked concurrently (Figure 2-2) and their home ranges were not contiguous.

Male home ranges overlapped the home ranges of females and juvenile males. The home range of M12 contained within it the home ranges of two radiocollared females in 1979 (Figure 2-3). It is likely that ranges of males overlapped ranges of at least four females and possibly as many as six.

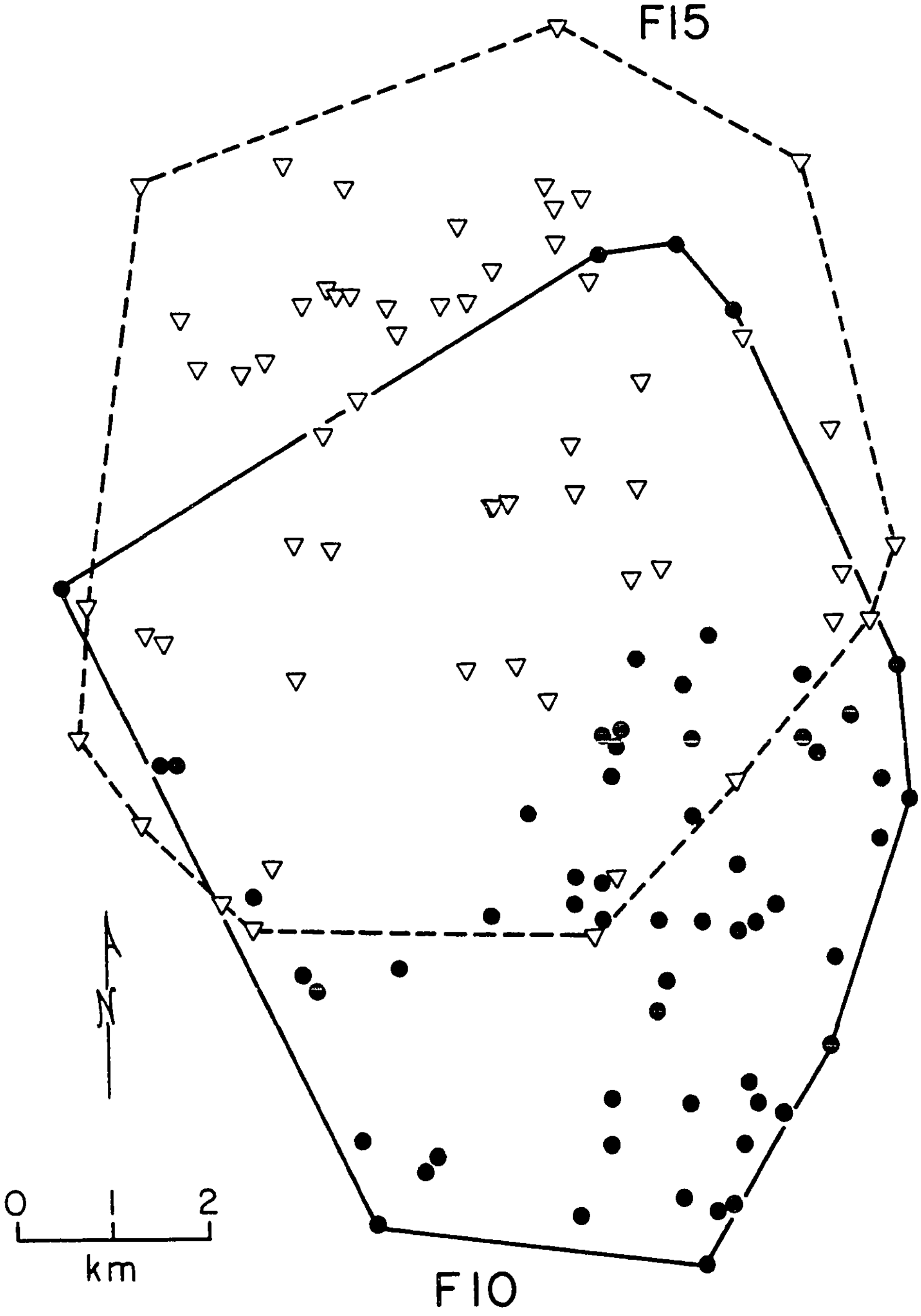


Figure 2-6. Overlap in the 1980 summer home ranges of adult female wolverine F10 and her yearling daughter F15.

Movement Patterns.--Radio locations on consecutive days (daily locations) were three times farther apart for males than they were for females. For the months of March through August, the average distance between daily locations for female wolverines was 4.2 km and for males, 12.3 km. The greatest distance for females was 15.6 km (adult female F7 in June 1980) and for males, 35.6 km (adult male M20 in June 1980).

The average distance between daily locations exhibited yearly variation. For F7, the average was 5.1 km (N=14) for May and June in 1979, when she had a home range of 99 km^2, and 8.0 km (N=17) for the same period in 1980 (an increase of 36%), when she had a home range of 176 km^2. The average distance for F10 also increased (32%) from 2.7 km (N=9) in 1979 to 4.0 km (N=11) in 1980, even though the size of her home range was essentially the same in both years (52 km^2 and 57 km^2, respectively).

The distance between radio locations on consecutive days (daily distance) was not necessarily an indication of distance traveled. During eight 1-hour continuous observations of active wolverines, the actual distance traveled was 33% greater than the straightline distance between locations at the beginning and at the end of the hour (Figure 2-7). The average rate of travel for adult male wolverines during these observations was 8.6 km/hr and for adult females, 4.6 km/hr. The greatest rate of travel observed for an unpursued wolverine was 10.6 km/hr for a male (M20) and 8.0 km/hr for a female (F7).

One of the major influences on late-winter movements for female wolverines was the presence of a natal den. In 1979, adult females F7

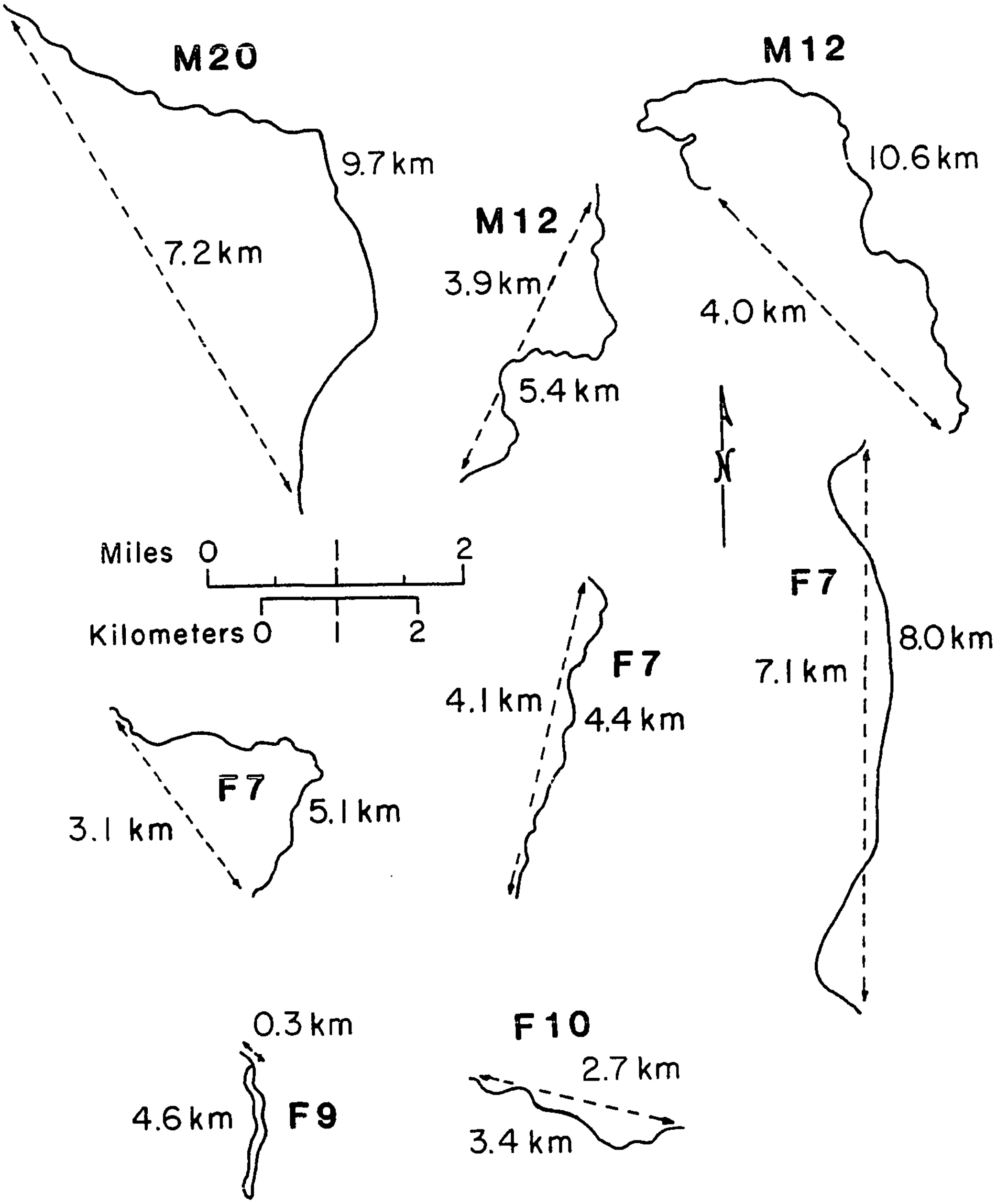


Figure 2-7. Distances moved by radiocollared male and female wolverines under continuous observation for 1 hour. The solid line depicts the actual route of the wolverine; the dashed line is the straightline distance between the locations at the beginning and the end of the hour.

and F10 were nursing juveniles during March and April; F9 was a young female that did not produce young in 1979. The movements of F9 in March and April were considerably different from those of the lactating females. Radiotracking locations in Figure 2-8 reflect this difference in the form of multiple locations at a central point (the natal den) for the lactating females and no concentration of radio locations for F9, the nonlactating female.

Similarly, movements in May and June for females with juveniles were influenced by the fact that females must periodically return to the young, which are left at rendezvous sites (see Chapter 3) while the female hunts. Radio locations under these circumstances tended to be clustered at rendezvous sites (see Chapter 3, Figure 3-2). For the 12 days on which F10 was tracked in May 1979, she was located at a rendezvous site at least once each day.

F7's movements showed a dramatic change in May 1980. During 1978 and 1979 and late winter 1980, F7 predictably could be found within the area of her 1979 home range depicted in Figure 2-3. Of 146 locations, only two were outside this area, both on 3 July 1978 about 2 km east of her 1979 home range, following the capture of F7's 4-month-old juvenile. On 9 May 1980, F7 was located 6 km north of the 1979 northern boundary (Figure 2-9a), the first of 16 days in which she was located in this new area during summer 1980. From 9 May until 7 June, she was found north of the 1979 boundaries 33% of the time. Her average distance between locations was 11.3 km; the average time interval between locations was 1.7 days.

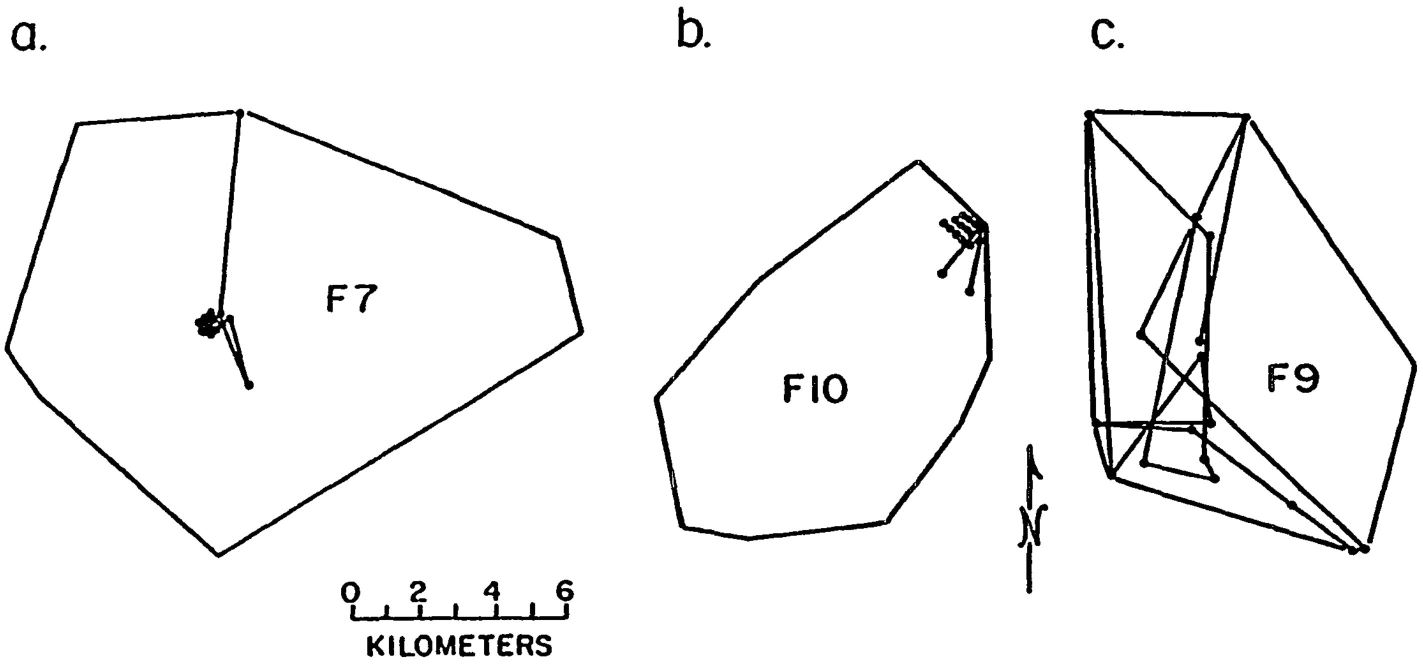
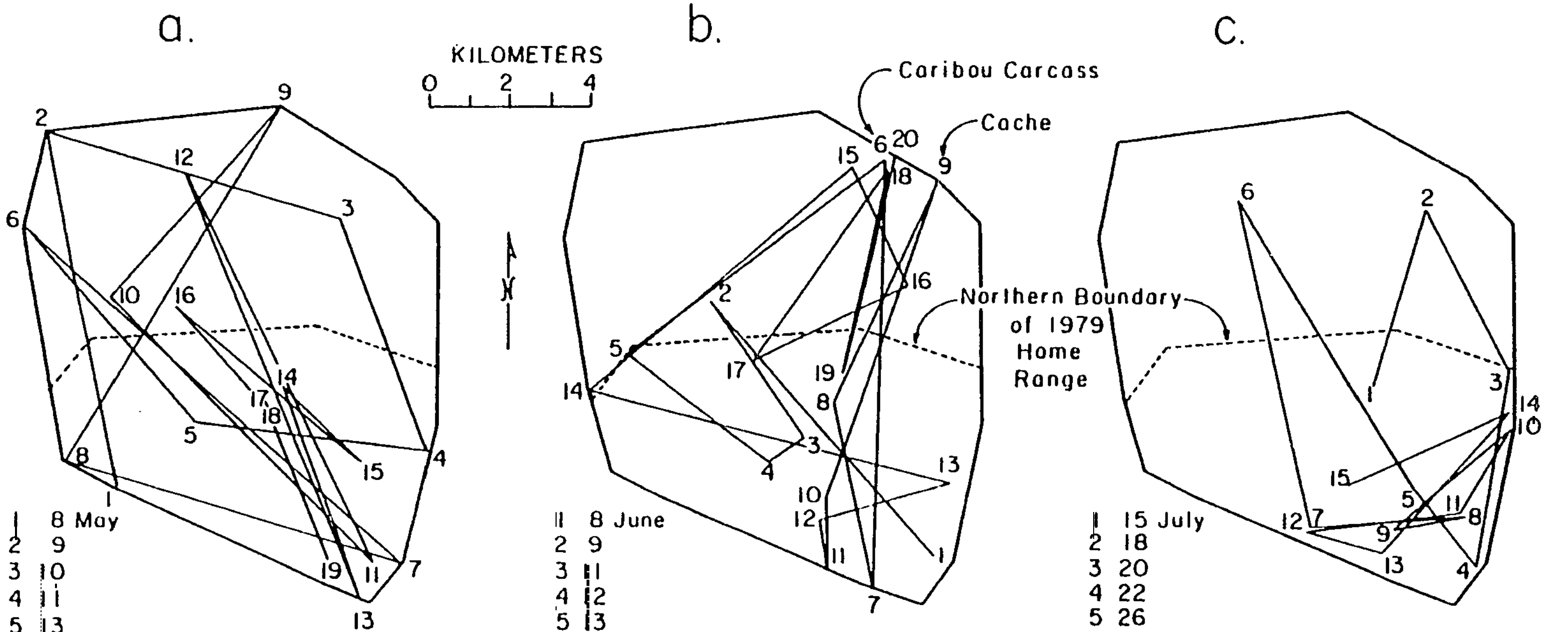


Figure 2-8. Radio locations for two lactating (F7, F10) and one nonlactating (F9) female wolverines in March and April 1979.



1	8 May
2	9
3	10
4	11
5	13
6	15
7	17
8	18
9	20
10	22
11	24
12	26
13	31
14	1 June
15	2
16	3
17	5
18	6
19	7

Average Distance = 11.3 km

Average Interval = 1.7 days

1	8 June
2	9
3	11
4	12
5	13
6	15
7	16
8	17
9	18
10	19
11	22
12	24
13	26
14	28
15	30
16	4 July
17	6
18	8
19	11
20	13

Average Distance = 8.1 km

Average Interval = 2.5 days

1	15 July
2	18
3	20
4	22
5	26
6	28
7	30
8	1 August
9	3
10	5
11	7
12	9
13	14
14	17
15	19

Average Distance = 6.8 km

Average Interval = 1.8 days

From 8 June until 13 July 1980, F7 was found north of the 1979 northern boundary 40% of the time (Figure 2-9b). On 15 June, she was at a caribou carcass in the northeastern corner of her 1980 home range and continued to visit the carcass area until at least 13 July. The average distance between locations was 8.1 km; the average time interval between locations was 2.5 days.

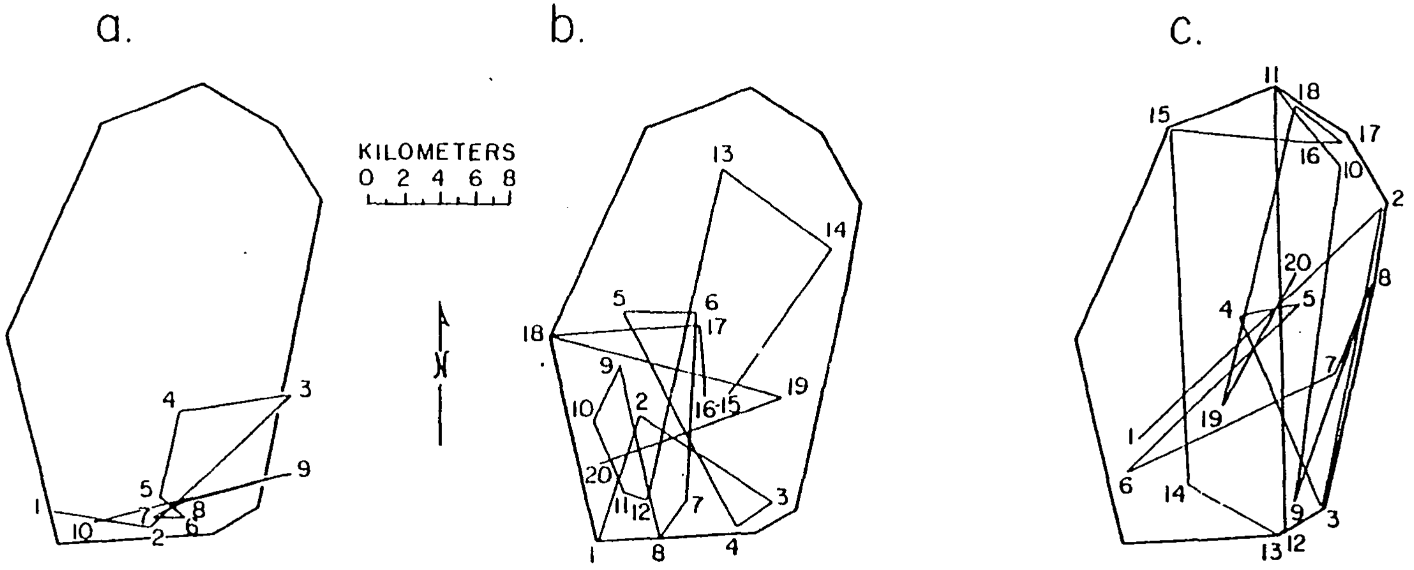
Locations from the middle of July until the end of August 1980 were largely restricted to the southern end of her home range (Figure 2-9c). Only 14% of her locations were outside the 1979 boundary. The average distance between locations was 6.8 km; the average time interval between locations was 1.8 days.

In comparison to the movements of F7, those of adult male M20 in 1980 resulted in increasing distances between radio locations from late winter 1980 through the following summer. M20's locations were all in the southern end of his home range in March 1980 (Figure 2-10a). The one location for February was also in this area. The average distance between these locations was 9.5 km; the average time interval was 2.9 days.

M20's movements expanded in May, but most of his locations from 5 May until 25 June were restricted to the southwestern portion of his range (Figure 2-10b); he was found only twice in the northeastern portion of his range during this period. The average distance between locations was 12.9 km; the average time interval was 2.7 days.

From 25 June until 19 August, M20's movements (Figure 2-10c) were concentrated in the eastern half of his range and involved extensive

Figure 2-10. Radio locations for adult male wolverine M20 during three periods from late winter through summer 1980. The average distance between locations and the average radiotracking interval are given for each period.



1	23	Feb
2	4	Mar
3	5	
4	5	
5	7	
6	8	
7	9	
8	10	
9	11	
10	24	

Average Distance = 9.5 km

Average Interval = 2.9 days

1	5	May
2	8	
3	9	
4	11	
5	13	
6	15	
7	17	
8	18	
9	24	
10	26	
11	26	
12	31	
13	1	June
14	6	
15	11	
16	12	
17	16	
18	22	
19	23	
20	25	

Average Distance = 12.9 km

Average Interval = 2.7 days

1	25	June
2	26	
3	28	
4	30	
5	4	July
6	16	
7	18	
8	20	
9	22	
10	26	
11	28	
12	31	
13	1	August
14	2	
15	4	
16	5	
17	6	
18	14	
19	17	
20	19	

Average Distance = 19.0 km

Average Interval = 2.9 days

movements between the northern and southern boundaries. During this period, the average distance between locations was 19.0 km; the average time interval was 2.9 days.

The distance between daily locations declined while wolverines were paired during the breeding season. The average distance between M20's locations on consecutive days from May through August was 14 km. However, his locations on 11 and 12 June, when he was paired with F9, were only 1 km apart (Figure 2-10b). M20 was possibly paired with another female on 31 July and 1 August 1980. On both days, he was located (though not actually sighted) in patches of dense willows located less than 1 km apart (Figure 2-10c). Breeding pairs of wolverines commonly rested in willows (personal observations). This fact and M20's limited movements suggest he was paired at the time. Distances between daily locations for female wolverines when they were paired with males further support this assumption. While the average distance between daily locations for F7 during summer 1980 was 8 km, the distance between the locations on the days she was paired with male wolverine M21 (5 and 6 June) was only 1 km (Figure 2-9a). Another female, F9, moved an average of 1 km per day during the 3 days she was paired with an unmarked male in August 1979.

Dispersal.--Dispersal was difficult to document because the distances traveled by dispersing wolverines were relatively great compared to the transmitting capabilities of their radio packages. The last radio location for juvenile M8 born to F7 in 1978 was in his mother's home range on 16 November 1978, the last day that tracking was carried out in 1978. When tracking was resumed the following March, the juvenile could no longer be found in the study area. In May his carcass was obtained from a trapper who reported capturing the animal in March 1979 in an area south of the Brooks Range 100 km from F7's home range (Figure 2-11, see insert). The date of capture could not be verified. It is possible that the juvenile dispersed in early March just before his reported capture because another male (M13), born to F7 in 1979, dispersed between 9 and 11 March 1980.

The area used by juvenile male M13 expanded shortly before his dispersal. M13 was born in March 1979. Radio locations of M13 were all in or near his mother's home range until 27 February 1980 when M13 was located away from his mother's home range for the first time, sleeping in an area approximately 10 km southeast of F7's range. On 7 March 1980, M13 was back in F7's home range in a snow tunnel (see Appendix B-e.) with his mother and a radiocollared adult male (M21). On the next day, the juvenile was again located outside his mother's home range near the 27 February location. He was in this area on 9 March as well, but on 11 March, the juvenile was found 60 km to the south along the same drainage where M8 was trapped the year before (Figure 2-11).

Although these are the only verified cases of dispersal, circumstantial evidence indicates that dispersal of young may occur at least as early as January and as late as May. Before this study was initiated, a female wolverine was captured, eartagged, and released in the study area incidental to other research. The animal was tagged in

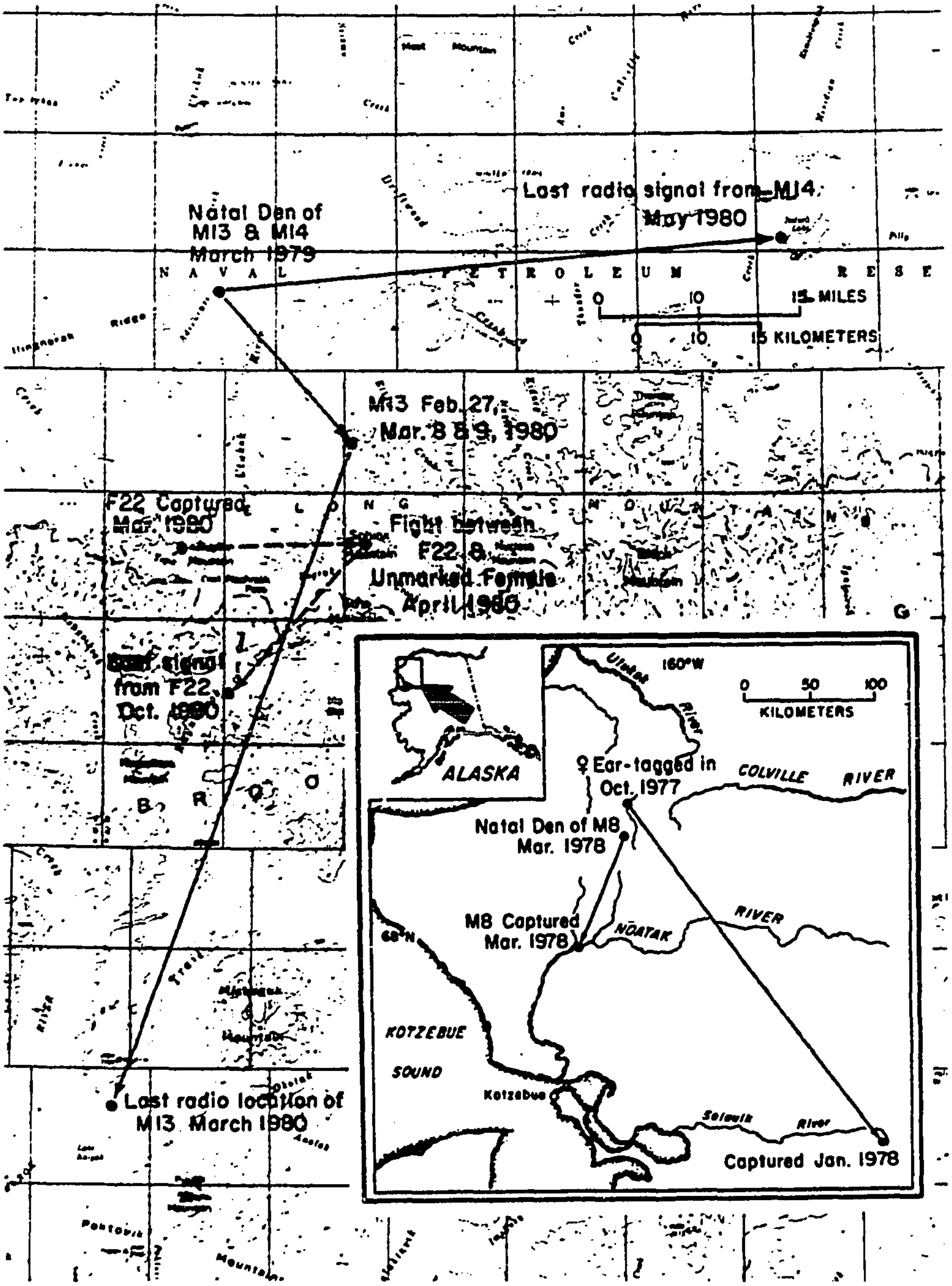


Figure 2-11. Possible and verified cases of dispersal by juvenile and subadult wolverines radiocollared in northwestern Alaska. The two longest movements are presented in the insert.

October, and a trapper reported taking an eartagged wolverine in January approximately 300 km south of the study area (Figure 2-11, see insert). Since it is very unlikely that any other wolverine had been eartagged in Alaska at that time, I assumed the tagged wolverine originated in the study area. Though the ear tags could not be recovered, they were reportedly the same color as those on the wolverine tagged in the study area. There is no way to know if the wolverine had been born in the study area; she may have been a transient. Her teeth showed no wear and only one cementum annulus was read from a premolar taken at the time of her capture. Because a canine tooth section from a 1-year-old male (M8) had only one cementum annulus, I believe the tooth section for the female indicated she was approximately 1 year old. In addition, her teats averaged <1 mm in length, suggesting a young wolverine.

One member of each of two litters born in the study area may have moved out of the study area in midwinter before they were a year old. Female juvenile F16 (sibling of F15) and male juvenile M14 (sibling of M13), both born in March 1979, were still in the study area in November 1979. However, when field work was resumed in February 1980, circumstantial evidence suggested that the two juveniles were no longer in their mothers' home ranges. F15 was captured on 14 February and her mother F10 on 24 February, but F16 was not recaptured. F16 had been eartagged on 29 May 1979, but she was not radiocollared. F16 probably would have been recaptured if she had still been in her mother's home range. Though neither M13 nor M14 was recaptured after November 1979, M13 was relocated nine times in his mother's home range between

25 January and 7 March 1980 just prior to his dispersal. On three of these occasions, he was with his mother. His sibling M14, however, was never seen with his mother again and was not relocated after November 1979. At that time, M14's radio signal was erratic so the radio may have been failing. On 17 May 1980, a signal corresponding to M14's was received 40 km east of his mother's home range (Figure 2-11), but the source of the signal could not be traced and the signal was never heard again.

A young male wolverine (M2) was possibly dispersing from the study area or passing through it in spring 1978. His radio signal was heard 10 times in a relatively small area (31 km^2) between his capture on 15 April and the disappearance of his signal after 6 May. A search was made within a 150-km radius of his last location, but no signal was received. At first I attributed the disappearance of his signal to radio failure, but after further experience with radiotracking wolverines in mountainous areas and knowing the distance that some dispersing wolverines covered, I believe it is possible that the male moved out of the study area. Whether this male was born in the study area is not known. His average testis length (20 mm) was less than that of the other three males captured in April 1978 (27 mm).

A similar incident occurred involving F22, a young female whose place of birth was unknown (length of teats and condition of her teeth indicated she could have been a yearling). On 18 March 1980, she was captured and radiocollared. She was recaptured on both the following 2 days in another trap 4 km from her original capture site. On 24 March she was 10 km to the east, and on 9 and 10 April, she was located in an area 8 km farther to the northeast. On 24 April she was again seen in that area fighting with an unmarked wolverine judged from its size to be another female. F22 eventually ran from the unmarked wolverine which gave chase for about 300 m; F22 continued running for another 400 m. She was seen the next day 3 km northeast of where the fight took place and then never located in the study area again. In October 1980, a radio signal corresponding to hers was heard by a biologist flying over the headwaters of the Kugururok River just south of the Brooks Range (Figure 2-11). Due to inclement weather, he could not pinpoint the location or verify the signal. If the signal was that of F22, she had moved approximately 15 km south of her original capture site.

Discussion

Home Range Size.—Until recently, most information on wolverine home range and movements was obtained by tracking wolverines in snow during winter. This method of collecting home range data is complicated by difficulties in consistently identifying individual wolverines and defining their residency status. Bjärvall's (unpubl. ms.) method of snowtracking denning females in March and April probably gives the most accurate estimates of home range using snowtracking techniques. In Bjärvall's study, two skiers followed a denning female's tracks each morning in suitable weather, one following the track from where it led away from the den and one following the track from where it led back to the den until they met or gave up tracking. In this manner, the identity of the wolverine was substantiated and the skiers could estimate the area they did not cover. This method of snowtracking to estimate home range, however, is limited to denning females in March and April.

The development of radiotelemetry was necessary before information could be obtained year-round for all sex and age classes. Hornocker and Hash (1981) initiated the first radiotelemetry study of wolverines in 1977 in Montana. Another radiotelemetry study was being conducted in southcentral Alaska by Gardner (1985) during the time my study was underway in northwestern Alaska. The three study areas are geographically and ecologically distinct. Because the investigators used different methods of collecting, analyzing, and presenting data from the three studies, I found it difficult to determine if differences in average home range size were caused by technique or by actual differences in the wolverine populations in the three areas.

In Hornocker and Hash's (1981) study, the average yearly home range for males (422 km^2) was smaller than both the average summer (626 km^2) and the average yearly (666 km^2) home ranges for males in my study area, and their average female yearly range (388 km^2) was larger than the average summer (94 km^2) and average yearly (103 km^2) home ranges for Driftwood area females. Hornocker and Hash's method of calculating yearly home range differed from mine in some respects. In their study, all locations for an individual wolverine were combined to obtain one yearly range estimate for that animal, regardless of how many years the animal was studied. Hornocker (pers. commun.) indicated that he used this approach because the wolverines' ranges did not differ appreciably from year to year. Hornocker and Hash (1981) recognized the problem of determining an average home range figure for a wolverine population without knowing the residency status of the study animals. In their study area, one female wolverine had a range of 963 km^2, which was as large as the largest male home range in my study area. They stated that the female's range was somewhat atypical, but they did not give an average home range size that excluded this female. Finally, an average summer home range was not presented for their study animals except for two lactating females.

Hornocker and Hash (1981) stated that the two lactating females in their study area had much reduced spring (Mar-May) and summer (Jun-Aug) ranges of 100 km^2 each; these ranges were 74% smaller than their average yearly range. By comparison, the average home range size (Mar-Aug) of lactating females in my study area (70 km^2) was 32% smaller than the average yearly range; however, as I pointed out above (p. 15), yearly range in my study could be underrepresented to a large degree.

I believe the difference in home range size between lactating and nonlactating females in my study area could be due to the small number of females in the sample and to the difficulty of locating lactating females away from their dens in March and April. About 17% of the difference in average home range size between lactating and nonlactating females was due to the greatly expanded home range of F7 in 1980 when she did not rear young. I do not believe this expansion was necessarily influenced by her nonlactating condition (see pp. 68-70). Furthermore, because lactating females spend an appreciable amount of time at their dens in March and April, they are much less likely to be found near home range boundaries during radiotracking flights than are nonlactating females. It would have been interesting to know Hornocker and Hash's (1981) average home range size for resident nonlactating females during March-August.

The method used for determining home range size for lactating females must be taken into consideration when comparing results between study areas. The ranges of the lactating females in Hornocker and Hash's (1981) study (100 km^2 each), in Gardner's (1985) study (92 km^2), and in my study (99 km^2, 56 km^2, and 55 km^2) were considerably smaller on the average (84 km^2) than the average (170 km^2) for three denning females in Bjärvall's (unpubl. ms.) study in Sweden (221 km^2, 180 km^2, and 109 km^2) even though the North American animals were tracked over a longer period of time. The larger home range size in Sweden may reflect actual differences between the Swedish and the North American wolverine populations. On the other hand, Bjärvall's method of snowtracking probably took him to the limits of his females' ranges considerably more often than did the radiotracking technique for investigators in North America, possibly resulting in more accurate estimates of home range size; the average size in the North American studies could be underestimated.

It appears that average male home range size in my study area is somewhat larger than that in other study areas, at least in summer. The largest home range in Gardner's (1985) study was 637 km^2 for an adult male from April 1980 to April 1981. The summer home range (10 Apr-15 Oct) for this male was 451 km^2. The average summer home range for three males (excluding juveniles) in Gardner's study was 385 km^2. Gardner did not calculate an average annual home range for male wolverines but instead cited Whitman and Ballard's (1984) estimate of 535 km^2 which they derived using a logarithmic curve analysis of wolverine home range data from the Susitna River study area. Hornocker and Hash (1981) calculated only an average annual home range (422 km^2). However, they did present data on two male summer home ranges (190.4 km^2 and 125.7 km^2) but gave no ages for these males. It is important to note the age of the wolverines because juvenile home ranges approximate the mother's home range.

Gardner (1985) determined that the summer home ranges of adult males in his study area were significantly smaller than those in my study area. He postulated that the difference was due to greater elevational range, more habitat diversity, and more stable and varied prey base in his area. However, I suspect that the proximate factor influencing adult male home range in summer is breeding activity (p. 66). The density and reproductive condition of females in the area are probably more important to male home range size than food or habitat. Ultimately, of course, habitat diversity and food availability are important because of their influence on the density of females, the size of female home ranges, and the number of males competing for females.

Home Range Overlap.--It is important to establish to what degree and by which segments of the population home range overlap occurs if average home range size is to be used to estimate population density or size. The exclusive use of summer home ranges for female wolverines in my study area was clearly evident (Figure 2-3). Hornocker and Hash (1981) stated that, in their study area, home ranges were not exclusive, overlapping between individuals of the same and opposite sex; however, they did not discuss overlap on a seasonal basis. They did point out that they were not always able to establish the residency status of individuals in their population, indicating that at least some overlap could have involved transient wolverines.

The data from my study demonstrate that it is important to establish the familial relationship of individuals of the same sex with overlapping home ranges. Females with overlapping home ranges might be mother-daughter combinations (see Chapter 3 and Figure 2-4). Home ranges of young males which have not yet dispersed may be overlapped by resident adult male home ranges. The range of adult male M21 overlapped that of M13 until M13's dispersal at 1 year of age. Juvenile M8's home range was overlapped by that of adult male M3 in summer 1978. Gardner (pers. commun.) verified that the only case of overlap in male wolverine home ranges which he observed in his study area involved a juvenile and an adult male.

It would have been interesting to have recorded the movements of adult female F19 through summer 1980 to determine if her range contracted after April when food becomes plentiful in the study area;

however, this could not be done because she had dropped her collar. Her frequent excursions into the home ranges of other females during winter 1980 (pp. 38, 44) probably resulted from impending starvation and attraction to baited live traps, for nearly all sightings of this female on the west side of the Utukok River were at baited traps. Once she killed and ate a red fox that was caught in one of the traps; she was also observed trying to kill another fox caught in a trap in the same area. She was livetrapped more times than any other wolverine and was the only adult wolverine to consume the bait after capture in the traps. At her last capture on 10 April 1980, she seemed lethargic. She had very worn teeth and was apparently an old animal. Hornocker and Hash (1981) noted that, in their study, both wolverines that starved to death visited bait stations frequently, relying heavily on the baits just before their deaths. Because F19 was still alive in early May, she probably survived; food becomes abundant in the study area by late May.

F24's movement to the south side of the Brooks Range in 1983 (p. 44) may also have been related to food resources. Hornocker and Hash (1981) do not discuss the overlap in wolverine home ranges which they observed in relation to time of year or to food availability. Other studies have shown that, during times of food shortage, resident animals may abandon their home ranges at least temporarily (Bailey 1981, Miller and McAllister 1982).

Hornocker and Hash (1981) postulated that human exploitation may be responsible for the overlap in home ranges of wolverines in their study area. They suggested that mortality from trapping in their study area may be severe enough to contribute to behavioral instability causing a breakdown in the territorial system. They stated that territorial defense by wolverines in the Montana study area was essentially nonexistent (citing Koehler et al. 1980). They pointed out that unexploited mountain lion (*Felis concolor*) populations showed a highly refined system of territoriality (citing Hornocker et al. 1969 and Seidensticker et al. 1973), while exploited populations were not territorial at all (citing Hornocker 1976). There was only one observed mortality in my study area during the study period (M17 in spring 1981). The lack of human exploitation could have contributed to the apparent exclusiveness of female home ranges in my study area, but I am reluctant to agree that intrasexual overlap of wolverine home ranges would indicate breakdown in territoriality (see pp. 108-112).

Movement Patterns.--It appears that movements of adult male wolverines during the summer are significantly influenced by breeding activity. While the distance between daily radio locations for males was four times that of females, rate of travel was only twice that of females. This suggests that male wolverines are more active, spend a greater proportion of their active time traveling, or travel more direct routes than females. Because males probably monitor the breeding condition of four to six females in their home range from at least May through August, they probably spend a greater proportion of their time traveling, and their movements would tend to be less circuitous and cover greater distances than those of females. Hornocker and Hash

(1981) stated that male wolverines in their study area made longer, more direct movements than females. Females had a "progressive travel pattern directed toward a more uniform coverage," while the males "traveled to the extremities of their range in relatively shorter periods than did females." This appeared to be the case in my study as well.

Differences in the distance between daily radio locations (daily distance) between females may be due, in part, to differences in home range size. For F7 and F10 in 1979, there was a 47% difference in daily distances. Because F7's home range was 51% larger than F10's that year, there was a higher probability of locating F7 at greater distances on consecutive days than there was for F10. However, when F7 expanded her range in 1980, the difference in home range size between F7 and F10 increased an additional 20%, but the difference between their daily distances only increased an additional 3%. This was because F10 increased her daily distance by 48% without increasing her home range size appreciably (3%). This suggests that factors other than home range size influence distance between daily locations.

The increase in daily distance from 1979 to 1980 for F7 and F10 was probably related to the presence of juveniles in 1979. It could be argued that the increase for F7 was solely the result of the increase in her home range size. However, F10's increase in daily distance was not associated with an increase in home range size. When raising young in summer, female wolverines return periodically to rendezvous sites and spend a relatively large proportion of time there. Radiotracking locations would have a higher probability of being recorded near these sites, resulting in smaller daily distances even though the actual distance traveled may be greater than in years when females did not raise young.

The reason for the increase in the size of F7's home range in May 1980 is not clear. When F7 was first observed in the new area, she was traveling rapidly and scentmarking vigorously. She appeared very interested in other scent that she encountered. It appeared that another wolverine had been in the area. Perhaps F7 was responding to the scent of a male in breeding condition. The greatest average distance between radio locations for F7 in summer 1980 (11 km) occurred in the period just prior to breeding (Figure 2-9a) and may have been related to the approach of the breeding season. However, it is questionable whether F7 expanded her home range in 1980 solely to seek a mate. Her use of the 1980 addition continued into August even though her 1980 mating was on 11 June within her 1979 home range boundary. The breeding male (M21) was present in her 1979 range during the preceding winter and was observed near her there on at least two occasions in April 1980. The male was observed in the 1980 addition as well.

It is not likely that F7's expansion occurred as a result of food shortages in her 1979 home range. The expansion occurred in May when food resources become abundant in the study area. In addition, the expansion occurred to the north, encompassing mainly low tussock tundra, which appears to have fewer food resources than does the higher terrain to the south and west. The presence of a caribou carcass in the northeastern corner of F7's 1980 home range certainly influenced F7's continued use of the 1980 addition through the middle of July, but it was not the factor which initiated the expansion of her home range. Food was apparently in short supply during winter 1979-1980 (see Chapter 4), but F10, the resident adult female to the south, did not expand her home range in summer 1980 even though she was sharing it with a yearling daughter.

Another explanation of F7's range expansion in 1980 is possible. The disappearance of an adult female residing north of F7's 1979 home range could have initiated the home range expansion of F7. In April 1980 (about a month before the expansion), a young female (F23) was captured in the area which was to become F7's 1980 home range addition. F23 was probably a yearling (see Table 1-1). She was initially sighted near the northern boundary of F7's 1980 home range addition. F23 ran into the 1980 addition when chased with a snowmobile and was captured and radiocollared there. The next day her radio collar was found lying on the ground 10 km north of the addition (Figure 2-4), indicating that her home range, if she was a resident, lay north of F7's. If F23 had been born in that area, it would indicate that an adult female had resided in the area the preceding summer. If this adult female died or dispersed, F7 may have expanded her home range to incorporate part of the neighbor's range. In territorial species, resident adults are known to extend their home ranges into adjacent areas upon the death of the neighboring resident (Erlinge 1968; Rogers 1977:132).

It is possible that F7 usually occupied the entire 1980 home range in years when she did not raise young, restricting herself to the southeast portion of her home range when she had young. However, there is no evidence to indicate that this is the case other than her use of the larger area in 1980 when she also had no young. F10 did not show a similar expansion in 1980 although she had no young. However, the continued presence of F10's yearling daughter in 1980 may have been a factor in this difference between the two females.

Dispersal.—Dispersal of juvenile wolverines occurred during their first winter, but not all juveniles dispersed. Female F15 was still in her natal area in July 1981 when she was 28 months old and radiotracking was terminated. She may have established residency near her mother's home range. Storm et al. (1976) found for red foxes that 80% of subadult males but only 37% of subadult females dispersed during their first winter. By the end of their second winter, 96% of the males and 58% of the females had dispersed at least 8 km from their natal areas in Storm's study. The distances traveled by dispersing wolverines may have been as great as 300 km in this study (Figure 2-11), but some female offspring may remain close to their mother's home range (see Chapter 3).

CHAPTER 3

SOCIAL BEHAVIOR

Results and Discussion

Female-Offspring Relationships.--Observations were made of female F7 and her 1978 and 1979 litters and of F10 and her 1979 litter. F7 and a male kit (M8) were both radiocollared on 29 June 1978 and radiotracked until 16 November that year. In 1979 female F7 had two new male kits (M13, M14) and female F10 had two female kits (F15, F16). I was able to radiocollar three of these four kits (M13, M14, M15) in late June 1979 when they were large enough to carry radio collars. Both M13 and F15 dropped their radio collars but were recollared in the fall.

Exact birth dates were not established. Radiotracking was not initiated in 1979 until 16 March, at which time denning was already underway for F9 and F10. In 1980 both F7 and F10 initiated what appeared to be denning attempts between 5 and 7 March; both abandoned the dens after 15 March. Factors which may have affected den abandonment are discussed below and in Chapter 4.

Females with young spent a large proportion of their time in the natal dens in March and April. In 1979 I located F7 on 14 occasions between 19 March and 17 April. She was away from her den on only two occasions, 2 km northwest of the den on 23 March and 5 km south of the den on 27 March. Adult F10 was located away from her den only twice in

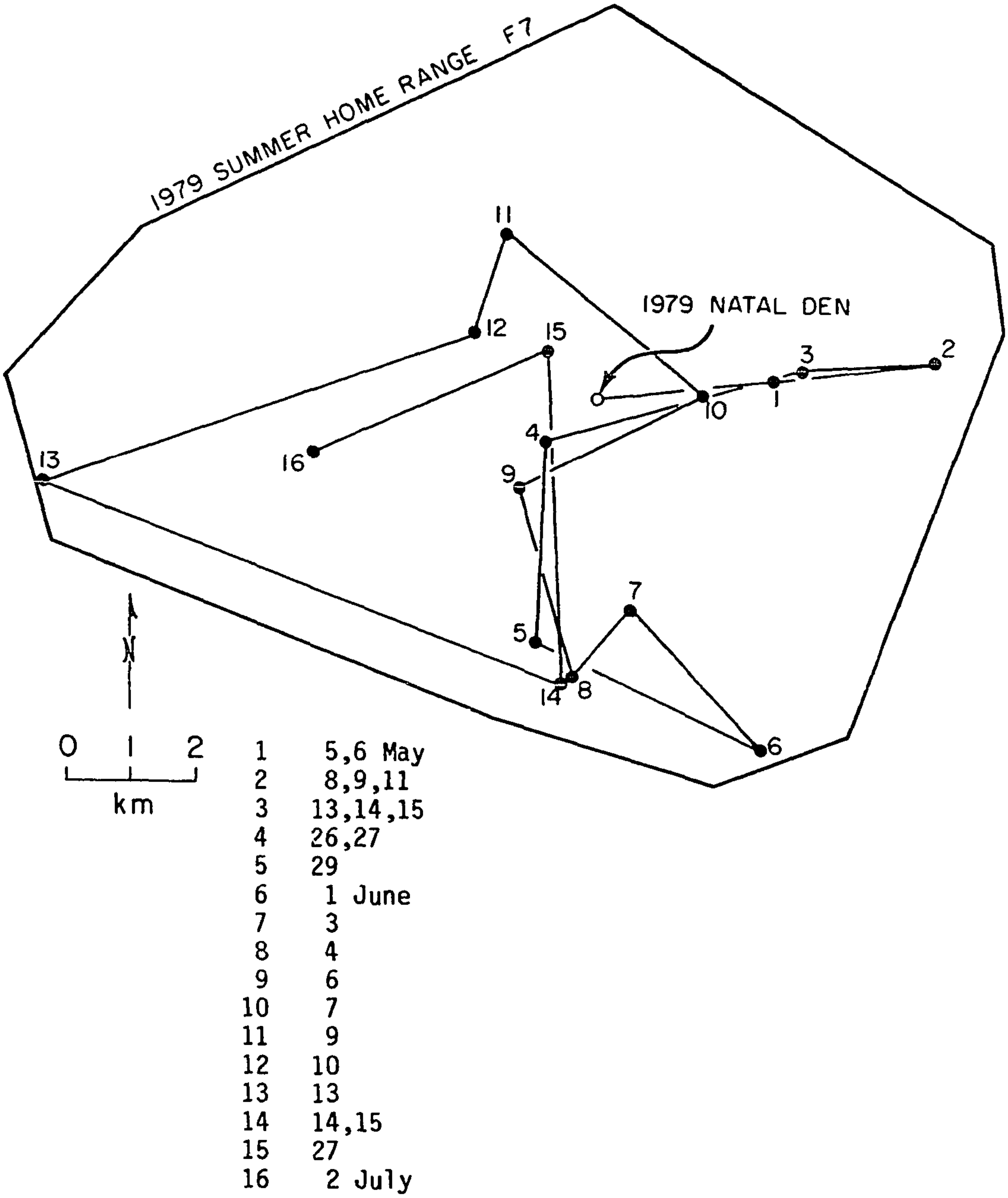
18 locations between 16 March and 18 April 1979, 2 km south of the den on 16 March and 2 km southwest on 27 March.

The timing of radiotracking flights may, in part, account for the high percentage of locations of denning females at their dens. The aerial radiotracking was usually carried out during the morning in March and April 1979. Of 18 radiotracking flights for which the time was recorded, 83% were made between 0900 and 1200. However, it appeared that F7 and F10 left their dens most often at midday during March and April. Ground observations at F7's den in 1979 indicated she was usually in the den between 2400 and 1200 and between 2100 and 2400; she was away from the den most often between 1300 and 1900. The four occasions when F7 was observed leaving her den fell between 1100 and 1300. This activity pattern may have been related to the midday peak in ground squirrel activity. In contrast, Bjärvall (unpubl. ms.) found that denning females in Sweden usually left their dens in the evening and returned sometime before morning. The major food source for these wolverines was caches of reindeer meat. Bjärvall suggested that wolverines in Sweden may have adopted nocturnal habits after years of persecution by hunters who track and shoot them.

The 1979 natal dens of F7 and F10 were kept under nearly continual visual observation during April, with the observers located 1.0 km and 0.6 km away, respectively, in a tent on the open tundra within sight of the dens. Both females were aware of the observers. The kits were not observed above ground, and the females rarely spent time in the general vicinity of the dens within view of the observers. The observers approached the den entrances on several occasions during the denning period and livetrapped F7 within 100 m of her den on 21 April 1979, but the females did not move their kits to new sites despite the disturbances. Both females appeared to abandon their dens between 28 April and 4 May due to spring melt conditions. Bjärvall (unpubl. ms.) stated that den abandonment by wolverines in Sweden due to human disturbance does occur and suggested that periodic moves to new dens regardless of disturbance may have evolved in response to a long history of hunters digging kits from dens.

After the natal dens were abandoned at the end of April 1979, it was possible to observe the females and kits from the air and occasionally from the ground. While the kits were still too young to travel with their mothers, the females hunted alone after leaving their kits at rendezvous sites (Figures 3-1 and 3-2). These sites were usually portions of snow tunnels remaining from winter (Appendix B) or remnant snowdrifts undercut by spring meltwater. Rendezvous sites used by F10 also included a rock cave and a boulder-strewn hilltop with no large snowdrifts in the vicinity of the kits.

The kits were periodically taken to a new rendezvous site. These moves, while sometimes triggered by disturbance from the observers, were made every 1 to 9 days regardless of disturbance, becoming more frequent as the kits grew older. By June, moves were made every day or every other day; the female would still leave the kits to hunt on her own. A minimum of 12 moves by F7 and her kits was documented between 28 April and 2 July 1979.



1	5,6 May
2	8,9,11
3	13,14,15
4	26,27
5	29
6	1 June
7	3
8	4
9	6
10	7
11	9
12	10
13	13
14	14,15
15	27
16	2 July

Figure 3-1. Rendezvous sites for female wolverine F7 and her two male kits from May to July 1979.

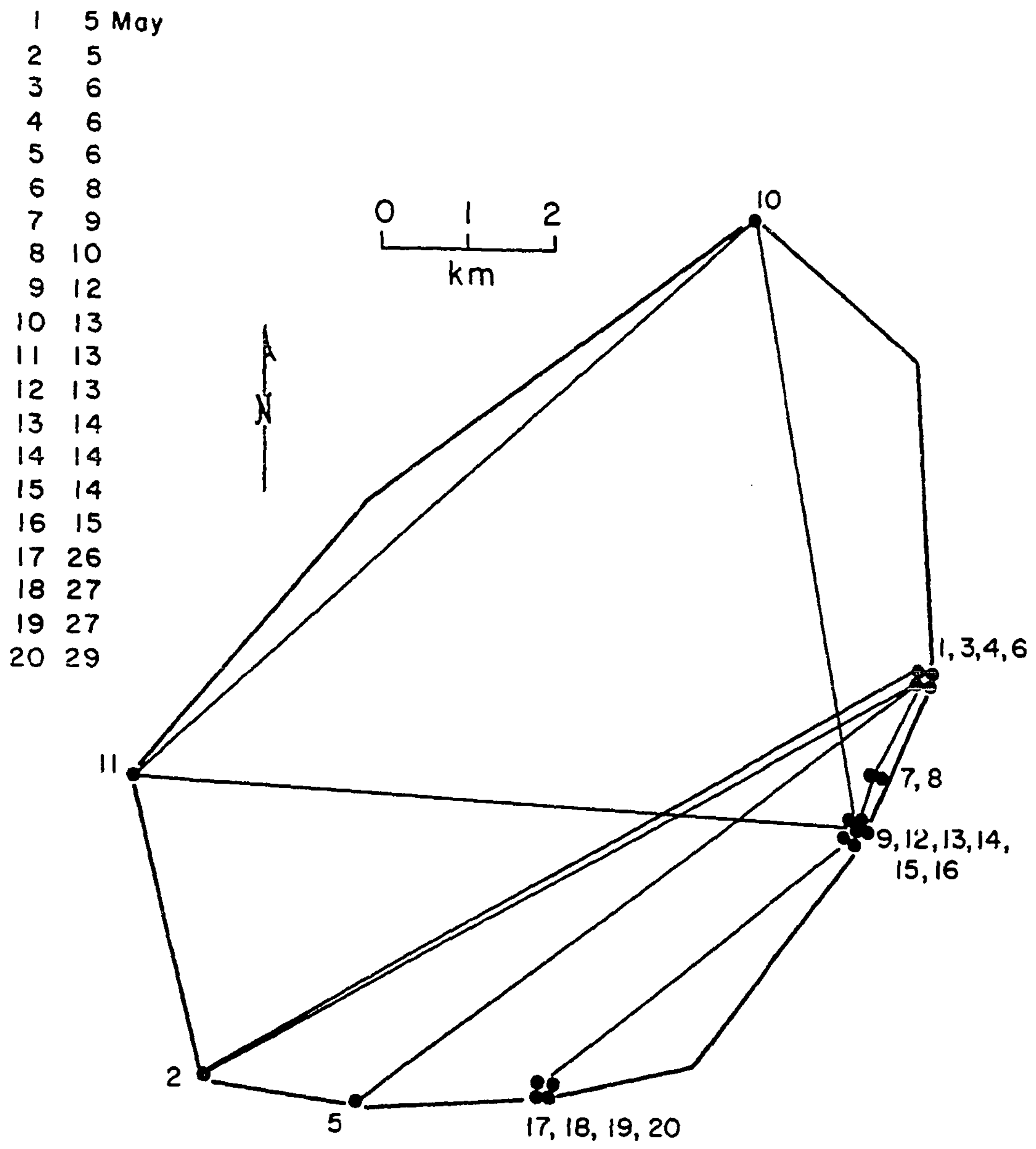


Figure 3-2. Radio locations of adult female wolverine F10 in May 1979 showing the concentration of her locations at rendezvous sites.

The longest observed distance between consecutive sites was 8.5 km between 13 and 14 June. The greatest distance that F7 was located from a rendezvous site was 12.2 km on 14 May. The average distance that F7 was located from a rendezvous site or suspected rendezvous site during May and June was 6 km (N=11).

The activity of F7 and her kits was observed at a rendezvous site on 2 June 1979 from 1030 until 1730. During this 7-hour period, the kits remained in an area of approximately 100 m^2 that included the upper portion of a large remnant snowdrift and the adjacent tussock tundra. The snowdrift had been undercut by meltwater that formed ice caverns beneath the drift with several entrances from the top and sides. The female remained with the kits most of the time but left the area to hunt at 1447 and returned at 1558. While at the drift, the female played with the kits periodically for a total of 55 minutes. She initiated three of six play bouts. The female spent a total of 52 minutes moving about the site, exploring the drift, rolling, digging, and grooming. She spent a total of 117 minutes resting and 20 minutes feeding on what appeared to be an arctic ground squirrel that she had brought back to the drift at 1558. During the remainder of the time, she was out of sight under the drift or behind tussocks and was probably resting.

The total time spent playing by one or both kits was 146 minutes; investigating the rendezvous site totaled 11 minutes. One or both kits rested for 119 minutes and fed for 21 minutes. Both kits were out of sight for the remainder of the time.

While the female was feeding on a ground squirrel on the snowdrift, she suddenly looked in the direction of the observers. She stood on her hind legs, began running down the drift, and then she disappeared into one of the holes in the drift. After repeating similar behavior for 42 minutes, she moved steadily away from the rendezvous site, stopping once to stand up to look in the direction of the observers. The kits did not accompany her and remained out of sight. The kits and female were located the next day 2.7 km away.

From 16 through 19 May 1979, nearly continuous observations were made at a rendezvous site where female F10 had taken her two female young between 10 and 12 May. The rendezvous site was a snow tunnel dug earlier in the winter. The young were playing and sleeping at the mouth of the tunnel between 0930 and 1100 on 16 May. During this time, F10 hunted near the rendezvous site and the kits remained outside the snow tunnel, but before F10 left on an extended hunt away from the rendezvous site, she carried at least one of the kits into the snow tunnel; the other one apparently followed. The kits did not reappear again during the entire observation period, probably because F10 became aware of the observers when she returned from the hunting trip. F10 left on these extended hunting trips on 16, 17, and 19 May between 1100 and 1300 and probably did the same on 18 May, but difficulties with the telemetry equipment prevented accurate documentation of her presence at the rendezvous site.

Though the kits were often left at rendezvous sites through June, they occasionally traveled with their mother as early as late May. I observed F10 carrying one of her kits under a snowdrift on 16 May, but on 27 May both kits were seen following the female to a new rendezvous site. The first time F7's kits were observed following her was on 29 May. By late June or early July, the kits had begun traveling with their mother regularly; by the end of July, the kits sometimes traveled without their mother but were rarely separated from each other.

In 1978 adult F7's male kit (M8) was captured on 29 June and radiotracked regularly through September. At the times of 10 radio locations from 29 June until 9 July, the kit was with his mother on all but one occasion (90%), 5 July, when the female was located 5.5 km from her kit. In 4 locations for August and 12 locations for September, the kit was with the female only 3 times (19%). The average distance separating them in August was 3.3 km and in September 3.5 km. In August 1979, F7 and one of her male offspring, M14, were together 6 times in 23 locations (26%). The average distance separating them was 2.3 km. Table 3-1 lists all the distances for the above observations.

Since M13 was not recollared until the end of August, only four radio locations are available for him in August. He was with his mother once. This male kit remained in his mother's home range until 7 March 1980. From 5 September 1979 until 7 March 1980, nine radio locations were obtained for him and F7; they were together on two occasions. The average distance separating them was 2.9 km; on four occasions, the kit was within 0.5 km of his mother (Table 3-1).

Because the siblings did not carry radio collars concurrently for more than a week during the tracking period, data on sibling

Table 3-1. Distances between female wolverine F7 and her offspring at the times of radio locations in northwestern Alaska, 1978-1980.

F7 and M8 1978		F7 and M13 1979/1980		F7 and M14 1979	
Date	km	Date	km	Date	km
29 Jun	0.0	19 Aug	4.0	4 Aug	0.0
30 Jun	0.0	20 Aug	0.0	4 Aug	2.8
1 Jul	0.0	23 Aug	3.6	4 Aug	4.0
1 Jul	0.0	24 Aug	1.7	5 Aug	2.8
3 Jul	0.0	5 Sep	9.1	5 Aug	2.8
3 Jul	0.0	28 Oct	0.2	6 Aug	2.3
5 Jul	5.5	13 Nov	0.1	8 Aug	1.1
5 Jul	0.0	9 Feb	0.5	9 Aug	0.0
8 Jul	0.0	10 Feb	0.0	9 Aug	0.0
9 Jul	0.0	28 Feb	5.9	9 Aug	0.0
3 Aug	0.0	4 Mar	7.0	10 Aug	0.0
23 Aug	3.1	5 Mar	3.6	11 Aug	2.0
30 Aug	7.5	7 Mar	0.0	12 Aug	5.8
31 Aug	2.7	8 Mar	13.0	13 Aug	7.2
2 Sep	2.3	9 Mar	13.0	13 Aug	1.9
3 Sep	4.2			15 Aug	1.8
6 Sep	4.1			16 Aug	4.0
7 Sep	4.8			17 Aug	1.8
8 Sep	0.0			19 Aug	4.0
11 Sep	0.8			20 Aug	0.0
13 Sep	2.3			23 Aug	3.8
18 Sep	2.9			24 Aug	2.7
21 Sep	5.5			27 Aug	1.9
22 Sep	0.0				
28 Sep	11.6				
28 Sep	3.1				

relationships are limited. In 18 days during August when M14 was located, M13 was observed with him on at least 10 days. On 6 days, M14 was located but M13 could not be found, though it is possible that even if he had been nearby, he could have gone undetected. On 23 August, the two siblings were separated by 6.8 km. On 27 August, M14 was located, but M13 was not, even though his radio was probably operational at that time.

Atypical movements of juveniles outside their mother's home range may precede dispersal. During their first year, home ranges of juveniles approximated those of their mothers (Figures 3-3 and 3-4). M13 was known to continue using his mother's home range until he was a year old. From 9 February until 9 March 1980, M13 was located 11 times in the study area before he dispersed on 10 March (Table 3-1). Of these 11 locations, M13 was with or near his mother on four occasions, was alone in his mother's home range on four occasions, and was 10 km southeast of his mother's home range on three occasions. Two of the three occasions when he was outside his mother's home range were just before his dispersal from the study area.

Several factors may have influenced M13's dispersal. M13 may have moved out of the study area in search of food. On all the occasions after 9 February when he was located in the study area, he was in or near holes dug into the snow. He was observed following his mother to one of these holes and also was seen sitting outside another while his mother was inside. Holes such as these were often the sites of cached

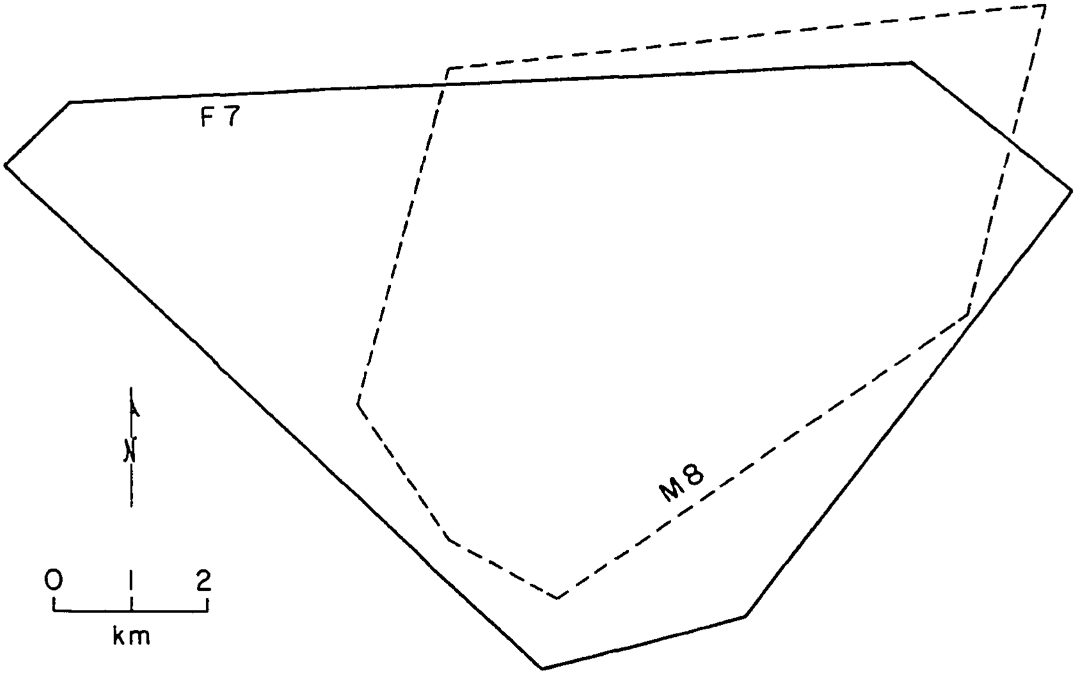


Figure 3-3. Home ranges of female wolverine F7 and her male kit (M8) from 29 June to 15 November 1978.

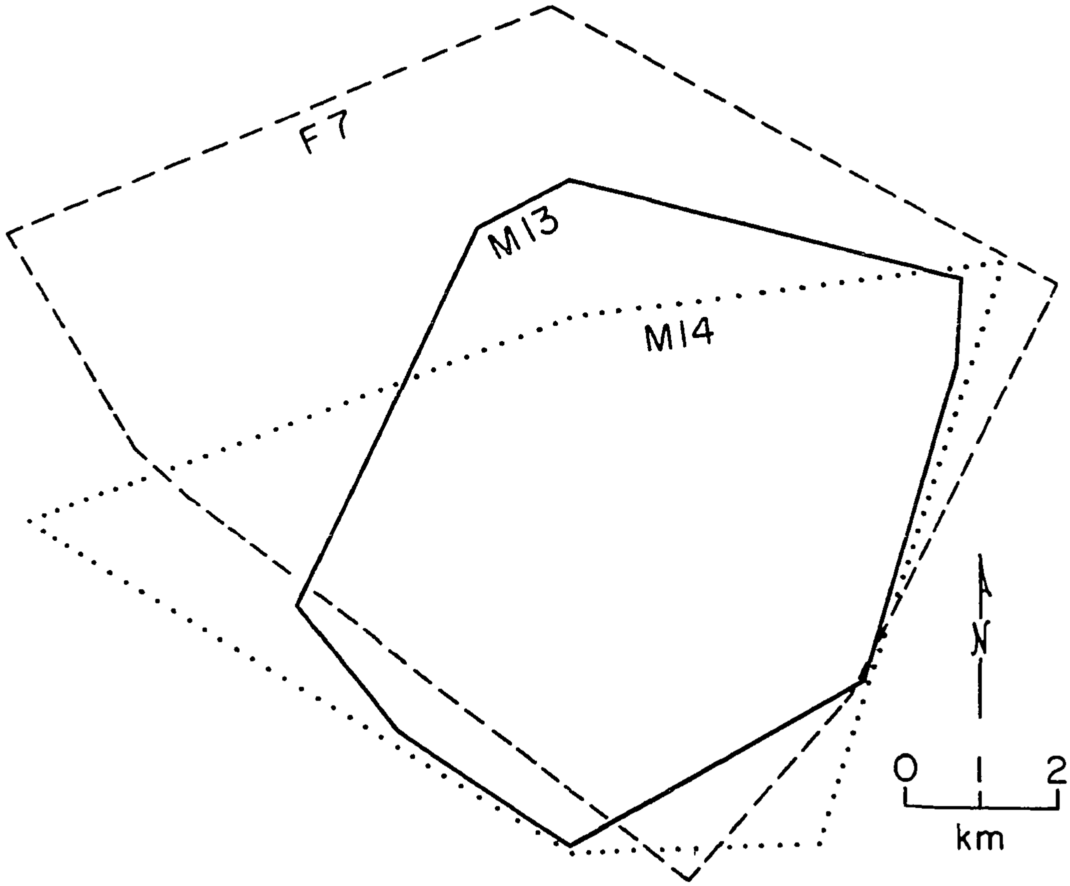


Figure 3-4. Home ranges of female wolverine F7 and her two male kits (M13, M14) from 31 July to 13 November 1979.

food items (see Chapter 4). There was no evidence to indicate F7 shared food with her yearling offspring.

Another factor which may have influenced M13's dispersal was confrontation with an adult male (M21). On 7 March, M13 was located in a snow tunnel with his mother and M21. On the following 2 days, he was located approximately 10 km outside his mother's home range, then he left the study area on 10 March. When the snow tunnel (see Appendix B-e.) was excavated in May, blood mixed with snow was found scattered along a side tunnel near the entrance. This side tunnel appeared to be more recently excavated than the rest of the snow tunnel and curved upward toward the surface; a similar situation was not found in any other excavated tunnel. The yearling male may have been attacked by the adult male and attempted to dig out of the snow tunnel to avoid him.

On the other hand, M13's dispersal may have been influenced by interactions with his mother, F7. I believe F7 was attempting to den on 7 March at the time M13 was located in the same snow tunnel with her and the adult male. F7 continued to use the snow tunnel for an additional 8 days after M13's dispersal but then abandoned the tunnel.

Finally, the approach of the breeding season may have had an influence on M13's dispersal. He might have dispersed at that time regardless of his interactions with other wolverines.

F15, born to F10 in March 1979, remained in the study area until she was at least 28 months old. As a juvenile, her home range probably approximated her mother's (see p. 80), but both wolverines had dropped their collars in early July and could not be tracked. In Figure 3-5, F15's home range during her first summer is shown as identical to her mother's. In the following summer as a yearling, F15's home range was centered farther to the north but still overlapped her mother's home range by over 60%. In 1981, when she was in her third summer, F15's home range appeared to be centered even farther north, but locations for her were limited, and her mother's range could not be determined that year.

From March through August 1980, yearling F15 was located an average of 5.9 km from her mother during 64 radiotracking flights. On only five occasions were they less than 1 km apart. The distance between mother and daughter increased markedly after March 1980. During March, F15 was located an average of 3.4 km (N=8) from F10. After March, the average distance separating the two increased to 6.0 km (April, 5.6 km, N=4; May, 6.4 km, N=12; June, 6.2 km, N=19; July, 5.6 km, N=14; August, 6.2 km, N=8).

The shorter average distance separating F10 and F15 in March was directly related to F10's use of a snow tunnel in the northern part of her home range, an area she seldom used after March. I assumed F10 was attempting to den in this snow tunnel; she was located in the tunnel 11 consecutive times between 4 and 15 March. On 10, 11, 14, and 15 March, F10 and F15's signals were coming from this snow tunnel at the same time. On 16 March, only the daughter's signal was received; the mother was not located. F10 apparently abandoned the den about this time. From 23 March to 26 April, F10 was located nine times. She was in or

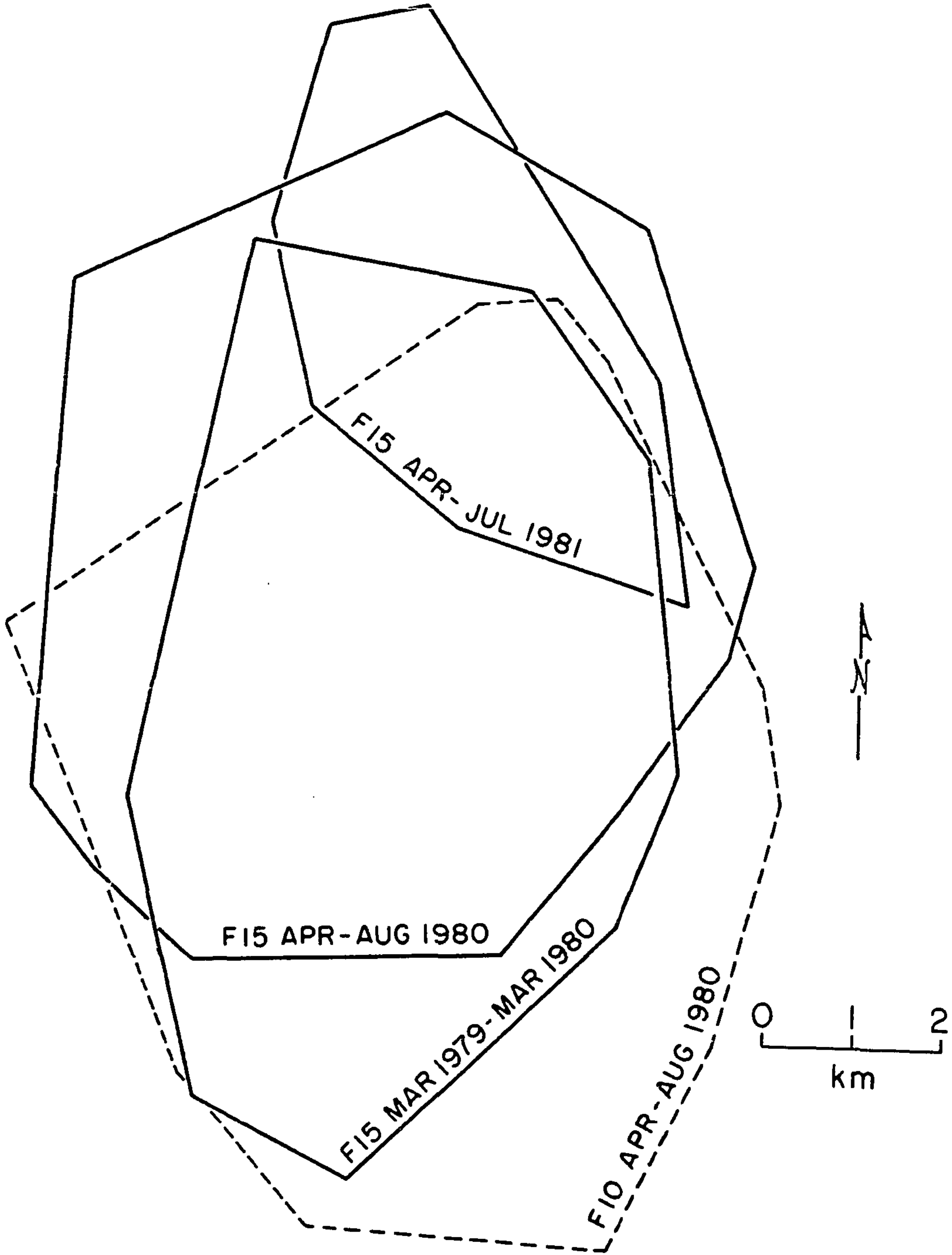


Figure 3-5. Home ranges of female wolverine F10 and her female kit F15 from March 1979 to July 1981, indicating a range shift to the north for F15. F10's radio transmitter was inoperable after August 1980.

near five different snow tunnels during this period, only one of which (29 Mar) was the original snow tunnel used in early March. The fact that the original snow tunnel was in the overlap area largely used by the yearling F15 and that F15 was located in the tunnel with her mother on four occasions during March accounted for the shorter average distance separating F10 and F15 in March. F10 remained largely to the south in the overlap area and F15 largely to the north after March (see Figure 2-6). The separation of F10 and F15 did not appear to be maintained through aggressive behavior because the two wolverines were observed playing together on 8 June 1980.

Breeding Behavior.--Breeding behavior was observed from the air on three occasions during the study (Table 3-2). Female F9 was observed breeding in 2 consecutive years, in August 1979 with an unmarked male and in June 1980 with M20. Female F7 was observed breeding in June 1980 with M21. The marked wolverines were known to be residents in the study area for at least 4 months before breeding occurred, and the breedings usually occurred within the known home ranges of the individuals involved. In one case, breeding possibly occurred outside the home range boundary of a female; the area where F9 bred in 1980 was 6 km southeast of her 1979 home range, but because her radio transmitter was inoperable in 1980, her 1980 home range boundary was not known. A visual location of F9 in February 1980 was about 2 km southeast of her 1979 boundary, suggesting a possible shift in her home range since summer 1979.

Table 3-2. Breeding behavior of three pairs of wolverines in northwestern Alaska, 1979-1980.

(F/M)	Date	Time*	Comments
F9/Un**	2 Aug 79	----	F9 observed alone for 1 hour
	6 Aug 79	1220	F9 with unidentified male, playing and resting together for 1 hour
		1900	Both resting
		2042	Copulation in progress, continuing for 12 minutes
		2125	Both active but not copulating
		2141	Both began moving away from the copulation site
		2243	Both together but not copulating
	7 Aug 79	0900	Traveling together
		2000	Both resting
	8 Aug 79	1030	F9 traveling ahead of the male by about 1 km; the male joined her in approximately 15 minutes
		2000	Both resting
	9 Aug 79	0930	F9 alone
		1607	F9 alone
F9/M20	6 Jun 80	----	M20 was 20 km NW of the breeding site
	11 Jun 80	1100	Traveling together
		1630	Both resting
		1830	Copulation in progress, continuing for 20-30 minutes
		1930	Both resting
		2300	Both resting
	12 Jun 80	0655	Both resting
		0747	Both resting
		1230	M20 hunting alone
		1330	M20 alone
	16 Jun 80	----	M20 was 9 km NE of F9's 1979 home range
F7/M21	1 Jun 80	1220	F7 with unidentified male
		1330	F7 apparently alone near a snowdrift
	2 Jun 80	0100	F7 alone
		1300	F7 alone
	5 Jun 80	0926	Copulation in progress, continuing for 56 minutes, then the wolverines parted briefly and recoupled for 20 minutes
		2100	M21 pursuing F7

Table 3-2. Continued.

(F/M)	Date	Time*	Comments
F7/M21, cont.	6 Jun 80	1230	Traveling together
		1255	M21 resting; F7 under a snowdrift
		1425	F7 resting; M21 may be under the snowdrift
		2045	F7 begins moving away from the snowdrift
	7 Jun 80	1000	F7 alone; still alone during the next 6 days (7 observations)

* Intermittent observations unless stated otherwise.
**Unidentified male.

Breeding pairs restricted their movements and remained together for 2 to 3 days. While a pair rested, males stayed within 1 m of the females. If females repositioned themselves farther away, the males would move closer to them. No body contact was observed during rest periods. The females usually initiated moves and took the lead when a pair traveled. The females showed interest in their surroundings, but males focused their attention on the females. While traveling, the males often tried to approach the females, but the females reacted defensively if approached closer than 2 m, turning abruptly to face the male and snarl or snap. Only once did a male (M20) appear to snarl at a female (F9). Males and females were never separated by more than a few meters except for two brief instances near the end of pair association.

Pair association was characterized by males aggressively attempting to subdue apparently reluctant females, generally resulting in agonistic interactions. An exception was noted on 6 August 1979. F9 and an unidentified male repeatedly investigated a rock outcrop together. Occasionally, F9 would suddenly dash away with the male pursuing her. F9 would then turn quickly to face the male, her forelegs spread apart and her rump raised. She would swish her tail rapidly from side to side, then run back to the outcrop. Both periodically rolled over and over separated by only a meter or so. Sometimes the female rolled, then the male approached the spot after she moved away. He sniffed the spot then rolled there himself. Once the female approached the male from behind and sniffed at his rump. When he showed no reaction, she swung around and bumped against him. The behavior of the two wolverines was decidedly playful in nature. Their play ended in a rest period at the end of an hour. When I returned to the site 7 hours later, copulation was in progress.

Copulatory behavior was similar in all cases, though I never observed initiation of copulation. The male had mounted the female from behind, his forelegs clasping the female's sides. Often the male grasped the scruff of the female's neck in his mouth, particularly if the female attempted to move. This neck bite was not maintained continuously. The wolverines rolled onto their sides periodically, and once F9 and the unidentified male rolled completely onto their backs while still clasped together. Several times F7 succeeded in breaking away from M21's grasp momentarily. No thrusting was apparent during the copulations I observed. After copulation, the separated wolverines rolled vigorously. F9 and the unidentified male remained active after copulation and moved away from the breeding site within an hour. F7 and M21 rested after copulation for at least 4 hours.

I am aware of only one other observation of a breeding pair of wild wolverines (Gardner and Ballard 1982:Appendix B) and two reports of wolverines that bred in captivity (Mohr 1938, Mehrer 1976). The description of breeding behavior observed in my study is in general agreement with that of Gardner and Ballard who described an observation (from the ground) of wolverines breeding on 9 June 1981 in southcentral Alaska. They reported vigorous and relatively continuous thrusting by the male during the first 50 minutes of copulation followed by intermittent thrusting for 49 minutes, for a total duration of approximately 99 minutes. In my study, initiation of copulation was not observed, which may account for the shorter duration of copulation bouts and the lack of thrusting observed. Long vigorous bouts of thrusting would have been detectable from the aircraft, but intermittent, less vigorous thrusting may not have been visible. However, the male periodically reestablished his hold on the female and at these times, thrusting may have occurred.

Gardner and Ballard (1982) reported very aggressive behavior (fighting and vocalization) for at least 15 minutes before initiation of copulation, and agonistic interactions occurred among all mated pairs in my study. The playful behavior of F9 and her unidentified mate on 6 August 1979 warrants elaboration since it was the only amicable interaction by a breeding pair that was observed. One or both of the wolverines may have been inexperienced and behaviorally immature. F9 was a young female (see Table 1-1) and almost certainly a first-time breeder. Sexual inexperience has been recognized in male mink (Mustela vison) and resulted in prolonged precopulatory behavior (MacLennon and Bailey 1972); however, the authors did not describe playful behavior. Also, interactions at the beginning of pair association may be less agonistic and more solicitous. The playful behavior associated in this case occurred the first time the pair was sighted. Pair association was the longest observed (2.3 days), suggesting that the pair was first sighted during the initial stages of their association.

Playful or solicitous behavior during breeding has been reported for other mustelids (Markley and Bassett 1942, Heidt et al. 1968, Hatler

1976), but it was not always clear when during the breeding season this behavior occurred. Markley and Bassett (1942) stated that marten (Martes americana) become more aggressive during the latter stages of the breeding season. During the postestrus period, the male marten tends to "annoy" the female, but her "antagonistic attitude" soon discourages the male from further attempts to mate. Hatler (1976) stated that sexual harassment by male mink actually resulted in the deaths of some females during the breeding season. The use of snowdrifts by wolverines during pair association appeared to be an attempt by the female to escape excessive attention from the male. Females sometimes hid or rested in cavities beneath the drifts. Agonistic behavior by the female may also serve to discourage harassment from the male.

These observations on wolverine breeding behavior substantiate Rausch and Pearson's (1972) conclusions from carcass examinations that wolverines breed during the summer and that the breeding season is several months long. However, they stated that wolverines apparently breed in May, June, and July, whereas this study indicates that August should be included.

It is not clear what determines the timing of copulation for a female wolverine and why the breeding season is so prolonged. Observations during this study suggest several possibilities. Young females may take longer to come into estrus, especially if it is their first breeding season. F9 bred on 6 August 1979 when she was probably about 17 months old (see Table 1-1), but she bred in June during the

1980 breeding season. Storm (1972) found that adult red fox vixens tend to breed 1 to 3 weeks earlier than 1-year-old vixens.

Females that are not raising kits may come into breeding condition earlier than females with kits. In 1978, while she was raising a male kit, F7 was traveling with an adult male in the middle of July. The kit was not with the pair. The pair was assumed to be breeding since mature males and females were not seen traveling together except when paired. In 1980, when F7 had no kits, she bred in early June. Perhaps estrus in a postpartum ovulator can be delayed by the demands of lactation.

Young females and lactating females are likely to be more nutritionally stressed upon entering the breeding season than mature females that are not raising kits. If nutrition is an important factor in the timing of estrus, females entering the breeding season after a particularly stressful winter due to old age or physical impairment are likely to be late breeders as well. Therefore, in a wolverine population, there are likely to be females at different levels of reproductive readiness. If, as results from Chapter 2 indicate, male wolverines maintain relatively large home ranges which encompass several exclusive female summer ranges, a male would have to travel extensively in order to "monitor" the breeding condition of the females in his range. A long breeding season would, therefore, be an advantage for the male in maximizing the number of females with which he breeds. To ensure that breeding occurs, it would be advantageous for female wolverines to remain in estrus until breeding has occurred and to be induced ovulators. Prolonged estrus and induced ovulation has been demonstrated for at least some of the mustelids (Ewer 1973:295). I found no evidence of female wolverines undergoing more than one pair bonding in a season as reported for marten (Markley and Bassett 1942); however, two copulations separated by 3.5 hours during one pair bond were documented (Table 3-3). Also, female wolverines can and do breed in consecutive years regardless of whether kits are produced from the previous year's breeding (see Chapter 1:Reproduction).

Other Social Interactions.--During the study, 15 interactions between wolverines (not including females with their juvenile young, mated pairs, or sibling groups) were observed (Table 3-3). Three interactions involved play behavior, four involved agonistic behavior, and four were neutral. In four instances, the type of interaction could not be determined because the wolverines were out of sight under the same snowdrift.

Adult male and female wolverines were sometimes located near each other even though they were not breeding. On 29 June 1978, I listened to the radio signal of adult male M3 for 2 hours without sighting him, while he apparently rested near an area where F7 was playing with her 4-month-old male kit. Later in July, M3 and F7 were observed traveling together in F7's home range; they were probably breeding, though this was never verified by observations of copulation.

On at least five occasions between 7 March and 1 April 1980, adult male M21 visited the immediate area of a snow tunnel being used by adult female F7. On 7 March, he was actually in the snow tunnel with the

Table 3-3. Intraspecific interactions by wolverines in northwestern Alaska, 1978-1980. The observations do not include those of mated pairs, sibling groups, or adult females with juvenile young.

Wolverines	Date	Comments
F7/F19/M13	9 Feb 80	All in the same area separated by less than 0.2 km, running in separate directions at the approach of the aircraft
F7/M21/M13	7 Mar 80	All in the same snow tunnel; no behavior observed; M13 dispersed 3 days later
F10/F15	10 Mar 80	Both in same snow tunnel; no behavior observed (but see discussion on p. 84 of text)
F10/F15	11 Mar 80	Both in same snow tunnel; no behavior observed
F4/Un*	26 Apr 78	Fighting
F4/Un	28 Apr 78	Fighting
F9/Un	10 Apr 78	Playing (see pp. 99-100 of text)
F22/Un	24 Apr 80	Fighting (see p. 59 of text)
F11/M12	7 May 79	Touched noses, then both went separate directions
F10/M12	13 May 79	F10 chased M12 away from her rendezvous site
F11/M12	31 May 79	Both together on a snowdrift, but M12 was disturbed by the approaching aircraft so no interactive behavior was observed
F10/Un	31 May 80	Both nosing around a rock outcrop separated by less than 3 m; F10 began moving away soon after she was sighted; the unmarked wolverine appeared frightened of the aircraft and did not follow her
F7/Un	1 Jun 80	The unmarked wolverine beside F7 ran under a snowdrift as the aircraft approached; no other behavior observed

Table 3-3. Continued.

Wolverines	Date	Comments
F10/F15	8 Jun 80	Playing
M8/Un	-- Sep 80	Playing (see pp. 99-100 of text)

*Unmarked wolverine.

female and her yearling male offspring M13 (see p. 83). On 1 June 1980, F7 was seen with a wolverine that disappeared under a snowdrift when the observers flew over. The unidentified wolverine could have been M21, but his radio collar had malfunctioned in late March, and visual contact was not maintained long enough to determine if it was M21 at that time. On 5 June, M21 and F7 were observed breeding; M21 was identified by his ear tags and bobbed tail.

M12's movements indicated that he periodically visited two radiocollared females (F10 and F11) through summer 1979 and was probably visiting other females farther to the west. Just before M12's capture on 7 May 1979, he was observed traveling past one of F10's rendezvous sites. He continued on into the home range of neighboring female F11. There he met F11, briefly touched noses with her, then continued on his way. In 28 radiotracking flights after his capture (8 May-23 Aug), M12 was located in F11's home range six times and in F10's home range nine times. All six of the locations in F11's home range were before July and, on three of the occasions, he was in proximity to F11. Three of M12's locations in F10's home range were before July and six were after July; only one radiotracking flight was made in July. Two locations for M12 were just north of F10's home range; the remainder were to the west of F10's and F11's home ranges.

M12 repeatedly visited F10 even though she was raising young. On 13 May 1979, M12 was not visually located, but his signal was received in the vicinity of F10's rendezvous site at 1315. The slow radio pulse indicated the male was resting. He was still resting when the observers returned at 1435, at which time the male ran past the rendezvous site within a few meters of the tunnel entrance. At the time of these observations, F10 was 5 and 8 km away, respectively, though her kits were in the snow tunnel at the rendezvous site. At 2240, M12 and F10 were running along the snowdrift near the rendezvous site, about 100 m apart, apparently disturbed by the tracking aircraft. On the following 2 days, M12 was located in F11's home range to the south, while F10 was located at the rendezvous site. Observations from the ground were made at the rendezvous site from 16 through 19 May 1979. On 16 May, M12 appeared at the rendezvous site as F10 was hunting nearby. M12 began following the female, but she turned and aggressively chased him for a few meters when he approached. He then left the immediate vicinity of the rendezvous site. About 2 hours later, F10 left the rendezvous site and remained away from her kits for about 6 hours. M12 was not located at the rendezvous site again until 20 May when his signal was received about 0.5 km from the site. F10 was believed to have abandoned the site on 20 May, possibly due to the presence of the observers.

Krott (1959) (cited in Haglund 1966) noted tracks of male and female wolverines together only in April and believed that male wolverines do not associate with the family group and are not even present in the area of the natal den. Haglund (1966) noted tracks of adult male and female wolverines together from January through March and saw a male and female together on 8 May.

While it appears that male wolverines do not assist in rearing young, males do apparently interact amicably with females that have young. In Bjärvall's (unpubl. ms.) study of denning female wolverines in Sweden during March and April, tracks of large wolverines believed to be males were observed several times at three of the four dens. One female very aggressively chased a male away from the vicinity of the den. But on 15 April, a male followed a female for more than 3.5 km and when he caught up to her, they ran around, climbed trees, and possibly mated. The male then bedded down and the female returned to her den. Later the male followed her tracks to about 1 km from the den, rolled in her urine spots, and bit little branches that he passed. In my study, male wolverines were known to visit females that were raising young in May, June, and July. The male's periodic association with females is most likely related to breeding and begins at least as early as March and well before pair formation. Some of the observations from this study suggest that once a male has bred with a female, he will subsequently spend less time in that female's range during the remainder of the season.

Playful behavior was observed between mated wolverines and between siblings and the dam. Playful behavior was also observed between wolverines that did not fall into these categories, but circumstances suggested the wolverines were probably familiar with each other. Play behavior between F9 and an unmarked wolverine in April 1978 and between M8 (offspring of F7) and an unmarked wolverine in September 1978 involved an unusually dark-colored wolverine, and both observations occurred in the same general area (east of F7's home range and south of F9's). In November 1979, an apparently old adult female, F19, was captured and assumed to be the unmarked wolverine in the observations above because of her very dark coloration and the fact that her capture site was near the area of these observations. She was also the same wolverine seen near F7 and her offspring M13 on 9 February 1980. During winter 1979-1980, she was repeatedly captured within F7's home range and radiotracked in adjacent areas, but no agonistic interactions were observed between her and other wolverines. The possiblity that F19 was related to F7 and F9 and even to other females in the study area is quite tenable. The fact that neighboring females in territorial mammals are likely to be related (Rogers 1977, MacDonald 1981, Lindstrom 1982) is probably at least partly responsible for the limited amount of aggression observed in field studies. Though males and females have been observed in aggressive encounters (e.g., preceding and following copulation and when females chase males from dens or rendezvous sites), actual fights between males and females have not been documented. Most fights probably occur between individuals of the same sex.

Hornocker and Hash (1981) stated that there was no sign of overt intraspecific strife of any kind during their snowtracking and radiotracking. In the present study, wolverines were observed fighting on three occasions (Table 3-3), and two males (M5, M6) had fresh wounds on their heads when they were captured in April 1978. Gardner and Ballard (1982) reported a wolverine that had probably been killed by another wolverine in their study area. Bjärvall (pers. commun.), while tracking wolverines in snow, found blood and hair where two wolverines had been fighting. All these instances of intraspecific strife occurred in the month of April, which suggests that the approach of the breeding season increases aggressive behavior or that wolverines are more intolerant of intruders at this time of the year.

Scentmarking.--Several methods of scentmarking were used by wolverines during this study. Urine was used most frequently and regularly along travel routes by both males and females during all seasons. The urine was usually deposited on protruding objects in the landscape. In 20 km of snowtracking a wolverine in October 1979 (probably M21), I noted a minimum of 40 urine deposits of which all but two were made on objects protruding above the snow surface. These objects included tufts of sedge, tussocks, and willow bushes. Urinations on clumps of exposed sod along the edge of a lake were accompanied by numerous scratch marks. Scratching was common at scent posts, particularly at the bases of larger willows. The same wolverine often deviated from its line of travel to mark protruding objects. In the two instances when the scent post was not noticeably elevated, the wolverines had still deviated to the spot. Larger protrusions seemed to have greater attraction, perhaps because they were more easily noticed, and the wolverines would deviate farther to these objects. Where protruding objects were numerous, marking appeared to occur at relatively regular intervals; when the wolverine crossed large expanses of undisturbed snow, it would often refrain from marking as frequently. The marking behavior of this wolverine was typical of wolverine behavior observed along most snowtracking routes. In October 1979, I observed male wolverine M13 urinating on a willow by lifting one leg as some canids do. Urination on the side of a snowdrift observed nearby could only have been made in this same manner. In contrast to urination, only one of seven defecations found along the tracking route was deposited near a particular object. This one scat was deposited beside a willow bush just after the wolverine left its bed. Defecation did not appear to be an active form of scentmarking though urination on older scats sometimes occurred; such scats, therefore, acted as scent posts.

The ventral gland and the anal sacs are probably used for scentmarking. Both male and female wolverines, as well as two male kits approximately 3 months old, were observed marking tussocks by straddling them and rocking with a side-to-side motion. Occasionally, a forward-and-backward motion was noted. It was not possible to determine if the ventral gland or anal sacs were being used.

I believe that scent gland secretions were sometimes being deposited without a rocking motion. While observing from the ground and the air, I could see wolverines stop and squat momentarily to urinate, but in some instances, a slight dragging motion forward was observed and was interpreted as marking behavior using glandular secretions. Since I was never able to verify this and because it was not possible to always differentiate between urination only and urination combined with "drag marking," this marking behavior was simply referred to as "marking." If rubbing was observed, then the behavior was treated separately and referred to as "rubbing."

While tracking wolverines in snow, I observed instances where the traveling wolverines deviated to a protruding clump of sedge or tussock, yet no urine was visible. Often the vegetation or snow was flattened where the wolverine had either sat or rubbed against the object, and a sweet musky odor was frequently detectable. Along a 10-km tracking route on 31 January 1979, a wolverine urinated approximately 35 times and "rubbed" 10 times. These rubbed areas always occurred less frequently than urinations. Likewise, when observing from the air, I noted wolverines "marking" much more frequently than "rubbing."

Large willows with base diameters of 6 cm or more were very often used as scent posts, particularly where they were solitary. So commonly were large willows used for marking that I could often predict a wolverine's line of travel while observing them from aircraft by noting where the large willows occurred ahead of it. It was not always possible to observe the wolverines marking the willows after they went beneath them, but in most of the instances that were observed, the scent was deposited near the base. A musky odor could usually be detected near the bases of willows that were marked along snowtracking routes. One male wolverine (M20) was observed visiting a large willow and pulling himself over a branch located about 1 m from the ground. He dragged his body over the branch rather than climbing over it, so that it was obvious that his ventral surface was making contact with the branch. While female F7 was traveling along the edge of the Utukok River, she stood on her hind legs on three occasions to sniff large willow bushes and marked at least one of them herself.

Sometimes freshly broken pieces of willows were seen on the ground beneath the marked bushes, and occasionally scratch marks or possibly claw or tooth marks were seen on the trunk. As I mentioned above, scratch marks in the snow were common. Urine was almost always observed under the bushes as well and was sometimes deposited over a distance of 10 cm or more, in a manner resembling canid urination using a raised-leg stance.

From calculations made in Table 3-4, it is possible to make some generalizations about scentmarking behavior by wolverines, at least during the summer. The average rate of scentmarking (including both "marks" and "rubs") was 0.5 marks per minute (N=19). Thirty-five of 206 marks (17%) were "rubs" (rocking motion observed); 8% of 36 marks by males were "rubs"; 20% of 163 marks by females were "rubs."

In three cases in which wolverines were observed from the air continuously for 1 hour, the average number of marks/km was between 3 and 7. Additional data on marks/km were not obtained due to the difficulty of measuring distance accurately. The average marks/km will vary depending on rate of travel (km/hr) and rate of marking (marks/min). Both of these factors are influenced by a wolverine's activity. For instance, during the time M20 was observed on 26 June 1980 (Table 3-4), he spent 15 minutes chasing a yearling caribou. The rate of scentmarking was the lowest observed; his rate of travel was the highest. Therefore, the number of marks/km (0.7) was very low relative to other observations. Wolverines rarely scentmarked while they were mousing intensely, digging for prey, or eating. If the time F7 spent

Table 3-4. Observations of scent marks made by wolverines in summer 1980 in northwestern Alaska.

Wolverine	Date	Duration of Observation (minutes)	Total Marks*	Rubs	Average Marks per Minute	Activity of the Wolverine
F7	4 May	60	13	0	0.2	Hunting and feeding
F7	15 May	60	36	15	0.2	Traveling
F7	17 May	15	6	1	0.4	Traveling
F7	18 May	15	14	7	0.9	Traveling
F7	20 May	12	7	?	0.6	
F7	20 May	12	4	0	0.3	Digging for 9 minutes
F7	22 May	15	5	0	0.3	Grooming and resting for 10 minutes
F7	15 Jun	7	9	0	1.3	Approaching a caribou carcass that she had visited earlier that day
F10	22 May	8	3	0	0.4	Traveling
F10	24 May	60	22	1	0.4	Hunting
F10	8 Jun	15	12	3	0.8	Traveling
F10	24 Jun	15	12	4	0.8	Searching for a caribou carcass or tracking F15
F10	24 Jun	15	9	1	0.6	Searching or tracking F15
F10	24 Jun	10	6	10	0.6	Difficult to keep her in view
F15	26 May	15	6	0	0.4	Traveling
F15	13 Jul	15	6	0	0.4	Traveling
M20	6 Jun	15	12	2	0.8	Traveling
M20	22 Jun	20	14	0	0.7	Traveling
M20	26 Jun	20	2	1	0.1	Chasing a caribou
M20	18 Jul	15	8	0	0.5	Mousing

* Includes "rubs."

eating on 4 May (29 minutes) is substracted from the total time observed, her rate of scentmarking while actually traveling would be twice that recorded. Wolverines also appeared to scentmark less when traveling together as a mated pair, at least during the period when the male is in proximity to the female. During his pair bond with F7, M21 was observed rubbing only twice. The rubbing occurred in a 30-minute period during which he was frantically attempting to reestablish visual contact with female F7 after temporarily losing sight of her.

A systematic attempt to study scentmarking was not made during this study, but the methods of scentmarking which were observed are similar to those described by other investigators for wolverines (Krott 1959, Haglund 1966, Pulliainen and Ovaskainen 1975, Koehler et al. 1980). Subjectively, it did not appear that marking was confined largely to home range boundaries. Wolverines appeared to mark throughout their home ranges. The intensity and frequency of rubbing appeared greater in situations where the wolverine was obviously excited and responding to olfactory stimuli, but rubbing was not limited to such situations. Urination and/or drag marking did not appear to be associated with an excited state in most instances.

The function of the various scentmarking techniques used by wolverines is unknown, but results from studies of other species suggest that the function of wolverine scentmarking with scent glands is dependent upon the particular gland used for scent deposition and the intensity and frequency of deposition. Ralls (1971) concluded that scentmarking in stoats (Mustela erminea) was probably an important agent for assessing asymmetry between dominant and subadult animals and that marking influenced an animal's self-confidence. Erlinge et al. (1982) examined the ecological significance of scentmarking by stoats, especially in relation to territory marking. Two types of marking were described: anal drag and body rubbing. When depositing anal scent, the stoats pressed the pelvis region against the substrate and moved forward with wriggling movements. The stoats appeared to be able to differentiate between their own odor and that of conspecifics in anal sac secretions. In body rubbing, they rubbed the ventral and front-lateral parts of their body on objects in their environment. The two types of marking were used in different situations. Anal drag was used to impregnate the home area, to mark new objects, and to mark over the scent of conspecifics. Body rubbing was associated with dominance in close aggressive contacts between conspecifics. Though stoats showed great variation in marking frequency, no consistent differences were observed between males and females. The authors noted the similarity between their findings and those of Rasa (1973) for dwarf mongoose (<u>Helogale</u> <u>undulata</u>). Anal gland secretions carried an individual's odor, whereas cheek gland rubbing was used during threat behavior. Rasa noted that the dwarf mongoose was unable to differentiate between individual cheek gland secretions but was able to detect differences in concentrations and time since deposition. The results of these studies suggest that wolverine "rubs" may be associated with the ventral gland and that "drag marks" involve the anal sacs. The excited state in which wolverines were often seen "rubbing" suggests an association with dominance status and the regularity of "drag marking" suggests familiarization with a home area.

General Discussion

The basic social system of Mustelinae has been referred to as "intrasexual territoriality" by Powell (1979). Powell's definition of a territory is an "area of exclusive use" that "implies priority access to resources" and "may imply defense (by aggression or by marking)." Ewer (1973) used the term "territory" to characterize the wolverine's spacing strategy based on Krott's (1959) observations that males exclude other males and that females are also mutually exclusive. Haglund (1966) and Pulliainen and Ovaskainen (1975) used the term "territory marking" when they described marking behavior by wolverines. Later, Pulliainen (1981) suggested that the term "territory marking" may be inappropriate for wolverines since the function of marking behavior is not clear. He suggested that scentmarking by wolverines may be related to patterns of resource use rather than to territorial defense based on his observations of similar behavior in pine martens (_Martes_ _martes_). Koehler et al. (1980) contend that wolverine scentmarking serves to separate wolverines temporally but not spatially. Hornocker and Hash (1981) concluded that territorial defense was essentially nonexistent in the wolverine population they studied, based on their observations of overlapping home ranges among the sexes (see Chapter 2). Though I use the term "home range" rather than "territory" in my study, there is evidence that at least female wolverines are territorial (i.e., defending areas of exclusive use) during at least part of the year. The general pattern of exclusive use of summer home ranges by female wolverines in the study area was so clearcut that the probable range of one female (F24) was predicted a year before she was captured based on home range data for the adjacent females. I observed both scentmarking and agonistic interactions by female wolverines, but more extensive studies would be necessary in order to demonstrate direct relationship to territory maintenance.

At least some of the confusion over territoriality could be explained by the complexity and flexibility of mammalian social systems. Studies of mammalian carnivores indicate that they have the ability to adopt different spacing mechanisms to meet changing environmental conditions. For example, recent studies have focused on the relationship of fluctuating food resources to the spacing strategy of the red fox (MacDonald 1981, Lindstrom 1982). In his study of bobcats (Lynx rufus), Bailey (1981) discussed the possible impact of environmental factors such as climate, habitat, den sites, and food on bobcat social organization. Hornocker et al. (1983) suggested that human exploitation can modify mustelid social systems. Their observations of intrasexual overlap in wolverine home ranges led them to speculate that human-induced mortality created behavioral instability in the social organization of wolverines in their study area. They predicted that, given favorable conditions and minimum exploitation, the wolverines would establish a functional, more traditional territorial system.

Removal of resident wolverines probably can cause changes in the social structure of wolverine populations, but intrasexual overlap in home ranges can be explained even in an intact territorial system. Studies of other species (Erlinge 1968; Rogers 1977:132) have demonstrated that when a home range is vacated (usually due to the death of the resident), neighboring individuals often attempt to expand their home ranges into the vacant area. If more than one individual attempts to establish residency in the area, conflict could occur, especially between individuals of near equal dominance (Ralls 1971). Where exclusive use of home ranges is not clearcut, wolverines may be in the initial stages of establishing territories. Territories may be more difficult to secure in heavily exploited populations where resident animals are removed at such a rate that most individuals establishing territories are immigrants unfamiliar with the area. Territoriality in such cases may still be functioning but at a level not readily apparent to investigators, especially in winter and early spring when wolverines are harvested.

Finally, intrasexual overlap in wolverine home ranges is probably not unusual for female wolverines even in unexploited populations (see Chapter 2). Female offspring of territorial species often share their mother's home range, the adult female either incorporating daughters within her home range or adjusting her home range to accommodate daughters. Lindstrom (1982) described the adaptive advantage that such a social system may have for red foxes. In red fox populations during conditions of increasing food availability, young, nonreproductive females remain within natal territories and family group size increases within the territories. Both the dominant pair of foxes and the daughters gain in fitness since the old vixen will be replaced by daughters if she dies, and the daughters have a higher survival rate as potential breeders living in their natal territory. In Rogers' (1977) study of black bears (Ursus americanus), young female bears tended to establish territories near their places of birth and mothers adjusted their territories to accommodate nursing daughters. Five adult females shifted their territories to include new areas away from their daughters. No mother shifted her territory toward the range of the maturing offspring, and no chases or fights were observed among close kin. Rogers suggested the adult females were better able to overcome the social pressures that were associated with range shifts than were immature or newly mature offspring.

A mechanism similar to what Rogers (1977) observed for black bears may have been operating in the wolverine population in my study area. A shift in home range utilization was apparently occurring in the case of F10 and her female offspring F15 (Figure 3-5). Data on annual movements of F10 and F15 are incomplete because of inoperative radio transmitters during part of the study period, but it was clear that utilization of the northern portion of her home range decreased for F10 during 1980 when F15 was a yearling using a portion of her mother's range. Further expansion northward by F15 as a 2-year-old may have been occurring in 1981.

CHAPTER 4

FOOD HABITS

Results and Discussion

Diet.--Most of the data on the wolverine's summer diet in northwestern Alaska was obtained by observing radiocollared wolverines, mainly from aircraft. Wolverines were observed eating, carrying, caching, or capturing 48 food items during 362 5-minute observation periods in summer (Table 4-1). The first 5 minutes of flight time over the wolverines was considered a sampling unit. There was only one food item per sampling unit, except for one case when a wolverine captured two ground squirrels within the same 5-minute period. Food items were not identified on 15 occasions but were visually identified or determined by the method of capture (such as mousing) on 33 occasions. Of the identified food items, 58% were ground squirrels, 18% were other small mammals, and 18% were caribou.

Wolverine food habits changed during the summer period (May-Aug). Wolverines foraged more often in August; the number of 5-minute sampling units in which foraging was observed was significantly higher in August than in the other summer months combined ($\chi^2=5.11$, $0.01<P<0.025$, df=1). In August, wolverine foraging and feeding activity involved ground squirrels much more frequently than all other food items combined ($\chi^2=12.27$, $P<0.001$, df=1). I believe the use of ground squirrels in August was directly related to the number and vulnerability of

Table 4-1. Number of times feeding behavior (eating, caching, or carrying food) by wolverines was observed from the air during 362 5-minute observation periods during summer in northwestern Alaska, 1978-1981.

Food Item	May	Jun	Jul	Aug	Total
Caribou	1	4	1		6
Marmot		1			1
Ground squirrels	3	1	4	11	19
Other small mammals	3	3			6
Ptarmigan		1			1
Total identified	7	10	5	11	33
Total not identified	3	2	1	9	15
Grand total	10	12	6	20	48
5-min observation periods	95	122	50	95	362

dispersing ground squirrels at this time of the year (Carl 1971, Green 1977).

The results presented in Table 4-1 and in the following observations suggest that diet was more varied in May and June than in August. Evidence found at a rendezvous site used by F7 and her kits on 2 June 1979 indicated that the wolverines had been eating ground squirrels, ptarmigan eggs, and microtines. During 149 minutes of hunting behavior on 4 June 1979, F7 made 34 searches for food items in tussock tundra. She pounced on seven occasions, probably for microtines but possibly for ptarmigan chicks, and was successful at least twice. In addition, she captured and cached an adult ptarmigan, found or caught a ground squirrel, and on two occasions appeared to find and eat some eggs.

Because so few radiotracking flights were made during winter, most data on winter food habits were obtained by analyzing scats that were collected along wolverine trails, at natal den sites, and at rendezvous sites. Many of the scats collected at rendezvous sites represent food eaten in early summer.

Eighty-two scats were collected along wolverine trails, most during November, February, and March 1979-1980. Caribou and ground squirrels occurred in 37 and 40% of the scats, respectively, and made up 35 and 32% of the total scat weight, respectively. Voles, lemmings, and shrews as a group occurred in 30% of the scats but made up only 6% of the total scat weight. The remains of birds and/or eggs occurred in only 11% of the scats and made up only 3% of the total scat weight. There were 13 g (3%) of unidentified food remains and 78 g (18%) of soil.

The frequency of occurrence and percent dry weight of the three most common food categories during three periods in winter are presented in Figure 4-1. Caribou remains were more frequent in scats from midwinter than from early or late winter ($\chi^2=6.26$, $0.02<P<0.05$, df=2), but the frequency of occurrence of ground squirrel and other small mammal remains showed no significant change during winter. The percent dry weight of caribou and ground squirrel remains showed seasonal changes that more or less corresponded to the changes in frequency of occurrence. This resulted from the fact that when caribou or ground squirrels occurred in a scat, each made up 80-100% of the total weight of all food remains in the scat in 80 and 85% of the scats, respectively. When other small mammals occurred in the scats, they made up 80-100% of the total food remains in the scat only 52% of the time.

The relationship between frequency of occurrence and percent dry weight is not exact. Note that percent dry weight is higher than frequency of occurrence for caribou in early winter and in midwinter but not in late winter (Figure 4-1a); percent dry weight is higher than frequency of occurrence for ground squirrels only in late winter (Figure 4-1b). In early winter and in midwinter, 62% of the heaviest scats (i.e., weighing more than the average for that period) contained caribou; as stated above, most contained 80-100% caribou. In late winter, 70% of the heaviest scats contained ground squirrels. None of the heaviest scats in any period contained the remains of other small

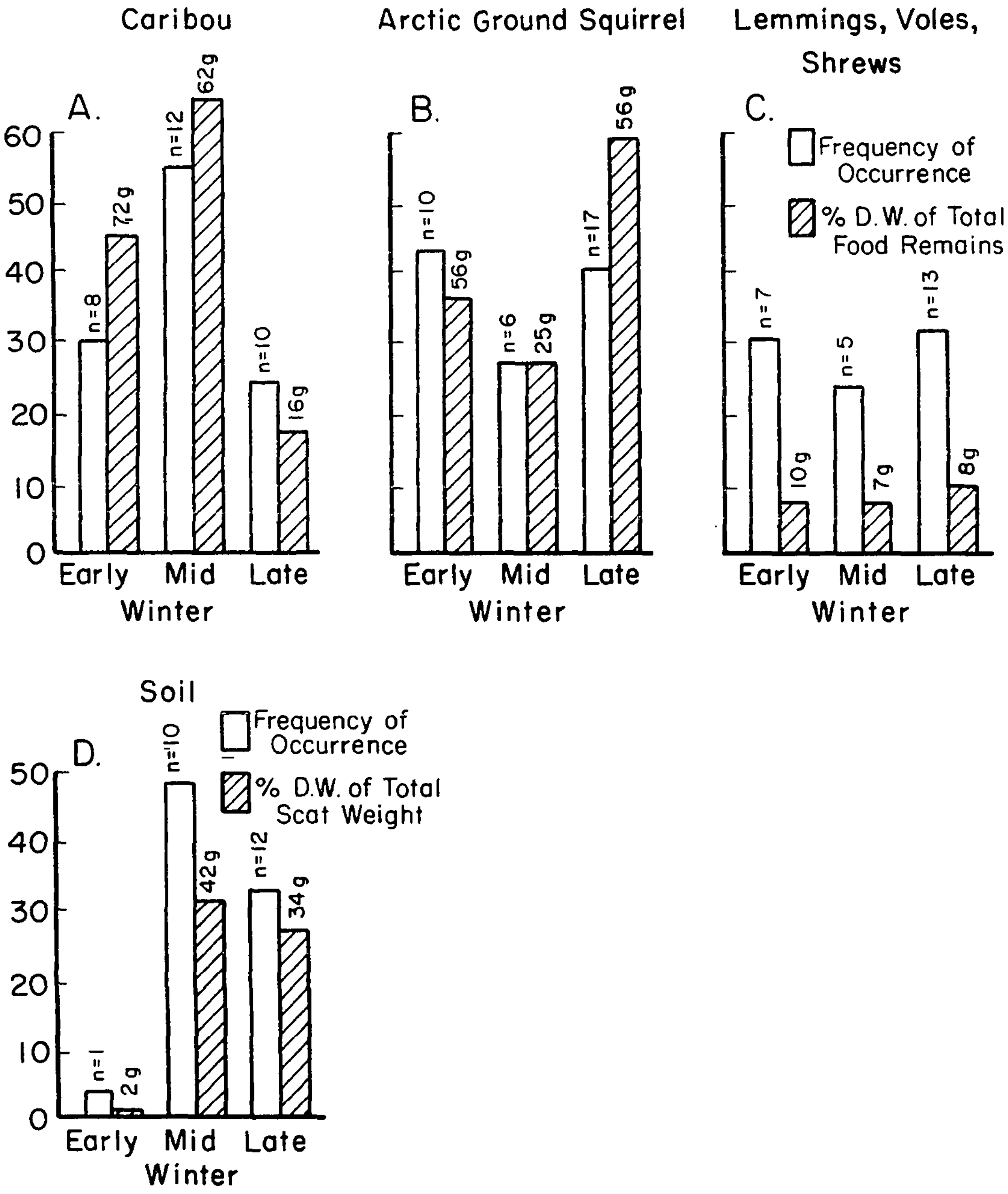


Figure 4-1. Frequency of occurrence and percent dry weight (D.W.) of the three most common food categories and soil ingested by wolverines in northwestern Alaska during three periods in winter.

mammals as the primary food category. These results suggest that the importance of caribou in the wolverine diet declined in late winter, whereas the importance of ground squirrel increased. Sources of caribou carrion may be exhausted by late winter, leaving wolverines dependent upon ground squirrels at a time when ground squirrels begin to become more available (see p. 132).

The percent frequency of occurrence of soil in the scats changed significantly through the winter (χ^2=9.94, $0.001<P<0.005$, df=2). Soil occurred more frequently and in greater proportions in mid and late winter than in early winter (Figure 4-1d). Most of the soil was associated with scats which contained ground squirrel remains. In early winter, 10% of the scats with ground squirrel remains contained soil, in midwinter 83%, and in late winter 50%. No scats with caribou remains contained soil in early winter, 33% contained soil in midwinter, and 20% in late winter.

Of 23 scats containing soil, 11 contained ground squirrel but no caribou; only 3 contained caribou but no ground squirrel. Four scats were made up entirely of soil. The remaining five scats contained a combination of food remains.

If it can be assumed that soil is passed through the intestinal tract at the same rate as caribou and ground squirrel remains, then it appears that soil is primarily ingested while wolverines are eating ground squirrels and that soil is more often associated with squirrels eaten in midwinter than in early or late winter. This is further supported by the proportionally lower percent dry weight in relation to frequency of occurrence for soil in midwinter (Figure 4-1d); because ground squirrels occur less frequently in scats in midwinter, soil by weight should be proportionally less. I believe the relationship of soil and ground squirrel remains is due to the use of cached ground squirrels, particularly in midwinter. Though fewer squirrels may be ingested in midwinter, those that are eaten are almost certainly cached squirrels in most instances (but see p. 131).

Scats collected at natal den sites represent food consumed primarily in March and April (late winter). Of 5864 g of scats collected at natal den sites (representing at least 300 individual scats based on the average weight of scats collected along wolverine trails), caribou and ground squirrels accounted for 92% of the dry weight of food items in the scats. The percentage of caribou and ground squirrels differed among years and among individuals (Figure 4-2). Scats collected at what was believed to be the location of F7's 1978 den contained 69% ground squirrel and 29% caribou remains by percent dry weight (Figure 4-2a). From scats collected at F7's 1979 den, the percentage of ground squirrel remains was only 40% and caribou was 52% (Figure 4-2c). Scats were not collected from F7's 1978 den until summer 1979 when the den site was discovered by a field assistant on 11 June 1979. The den site was recognized by the piles of scats and broken, matted vegetation where the tunnels and beds had been located. F7 and her 4-month-old kit had been captured in June 1978 in a nearby drainage at a rendezvous site. The high percentage of ground squirrel remains in the scats collected at the 1978 den could have been due to the den site

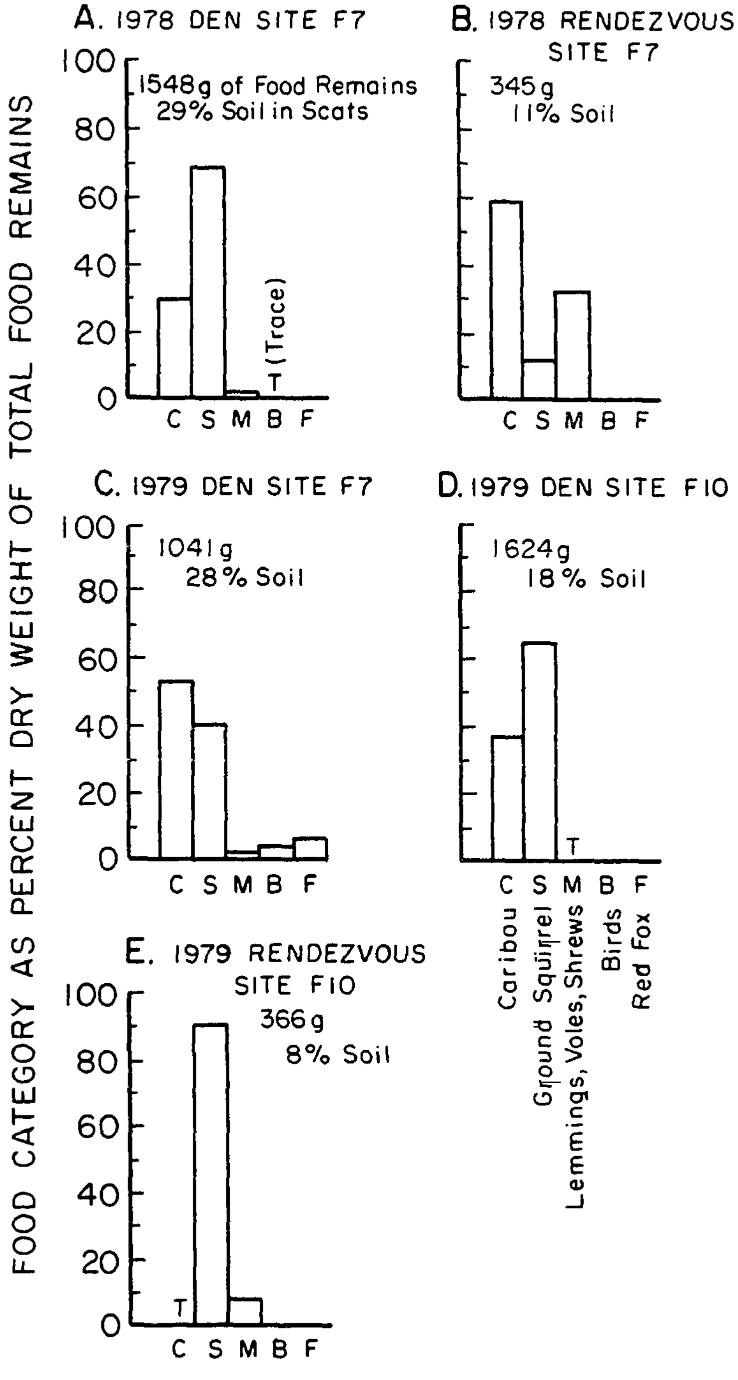


Figure 4-2. Percent dry weight of food remains collected at wolverine natal den sites and rendezvous sites in northwestern Alaska and the percentage of the total scat weight made up of soil.

itself having been used periodically as a rendezvous site during May and June 1978. F7's 1979 den was used only until 29 April, so the scats from this den represent food eaten in March and April 1979, which is the denning period.

Scats collected at F10's 1979 den contained 63% ground squirrel remains and only 37% caribou (Figure 4-2d). A relatively high percentage of ground squirrel remains by weight was found at the den, though F10 was known to have abandoned the den in late April 1979. The soil associated with food remains from this den was 10% less than soil in scats collected at F7's 1978 and 1979 dens. This difference in soil content suggests that more of the squirrel in food remains at F10's den were fresh kills and that fresh squirrels may be more available to F10 than to F7 in late winter. This assumption is not unreasonable since F10's home range contains more suitable ground squirrel habitat with higher terrain and numerous south-facing slopes.

Scats collected at rendezvous sites were deposited primarily during May and June. At a rendezvous site used from 12 May to 20 May by female wolverine F10 and her two kits, a much higher percentage of ground squirrel remains (89% of the dry weight of all food remains) was found than that at any other scat collection site (Figure 4-2e). Soil in the scats accounted for only 8% of the total scat weight. This snow tunnel was probably dug during the winter. The tunnel had thawed so that, by the time the kits were moved there, only the first 7 m of the tunnel were usable. The kits were being kept in a bed 4 m from the entrance. Scats were collected from the area surrounding the tunnel entrance.

Most of the scats were deposited in several large piles and probably represented food eaten only between 12 and 20 May.

Scats from a rendezvous site used by F7 and one kit were collected on 29 June 1978, at which time the two wolverines were still using the site. The date of the initial establishment of the site is unknown. Most of the scats probably represent food items eaten in May and June. The skeleton of a caribou was found about 600 m from the site. It was probably the remains of a caribou which died during the spring migration in May or June. As might be expected, caribou ranks high (58%) among food remains in the scats from this site (Figure 4-2b). Microtine remains were very high (23% by weight) relative to the other scat collections analyzed. The black matrix of these scats (as opposed to the more common white matrix found in winter scats, see pp. 137-138) probably resulted from a diet rich in protein from the caribou carcass. The black matrix accounted for 12% of the total scat weight from this site.

Some information on winter food habits was gained from examining areas where wolverines had been digging along their travel routes. In approximately 80 km of tracking wolverines in winter, 186 "digs" were found that could be attributed solely to wolverines. Of these, 110 had been dug into earth with no indication that a food item had been present. Fourteen were snow tunnels which were too deep to determine the contents. Six "digs" had flecks of blood indicating that the food items were fresh kills, probably microtines. Sixteen "digs" had ground squirrel remains (usually just a few hairs), 16 had caribou bone fragments, 5 had ptarmigan feathers, 1 had a whole shrew, 1 had a dried, mud-caked duck carcass, and 3 had eggshells. The remainder of the "digs" had been dug into snow with no evidence of food remains.

Foraging Behavior.--Wolverines hunting in summer coursed through their home ranges at a steady, moderate pace making many brief stops lasting 2-10 seconds to investigate odors or objects along the way. If a vole or lemming was discovered, the wolverine would pounce in the typical mousing posture of other carnivores. Sometimes pounces were interspersed with digging.

Ground squirrels were chased until they were captured or escaped into burrows. Wolverines rarely attempted to dig squirrels from extensive burrow systems, but if a burrow was shallow, the wolverine usually attempted to dig for the squirrel. Most often these shallow burrows were holes located beneath tussocks. The wolverine would alternate digging on opposite sides of a tussock, quickly hopping from one side to the other. Usually, the squirrel would attempt to run from the burrow after the wolverine had been digging for 5-10 minutes, and the wolverine would often capture the squirrel at this point. If the squirrel escaped into another shallow burrow, the wolverine followed and resumed digging.

While hunting, wolverines were observed to eat the contents of nests immediately, but other food items were sometimes carried and eaten later, taken to kits at a rendezvous site, or cached. Sometimes the item was left lying on the ground and returned to after the wolverine had finished searching the surrounding area for other food items or finished caching a different item. One wolverine (F9) that had killed two ground squirrels in rapid succession at the same site cached one of the squirrels 2 km from the kill site, then immediately returned to the kill site by the same route and carried the second squirrel several meters away and began feeding on it. This tendency for carnivores, during a hunting period, to cache food items before eating is common (Oksanen 1983). Nearly all ground squirrels eaten in winter were probably cached the preceding summer (see discussion below).

On three occasions in summer, wolverines were observed chasing caribou but no kills were made. A female wolverine (F7) was chasing two cows with calves when she was located on 3 June 1980, and she continued to chase the caribou for another 5 minutes without stopping. She was easily outdistanced by the caribou. On 12 June 1980, a male wolverine (M20) spent approximately 20 minutes chasing several groups of cows and calves. The caribou did not appear to be particularly disturbed by the wolverine, running only if the wolverine approached within 100 m. One cow with a calf attacked the wolverine, striking out at him with her front hooves. On 26 June 1980, this same male wolverine chased a yearling caribou for 15 minutes for approximately 3 km but was never able to approach closer than 35 m. Caribou appeared to outdistance wolverines easily during summer. As far as can be determined, caribou eaten by wolverines in summer in the study area were obtained as carrion.

Wolverine predation on caribou may be more common in winter, but few caribou are available in the study area at this time. An unmarked wolverine in the Driftwood area was observed trying to kill an adult bull caribou in October 1980. When it was first observed, the caribou was limping and bleeding from a foreleg as it moved along the Utukok River. Soon afterwards, a wolverine was observed running across the frozen river directly toward the caribou. When the bull became aware of the wolverine, it spun around and lowered its antlers. The wolverine quickly changed direction and ran behind the caribou, and the caribou turned to fend it off again. This was repeated several times while the wolverine remained about 5 m from the caribou. Finally, when the wolverine attempted to close with the caribou, the bull turned and ran, and the wolverine pursued it (J. A. Kermoian, pers. commun.). The wolverine chased the caribou for at least 8 km. I saw spots of blood in the caribou tracks along the route, but I was unable to determine the outcome of the chase since bad weather conditions prevented further tracking.

I received a report of a wolverine killing a yearling caribou on the arctic coastal plain north of the study area on 13 March 1978 (M. Kunz, pers. commun.). The episode occurred near Inigok Camp between Lonely and Umiat and was witnessed by all the camp personnel. The wolverine attacked the yearling, which was separated from the rest of the caribou in the area, by jumping on its back, upper neck, and the back of its head. The wolverine hung onto the caribou with its teeth and claws. Once the caribou fell, it did not get up again. About 2 days later a wolverine was observed near Lonely chasing a band of caribou for about 5 km along the beach. The wolverine remained in the area for 2 days, but no kills were observed.

Caching Behavior.—Caching behavior, observed on nine occasions, occurred throughout the summer (Table 4-2). Some caches were made by depositing the food item under a remnant snowdrift, but most were made by burying the item beneath a few centimeters of soil. Wolverines were observed caching freshly killed ground squirrels by digging a shallow hole in the tundra, then pushing soil or vegetation over the squirrel with their noses. Juvenile M8 cached a caribou leg on 4 September by merely pushing soil and vegetation over the leg with his nose. At one point, he appeared to pick up some vegetation in his mouth and deposit it on the cache. Caches were made between 0.5 and 2.0 km from the kill site.

Adult male wolverines were observed capturing, carrying, consuming, or caching food only 7 times compared with 43 times for females or their offspring. However, adult males were only sighted 74 times compared to 306 times for females or their offspring. When the number of sightings is considered, the number of observations of wolverines with food was not significantly different between adult males and females or their offspring.

While radiotracking wolverines in the winter, it was common to find a wolverine partially or wholly hidden in a freshly excavated hole in the snow with soil and vegetation spread around on the surface of the

Table 4-2. Observations of wolverines caching food in northwestern Alaska, 1978-1981.

Date	Wolverine	Item	Cache Site
28 May	AM*	Caribou	Under a snowdrift
4 Jun	AF	Ptarmigan	Under a snowdrift
18 Jun	AF	Caribou leg	Tussock meadow
31 Jul	AF	Ground squirrel	Upland tundra
2 Aug	AF	Ground squirrel	Tussock meadow
12 Aug	AF	Ground squirrel	In drainage with sedge in a tussock meadow
12 Aug	AF	Ground squirrel	In drainage with sedge in a tussock meadow
2 Sep	AF	Ground squirrel	Upland tundra
4 Sep	JM	Caribou leg	Upland tundra

*AM=adult male; AF=adult female; JM=juvenile male.

snow. In one instance, a male wolverine (M20) was half submerged in the snow, his tail and haunches protruding above the surface. At my approach, the wolverine ran from the hole where he had been feeding on a ground squirrel frozen into the soil. Half of the squirrel's body was still in the hole. The carcass was shredded and unfrozen where the wolverine had been gnawing. It appeared as though the sides of the hole had also been gnawed, suggesting that this is how much of the soil in the scats is ingested. The squirrel was located 10-15 cm below the ground surface under about 25 cm of snow. The hole was symmetrical, about 12 cm in diameter, and located in a large expanse of low-lying tussock tundra. This hole was similar to others I found while tracking during the winter. Often vegetation and soil were scattered over 3 m^2 with the small symmetrical hole located at the center of the disturbed area. A ground squirrel found in one of these holes (6 March 1980) must have been cached while temperatures were still warm, for the odor of decay was detectable. The opening of the hole was 30 cm by 58 cm in a tussock and sedge meadow. The hole was dug through 32 cm of snow and 10 cm of soil.

Eggshells found in three holes on 30 March 1981 must have been cached the preceding spring. These holes were located approximately 50 m apart in a sedge meadow. The snow cover was about 10 cm deep and the holes were about 5 cm into the soil.

One cache excavated by a wolverine on 21 October 1979 contained a dried duck carcass caked with mud under 20 cm of soil and nearly a meter of snow. The wolverine had detoured directly to the cache location, a distance of 10 m perpendicular to its line of travel.

Most of the caches utilized in winter were apparently made before the ground was frozen. Very few freshly made caches were found in winter and none contained appreciable amounts of food (usually just a shrew or fragments of ground squirrels or ptarmigan). Snow tunnels excavated in May that were used by wolverines in winter contained no food other than caribou bone or hoof fragments.

Wolverines were probably not responsible for making all the caches they utilized. Red foxes, common in the study area, are known to make food caches (MacDonald 1976). Many of the caches excavated by wolverines could have been originally made by red foxes. When a wolverine intercepted the tracks of a red fox, it would often deviate from its travel route to follow the fox tracks, sometimes over several kilometers.

Grizzly bears were responsible for making some of the caches used by wolverines in the winter. During the summer, grizzly bears were commonly seen at caribou carcasses which they had covered with soil and vegetation. The remains of a caribou fed on by a wolverine (F9) on 26 March 1979 were probably buried by a grizzly bear the preceding summer. The wolverine had excavated an elliptical hole about 10 cm across and 10 cm deep into the frozen ground and was gnawing on the caribou remains when I arrived at this site. A portion of a lower leg and the esophagus were visible beneath 4 cm of frozen soil. A strong odor of rumen and decay was evident. Usually, very little meat and often only a few bones were left at sites where bears fed.

Some caribou remains fed on by wolverines in winter probably were not cached but left lying on the tundra during the summer. The remains of three caribou calves were found in F7's home range in August 1979. One had not been fed on but lay decomposing in shallow water on the tundra.

It is not clear whether wolverines locate food caches through olfaction or by remembering cache locations; both factors are probably involved. MacDonald (1976) suggested, based on observations of captive foxes, that red foxes are able to remember cache locations exactly. However, his trials on cache recovery were made within days of the caching episodes. Memory must play some part in cache recovery because foxes in MacDonald's study could routinely recover their own caches but not those of other foxes, which apparently they found by chance. In winter, a wolverine usually traveled a more or less direct route through its home range, occasionally deviating to either side to investigate an object or odor. Periodically, a wolverine's more or less straight track would be interrupted by a series of tracks turning and doubling back several times over an area and, in most cases, a hole or several holes could be found among the criss-crossing tracks. Often this same pattern occurred where a wolverine had intercepted the fresh tracks of a weasel. Whether the wolverine was searching for the weasel or a cache of microtines which may have been made by the weasel could not be determined. This same zig-zag searching pattern was used by an adult female (F7) when she located three cached ptarmigan eggs in March 1981. The pattern gave the impression that the wolverine was searching, but whether she knew the general location of the caches or smelled the eggs and began to search for them is not known.

Some of the ground squirrels in the winter diet may be dug out of hibernation either while they are still alive or after dying due to starvation or exposure. Green (1977) stated that overwinter survival of hibernating ground squirrels probably depends on the amount of stored fat and the quality of the hibernacula. However, little is known about the qualitative differences in hibernacula or the survival rate of hibernating ground squirrels. On 24 March 1980, I found a hole which a wolverine had excavated through 15 cm of snow and 25 cm of soil in upland tundra with a slope of less than 10°. At the bottom of the hole was an enlarged cavity with ground squirrel hairs in it. The symmetrically round hole leading to the cavity was 17 cm in diameter. The enlarged cavity could have been a hibernacula. The average depth to the nest cavity of 20 hibernacula excavated by Melchior in northwestern Alaska (unpubl. data) was 42 cm with a range of 15-85 cm. These hibernacula were all in embankments or Fellfield slopes having an average slope of 24° with a range of 4-55°.

General Discussion

Wolverines appeared to be opportunistic in their food habits, responding to temporarily abundant or easily procurable food. Their diet reflected annual and seasonal changes in food availability. Late winter marked the beginning of a plentiful and varied food supply for wolverines in the study area. Ground squirrels emerged from hibernation from late March to mid-May. The earliest date of emergence observed during the study was 9 March 1980, though emerging squirrels were usually not a common sight until late March or early April. Immediately following emergence from hibernation, squirrels began setting up breeding territories and were particularly aggressive toward each other at this time. Green (1977) reported that agonistic interactions peak 2 to 3 weeks after the first squirrels emerge and that squirrels are particularly vulnerable to predation at this time. Therefore, it is not surprising that a relatively high proportion of squirrel remains occurred in scats collected at the natal den sites and along tracking routes in March and April. Wolverines were still eating cached ground squirrels in March; however, the decrease in the proportion of soil in scats from January and February to March indicates that the wolverines began to take freshly killed ground squirrels in March.

Other food items began to increase in the diet in May. Microtine remains in scats and observations of wolverines capturing or eating microtines were highest in May and June, a time when microtines become vulnerable to predation as their nest sites and runways are exposed by melting snow. Birds and eggs were more available in June, the peak of the nesting season. The spring migration of caribou through the study area usually begins in late May, and calving peaks between 2 and 10 June. Adult caribou dying during migration or calves dying at birth and shortly afterward provided carrion for wolverines at this time of year. Both wolverines and grizzly bears were sighted on caribou carcasses disproportionately more often in June, suggesting that caribou carrion is more available in June than in any other month.

As the summer progressed, ground squirrels made up an increasing proportion of the diet as other food items became less available and ground squirrels again became particularly vulnerable to predation. The significantly higher number of ground squirrels which wolverines were observed eating in August coincided with the peak in ground squirrel dispersal. At this time, ground squirrels were the most important food item in the wolverine's diet.

Berries and insects, which wolverines have been observed eating in summer in other studies (Krott 1959), did not occur in appreciable amounts in the study area and no evidence of wolverines using these foods was documented.

By early October, the availability of food for wolverines had begun to decline. Sightings and fresh sign of caribou and ground squirrels were essentially absent by the end of November. Ground squirrels began to drop off in the diet by midwinter and most of those that were eaten were probably obtained from caches made in summer and fall.

Ground squirrels were a staple in the diet of wolverines during most of the year. Squirrels reportedly do not undergo dramatic changes in abundance from year to year; the number of resident adult ground squirrels and the number of young produced and dispersing in the fall remain fairly constant (Carl 1971, Green 1977). However, the number of squirrels available as food for wolverines during winter may fluctuate depending on several factors.

Red foxes probably capture and cache considerable numbers of ground squirrels, particularly in August when ground squirrels are dispersing. During winter, utilization by foxes of alternate prey, mainly ptarmigan and microtines, may leave a large percentage of ground squirrel caches available for wolverines in years when ptarmigan and microtines are abundant; red foxes were observed capturing both food items in winter. The number of ptarmigan and microtines, however, did not appear to be high during most of the study period. High numbers of microtines were observed by biologists in the study area during the 2-year period preceding the study (J. C. Coady, unpubl. data), but when the field work was initiated in spring 1978, so few microtines were captured in snaptraps that trapping was discontinued. Arctic foxes were also numerous just before the study began (J. L. Davis, pers. commun.), indicating a high lemming population at that time, but they were rarely seen during the study. Only in spring 1980 was there some evidence of an increasing microtine population. In that year, microtines were observed around the field camp more frequently and avian predators such as short-eared owls (Asio flammeus) and long-tailed jaegers (Stercorarius longicaudus) were seen more commonly than in 1978 and 1979. The ptarmigan population was high at the beginning of the study in spring and fall 1978 but showed dramatic reductions by spring 1979 and through winter 1979-1980.

The size of the red fox population itself may influence the number of ground squirrel caches available to wolverines in winter. Red foxes were the only predators in the study area besides wolverines that regularly captured and cached ground squirrels. If fox populations are high and reproduction is good, many food caches may be made by foxes in the study area. A. B. Sargeant (pers. commun.) observed juvenile foxes making food caches even before they were old enough to leave the area of their natal den. The red fox population, which was high at the beginning of the study, declined noticeably over the study period. Fox hair and bones totaled 5% of the dry weight of the food remains in scats collected at the den of F7 the preceding winter (Figure 4-2c). Fewer foxes in the study area may have resulted in fewer ground squirrel caches available during winter 1979-1980 and would have meant fewer caches of other food items as well. Foxes in the study area were known to make caches in winter that were later excavated by wolverines.

Caribou were a primary food item for wolverines in the study area, but the availability of caribou may be influenced by several factors. Shifts in their use of winter ranges change the migration routes to the calving ground. Three important wintering areas for the WAH caribou were identified during the study period (Davis et al. 1982). Caribou wintering in the Selawik-Buckland area migrate directly through the study area on the way to the calving ground. Some of the caribou wintering in the central Brooks Range may pass through the eastern portion of the study area by traveling west along the northern foothills before turning north to the calving ground. But caribou wintering on the arctic coastal plain do not migrate through the study area in spring. The number of caribou using a particular wintering area varied substantially between years during the study (Davis et al. 1982). In those years when a large proportion of the herd wintered in the central Brooks Range and especially on the arctic coastal plain, fewer caribou would have been available to predators and scavengers in the study area during spring.

The total number of caribou in the WAH would also affect the number of caribou available to predators and scavengers. A major population decline in the WAH occurred between 1970 (240,000 caribou) and 1976 (75,000 caribou). Davis and Valkenburg (1978) estimated the herd was increasing at an average annual rate of 14% during the study period.

In some years, a disproportionate number of caribou may succumb to disease and/or parasites. Neiland et al. (1968) documented unusually high numbers of retained placentas in caribou from the WAH during the early 1960's. In June 1978, caribou biologists observed what appeared to be an unusual number of dead caribou in the study area. Though the cause of death in many cases was not determined, high parasite loads were obvious in several instances.

The distribution and abundance of predators in the study area could also influence the amount of carrion available to wolverines. Grizzly bears were observed killing caribou, both adults and calves, in the study area, but many of the caribou carcasses which grizzlies fed upon were scavenged by them (Reynolds 1980). Bears of all sex and age classes preyed upon or scavenged caribou, though Reynolds stated that some bears were more successful than others at killing caribou or maintaining possession of carcasses. Reynolds did not consider his data sufficient to estimate the extent of grizzly bear predation and scavenging on WAH caribou. Because the wolverine study area is located in an area of relatively high bear density in NPR-A, bear predation may provide a substantial amount of carrion for wolverines. On the other hand, because bears themselves are scavengers, they may consume more carrion than they provide, at least in some years.

James (1983) estimated that the wolf pack in the study area killed approximately 136 caribou from 20 April to 13 September 1978. No estimates were available for other years of the study. Most of the caribou kills were probably located in the central portion of my study area where radio locations of the wolf pack were concentrated.

It appears that the availability of food for wolverines was relatively low during the study, particularly after winter 1978-79. Food availability during winter 1978-79 was probably fairly good due to the unusual number of caribou dying during the preceding summer and to high ptarmigan and red fox populations. The results of the food habits analysis indicated that caribou remains may have been critical to the survival of wolverines in the study area during midwinter 1979-1980. Most of the caribou eaten in winter died before November. The remains of caribou carcasses that were available for winter use were mostly the remnants of carcasses buried by scavengers or bone and hide left lying on the tundra near carcass sites. It was not unusual to find winter scats (10%) that were made up entirely of caribou bone fragments held together by a white powdery matrix. Sometimes the only excrements found along winter trails of wolverines were small amounts of chalky liquid. Kruuk (1972) analyzed the very fine white powder in spotted hyena (Crocuta Crocuta) droppings and found that it consisted of $Ca_3(PO_4) \cdot 1.5Ca(OH)_2$ which is also the formula for inorganic matter in bone. He concluded that bone is digested by the hyena and only the inorganic matter is excreted. Bone may contain up to 40% organic matter, mostly collagen. Kruuk postulated that hyenas are able to use all the organic matter present in bones, not just the marrow. Van Zyll de Jong (1975) suggested that wolverines are morphologically and behaviorally adapted to a scavenging lifestyle, and Ewer (1973) referred to the wolverine as the "hyena of the north."

Wolverines are viewed largely as scavengers though most investigators recognize the ability of wolverines to make their own kills when the opportunity is available. In all studies reporting on wolverine food habits, large herbivores have been the most important food item in the winter diet (Pulliainen 1963; Makridin 1964; Haglund 1966; Myrberget et al. 1969; Rausch and Pearson 1972; Myhre and Myrberget 1975; Hornocker and Hash 1981; Gardner 1985; Bjärvall, unpubl. ms.; and others). Wolverines have been known to kill prey as large as moose (Haglund 1974), but most investigators agree that larger mammals are usually obtained as carrion in the wolverine's diet. In the present study, caribou composed a major portion of the wolverine's winter diet despite the fact that caribou do not generally occur in the study area during most of the winter. In this area, where caribou occur in large numbers only during the summer, wolverines apparently were able to subsist during winter 1979-1980 on caribou remains composed mainly of bone and hide, occasionally supplementing their diet with ground squirrels gnawed from the frozen tundra. The wolverine's ability to survive the most severe time of the year on such a meager diet attests to its efficiency as a scavenger.

There is evidence that such a restricted diet in winter 1979-1980 may have had some effect on wolverine reproduction in the study area. One adult female wolverine (F19) was considered to be malnourished that winter, perhaps even on the verge of starvation, based on her poor physical condition and the unusual number of visits she made to baited live traps (see Chapter 2, pp. 64-65). In addition, the spring of 1980 was the only spring in 4 years (1978-1981) in which one adult female wolverine (F7) failed to produce young (see Chapter 1: Reproduction). None of the three other radiocollared adult females were known to have young that summer as well. Though the wolverines were able to survive the winter, their reproductive potential may have been limited by food shortages. A significant reduction in the number of caribou carcasses in the study area due either to a caribou population decline or a change in migration patterns could result in a decline in wolverine numbers in the study area, at least in years when other food resources are scarce. A long-term reduction in the WAH caribou population would almost certainly be detrimental to the productivity of wolverines in the study area.

CHAPTER 5

WOLVERINE HARVESTS IN NORTHWESTERN ALASKA

Results and Discussion

Wolverine harvests from Game Management Unit 26 (GMU 26) have been recorded since 1959. Until 1969, records were obtained through a bounty program whereby $15 was paid for wolverines submitted to village agents. The bounty program was discontinued after 1969 and 2 years later the sealing program was initiated. The reported harvest of wolverines in GMU 26 from 1959 to 1983 was as high as 42 and as low as 2 with an average of 14 wolverines per year (Table 5-1). Most of the wolverine harvest is reported from GMU 26A, which includes NPR-A and the study area (Figure 1-1).

The extent of the unreported harvest is unknown, but it is generally accepted that wolverine harvests in GMU 26 are not well represented by the sealing program. Wolverine hides taken within GMU 26 by residents of the unit are nearly always used locally, and the residents have little incentive to seal the hides. During the 1977-78 trapping season, I purchased 22 wolverine carcasses from hunters and trappers in GMU 26 at $20 per carcass. Upon examining ADF&G sealing records for that season, I found that only two (9%) of the purchased wolverines had been sealed. In addition, W. C. Hanson (pers. commun.) purchased the hindquarters of wolverines taken by residents of Anaktuvuk Pass from 1975 to 1979 as part of a research program he was conducting

Table 5-1. Reported wolverine harvests in Game Management Unit 26 from bounty records between 1959-1960 and 1968-69 and from sealing records between 1971-72 and 1982-83.

					Number of Wolverines Harvested by the Following:		
Trapping Season	Total	Males	Females	Unknown	Unit Nonresidents	Unit Residents	Unknown
1959-60	13						
1960-61	31						
1961-62	8						
1962-63	10						
1963-64	42						
1964-65	2						
1965-66	11						
1966-67	33						
1967-68	29						
1968-69	11						
1969-70	-	-	-	-	-	-	-
1970-71	-	-	-	-	-	-	-
1971-72	2	2	0	0	0	1	1
1972-73	5	5	0	0	1	4	0
1973-74	5	4	1	0	5	0	0
1974-75	3	2	1	0	2	1	0
1975-76	11	9	2	0	7	4	0
1976-77	15	10	5	0	12	3	0
1977-78	12	5	5	2	4	8	0
1978-79	9	6	3	0	2	7	0
1979-80	10	7	2	1	8	2	0
1980-81	12	11	1	0	12	0	0
1981-82	21	19	2	0	18	3	0
1982-83	6	6	0	0	6	0	0

in northern Alaska; the purchase price was $15 per wolverine. In 1977-78, only 4 of 20 (20%) wolverines harvested in GMU 26 and purchased by Hanson were sealed. Using Hanson's data and the sealing records, I determined the total known harvest for GMU 26 in 1977-78 was a minimum of 48 wolverines, of which only 12 (25%) were sealed. These 48 wolverines approximate the actual average annual harvest for GMU 26 better than the average of 14 reported on the sealing forms. Wolverines purchased by Hanson but not sealed in 1975-76 numbered 19 for a total known harvest of 31; in 1976-77, 9 for a total known harvest of 24 (all samples in fall 1976 were lost to spoilage and not included); in 1978-79, 11 for a total harvest of 20. These figures are minimums because I subtracted one wolverine from Hanson's data for every wolverine in the sealing records reported by Anaktuvuk residents even if the date and location on the sealing form did not correspond to any in Hanson's collection. I believe the reported harvest from GMU 26 may represent 10% or less of the actual harvest in some years and probably rarely represents more than 50%. In the years for which Hanson's data are available, the average harvest was at least 31 wolverines per year; this harvest is a minimum for GMU 26 because it does not include an estimate of unreported wolverines taken by residents of other villages.

The number of unit nonresidents taking wolverines in GMU 26 influences the size of the reported harvest. During the past six trapping seasons, the reported harvest from GMU 26 averaged 11 wolverines per year. In 1981-82 it was more than double the average for the other five seasons (Table 5-2). Of the 21 wolverines reported in

Table 5-2. Characteristics of the reported wolverine harvest (for wolverines of known sex) taken in Game Management Unit 26 from 1977-78 to 1982-83. The 6-year period was divided into two groups to provide subsamples of sufficient size for statistical testing.

Trapping Seasons	Total Reported Harvest of Known Sex	Males	Females	Taken in the Denning Season		Taken by Shooting		Taken by Shooting in the Denning Season	
				Males	Females	Males	Females	Males	Females
1977-80	28	18	10	4	7	11	7	3	7
1980-83	39	36	3	23	2	24	2	20	2

1981-82, 8 (38%) were shot by two hunters (taking 3 and 5, respectively) who used aircraft to take wolverines by landing and shooting. These two individuals were not residents of GMU 26. Unit nonresidents are much more likely than residents to seal wolverine hides because nonresidents often sell hides through the commercial fur market or have them processed by commercial tanneries and taxidermists.

In the following discussion, I examine the sex ratio of the reported harvests in GMU 26 during the last 6 years. My purpose is to point out factors which may have influenced sex ratios. The sex ratios of furbearer harvests often do not reflect the actual sex ratio of the population. Changes in the sex ratio of harvested wolverines may reflect changes in the population structure brought about by changes in harvest pressure, but they may also reflect changes in the harvesting regime (i.e., timing, method, and location of the harvest). A consideration of wolverine behavior and ecology in the analysis of harvest statistics is important.

The proportion of males in the reported harvest from GMU 26 (Table 5-2) has increased significantly (χ^2=8.31, 0.001<P<0.005, df=1) during the last six trapping seasons. In the first three seasons (1977-78 to 1979-1980), 28 wolverines were sealed, of which 64% were males; in comparison, in the last three seasons (1980-81 to 1982-83), 39 wolverines were reported, of which 92% were males (Table 5-2).

The timing of the harvest in relation to the denning season (Mar-Apr) was examined. During the last six trapping seasons, 54% of the harvested wolverines were taken in the denning season, which is significantly different (χ^2=46.38, P<0.001, df=1) from what would be expected if the harvest were distributed equally over the trapping season (Nov–Apr). In addition, the percentage of the harvest that was taken during the denning season in the first three seasons (39%) was significantly different (χ^2=3.95, 0.025<P<0.05, df=1) from the percentage that was taken in the last three seasons (64%).

With the harvest occurring primarily in the denning season, a high proportion of males might be expected in the reported harvest if juveniles disperse just prior to the breeding season (p. 80) and if dispersers involve a higher proportion of males than females. However, if lactating females are more vulnerable to trapping in the denning season because of increased nutritional demands, an increase in the number of juvenile males harvested in the denning season may be offset by the number of lactating females trapped. Knowing the sex and age structure of the harvested wolverines would be necessary to evaluate whether this compensating mechanism is operating.

The methods used to take wolverines may also influence the proportion of males in the wolverine harvest in GMU 26. A greater proportion of wolverines was shot (66%) than was trapped in the 6-year period I examined (Table 5-2), but the proportions were not significantly different between 1977-1980 (64%) and 1980-83 (67%). However, the proportion of shot wolverines that were taken in the denning season was considerably lower in 1977-1980 (56%) than in 1980-83 (85%) though the difference was not significant (χ^2=3.57, 0.05<P<0.10, df=1). Results from my study indicate that denning females may be less vulnerable to shooting than are males or nondenning females during the denning season because of the large amounts of time that denning females spend in their dens at this time of the year (pp. 71-72). In years when a high proportion of females is denning, the proportion of males in the harvest should be related to the proportion of the harvest that is shot in the denning season. Trapping should not affect the harvest in the same manner. Female wolverines continue to forage in their home ranges during the denning season, though the proportion of time they are vulnerable to shooting is considerably less than for nondenning females. The chance that a female will encounter a trap in her home range is probably greater than the chance that a hunter will encounter the female during a trip through her home range. Though the sample size is too small for statistical testing, data from my study area suggest that attempts to capture denning females were more successful when wolverines were livetrapped than when they were shot using Cap-Chur guns from helicopters or snowmobiles.

The amount of hunting pressure may modify the effect of late-season shooting on the proportion of males in the harvest of wolverines in GMU 26. The chances of encountering a denning female increases with the amount of time hunters spend in her home range. I was successful at sighting denning females on only 12.5% of the radiotracking flights I made between 16 March and 18 April to locate known denning females (N=32). I was not able to sight F10 until the ninth flight to her home range. In contrast, I sighted a radiocollared, nondenning female (F9) on 100% of the radiotracking flights (N=17) and a radiocollared male

(M20) on 80% of the radiotracking flights (N=10) during the denning season. Hunters would have an even smaller chance of sighting denning females because hunters would not have the advantage of the radiotelemetry equipment.

Under present conditions in GMU 26A, hunters using aircraft probably take higher proportions of male wolverines in the denning season than hunters on snowmobiles. Most hunters using aircraft are not residents of GMU 26; their flights through the unit are infrequent, cover relatively large areas, and are not often retraced in the same season. Hunters on snowmobiles, on the other hand, are most often residents of the unit; though some may make long trips through portions of GMU 26A that are not repeated in the same season, others cover areas over and over again as they travel to and from the villages. The chances of sighting and shooting a denning female in that area increase as the number of times hunters pass through an area increases.

At some point, however, harvest pressure around villages may be so high that the proportion of males in the harvest increases. Often, the greater proportion of males in furbearer harvests is explained by the larger home range size of males, which makes them more vulnerable to trapping and hunting. However, I believe that invoking home range size differences to explain the disproportionate sex ratio of furbearer harvests is a simplistic approach to explaining a much more complicated process. Home range probably relates to the disproportionate sex ratio of wolverine harvests not only because the male's home range is larger than the female's, but also because there are fewer male home ranges available than female home ranges, causing males to remain in the transient population for longer periods of time than females; transients move over longer distances than resident animals and are probably more vulnerable to hunting and trapping. Transients are more likely to move into areas that are being trapped or to leave longer trails that can be tracked by hunters than are resident animals. As the resident wolverines are removed, the proportion of the population in the area that is transient increases. If harvest pressure continues, most wolverines taken in the area will be transients, most of which are probably males (p. 70).

An increase in food resources for wolverines in GMU 26A may influence the proportion of males in the harvest by increasing the proportion of females that den, making fewer females vulnerable to shooting and possibly to trapping if food resources were abundant. There is some indication that food resources may have increased in GMU 26A over the last six trapping seasons, particularly in the northern foothills of the central Brooks Range. The number of caribou in the WAH had decreased to about 75,000 animals in 1976; only a few thousand were known to winter in the central Brooks Range that year. From that time, the herd steadily increased by about 15,000-20,000 per year. In 1981-82 and 1982-83, 20,000-50,000 caribou wintered in the central Brooks Range (J. L. Davis, pers. commun.). This number of wintering caribou undoubtedly increased the amount of carrion available to wolverines in the central Brooks Range. In addition, mortality of moose along the central Colville River increased substantially preceding or during winter 1980-81. The percentage of short yearlings in the April 1981 survey was only 7% compared to an average of 19% in the preceding 4 years, indicating an increase in calf mortality (Coady 1981). If caribou and moose are important food resources for wolverines in the central Colville drainages, then food resources should have been good for wolverines from 1980 through 1983, and there may have been an increase in the proportion of females denning. Most of the reported harvest (92%) came from the central Colville drainages from 1980 through 1983.

Of course, the change in the sex ratio of the harvest from 1977-1980 to 1980-83 could have resulted from a general increase in the proportion of males in the wolverine population. I compared the sex ratio of wolverines caught before the denning season in 1977-1980 with that in 1980-83. (I assumed that a disproportional use of harvest methods before the denning season would not bias the sex ratio.) There were 13 males and 4 females (76% males) in the reported harvest in 1977-1980 and 13 males and 1 female (93% males) in 1980-83. Though the sample is too small for statistical testing, the numbers suggest that the proportion of males in the population before the denning season may not have been different between 1977-1980 and 1980-83.

Could the increase in the proportion of males in the 1980-83 harvests have been related to a substantial increase in the number of male wolverines immigrating into the area during the denning season in this period? Without data on the age of harvested animals, this question is difficult to answer; most males immigrating into the area would be young animals. Indications of increased reproduction or decreased harvest pressure in adjacent areas might suggest that immigration could have increased in GMU 26A. An analysis of harvest statistics from the adjacent GMU's (23, 24, and 25) indicates that there was no appreciable decrease in the number of hunters and trappers, no increase in the average number of wolverines taken by trappers and hunters, and no increase in the maximum number of wolverines taken by the most successful hunters and trappers.

In summary, the sex ratio of wolverine harvests in GMU 26 can be affected by changes in the productivity and structure of the wolverine population in and adjacent to the harvest area; by changes in harvest methods, timing of harvests, location of harvests, and intensity of harvest pressure; and by changes in food resources in and adjacent to the harvest area, which affect productivity, movements, and vulnerability to hunting and trapping. In GMU 26 in particular, where a large proportion of wolverines harvested is taken by shooting, the sex ratio of the harvest should be evaluated with the following factors in mind:

1. the proportion of the female segment of the population that is denning,
2. the proportion of the wolverines in the harvest that is shot during the denning season,
3. the proportion of the harvest reported by nonresidents using aircraft to take wolverines, and

4. the proportion of the harvest taken in areas that are either lightly or very heavily harvested.

CHAPTER 6

WOLVERINE MANAGEMENT CONSIDERATIONS IN NORTHWESTERN ALASKA

The Alaska Department of Fish and Game is mandated by the Constitution of the State of Alaska to manage furbearers on the sustained yield principle for the benefit of the resource and the people of the State according to the Species Management Policies of 1980 (Alaska Department of Fish and Game 1980). In most areas of the state, the Department's policy is to manage furbearers for optimum sustained yield of economic benefits. The Department recognizes that responsible management must be based on scientific knowledge, and the primary goal of my research was to determine those aspects of wolverine behavior and ecology that are important to the management of wolverines in northwestern Alaska. Knowledge of wolverine population size, productivity, and survival is fundamental to wolverine management. The following discussion is a synthesis of the results presented in the preceding chapters as they apply to wolverine management in GMU 26A.

The status of food resources both in and adjacent to GMU 26A is probably the most important factor influencing wolverine populations in northwestern Alaska at this time. In all the studies of wolverine food habits I have reviewed (see p. 138), large ungulates have been the primary food resource, at least in winter. Most of the ungulates are probably obtained as carrion. The size, distribution, and movements of the WAH and the Teshekpuk Lake caribou should be considered key factors influencing wolverine population size in GMU 26A, except perhaps in the central Colville River drainage where moose may play a substantial role. The results of the food habits analysis in this study (Chapter 4) emphasize the importance of caribou in the diet of wolverines in the study area, and the examination of stomach contents from 22 wolverine carcasses collected from the coastal plain in 1977-78 indicated that caribou was the primary winter food for wolverines in that area (Magoun 1979). Though no information was gathered on the food habits of wolverines along the central Colville River, wolverines there have been observed feeding on moose (H. V. Reynolds, pers. commun.), and caribou are undoubtedly an important food, particularly in years when caribou bands winter in that area. Van Zyll de Jong (1975) suggested that there is a "direct relationship between the biomass and turnover of large herbivore populations and the abundance and distribution of wolverines." In Norway, noticeable shifts in areas used by wolverines have been attributed to changes in reindeer distribution (Kvam and Sorenson, in press). Because the number and distribution of wintering caribou can change considerably from year to year in GMU 26A (J. L. Davis, pers. commun.), productivity and movements of wolverines may fluctuate more widely and show more regionalized differences than wolverine populations in other GMU's where food supplies are more stable.

Estimate of Population Size

Average summer home range size for wolverines in the study area was used to calculate a minimum population size for resident wolverines in

GMU 26A. Approximately 39,600 km^2 (foothill region) of GMU 26A is similar in habitat and terrain to the study area; the remaining 74,650 km^2 (coastal plain) is made up of wet tussock tundra and hundreds of tundra ponds and relatively little topographic relief. Because the habitat of the coastal plain is substantially different from that of the study area, I do not believe that wolverine density estimates from the study area can be applied to the coastal plain. Wolverines of different sex and age groups, including reproductive females, have been harvested from the coastal plain (Magoun 1979), indicating that resident females do occur there. However, there are no data available to calculate the density of resident wolverines on the coastal plain. Therefore, the resident wolverine population estimate for GMU 26A presented below is based on the population size projected for the foothill region only. Taking this conservative approach, the estimate for the resident wolverine population in GMU 26A is a minimum estimate.

To derive the estimate of population size, I made the following assumptions:

Assumption 1 - Summer home range size provides the best estimate of density for resident female wolverines because little overlap in home ranges occurs at this time of the year in the study area, except for females with yearling daughters.

Assumption 2 - One out of every five resident females shares her home range with a yearling daughter; of the five resident females in the study area in 1979 (Figure 2-3), only one (F10) was known to produce a female kit that remained in her home range in 1980 (Figure 2-4).

Assumption 3 - Summer home ranges of resident males do not overlap. Data were insufficient to determine if there was overlap in male home ranges. Results from studies of other solitary carnivores suggest that overlap probably does occur for male wolverines in summer. However, since I have no estimate of the degree of overlap in the male segment of the population, I assumed that no overlap occurred; this results in a conservative estimate of male density which may be offset somewhat by the fact that male summer home range size may have been underestimated (pp. 36-38).

Assumption 4 - All areas of the foothill region are occupied by resident wolverines at the density observed in the study area.

Assumption 5 - The reproductive rate for female wolverines observed in the study area is applicable to the resident wolverine population in the foothill region of GMU 26A.

Based on the average female summer home range size of 94 km^2 (p. 33), I estimated there are 421 resident adult females in the foothill region of GMU 26A. If one of every five of these females shared her home range with a yearling daughter, the number of yearling females equals 84. At a reproductive rate of 0.6 kits/year/female (pp. 26, 28), the number of kits in the fall population equals 252. A minimum of 64 resident adult males would occur in the foothill region based on an average male summer home range size of 625 km^2 (p. 36). Therefore, the resident fall population of wolverines in GMU 26A is 821 animals.

The fall population of wolverines in GMU 26A undoubtedly includes some transient wolverines. In the fall, juveniles have not yet begun to disperse (pp. 54-58), so transients in the fall population include only wolverines over 1 year old. Transients probably make up an important segment of the wolverine population in terms of harvest and population maintenance. However, no information is available on the survival rate of transients or the length of time they remain transient. A realistic estimate of the number of transients in the population estimate is impossible at this time.

Clearly, 821 wolverines should be considered a conservative estimate of the resident fall wolverine population in GMU 26A, but one subject to considerable error. The density of wolverines in the foothill region based on this estimate is 1 wolverine/48 km^2. If the 821 were spread over GMU 26A as a whole, including the coastal plain, the density would be 1 wolverine/139 km^2.

The estimated density of wolverines in GMU 26A of between 1/48 km^2 and 1/139 km^2 is similar to densities calculated for other populations studied with radiotelemetry. Hornocker and Hash (1981) estimated a density of 1 wolverine/65 km^2 in Montana based on capture-recapture, radiotelemetry, and observations of wolverine trails in snow. Their estimate probably included resident adults and juveniles as well as some transients. Whitman and Ballard (1983) derived a density of 1 wolverine/209 km^2 for the population in the upper Susitna River basin in Alaska. This estimate included adults and juveniles but not transients. Because of the lack of data on female home range size, Whitman and Ballard assumed that adult female wolverines occupied similar-sized home ranges as males. They stated that "if female home ranges were known, the population estimate would probably be somewhat higher." The home range size used by Whitman and Ballard for female home ranges was 627 km^2. If they had used 300 km^2 for female home size, a more realistic estimate in view of the data from other studies (see

Chapter 2), the estimate of the number of adult females and juveniles would have been doubled and their density estimate would have been approximately 1 wolverine/125 km^2.

Evaluation of Harvest Pressure

The Alaska Department of Fish and Game recognizes that high wolverine pelt prices and a strong domestic demand provide incentive for heavy trapping and hunting pressure on wolverines in the northwestern and arctic regions of Alaska (Alaska Department of Fish and Game 1980). The Department recommends that restrictive regulations or season closures be implemented in areas where they are the only viable solutions to protecting the resource and preventing overharvest. The analysis of the harvest statistics in GMU 26 (Chapter 5) suggests that the actual harvest of wolverines is between 30 and 100 wolverines per year. Managers may question whether a harvest of 100 wolverines is sustainable in GMU 26.

To investigate this question, I first looked at the characteristics of the wolverine population in the study area, an essentially unharvested population. Table 6-1 is an example of survival and fecundity schedules that could prevail in the study area and result in a stationary wolverine population. Fecundity (m_x), the average number of female kits per female per year, was based on the reproductive rate observed during the study (0.6 kits/female/year, see pp. 26, 28). A 50:50 sex ratio for litters was assumed. Females do not produce kits

Table 6-1. Survival and fecundity schedules for a hypothetical wolverine population when the exponential rate of increase (r_s)* = 0.

Year	Survival to Year X (l_x)	Survival from X to X+1 (p_x)	Fecundity (m_x)
1	1.000	1.000	0.0
2	1.000	0.500	0.0
3	0.500	0.906	0.3
4	0.453	0.906	0.3
5	0.410	0.906	0.3
6	0.372	0.906	0.3
7	0.337	0.906	0.3
8	0.305	0.906	0.3
9	0.277	0.906	0.3
10	0.251	0.906	0.3
11	0.227	0.906	0.3
12	0.206	0.906	0.3
13	0.186	0.000	0.0

*Caughley (1977:107-110).

until they are at least 2 years old. I assumed that no wolverine survived past the age of 12 years, based on the largest number of cementum annuli (11) recorded for a wolverine in northwestern Alaska (Appendix C), and that no kits were produced in the last year. Fecundity was assumed to be the same for all other age classes since I had no evidence that indicated a decrease in fecundity with age.

The survival rate (p_x) in Table 6-1 was determined in the following manner. I assumed that all female kits survive and do not disperse in their first winter. I also assumed that 50% of the female yearlings disperse in their second year (p. 57, 70). These are broad assumptions but were based on limited observations of female wolverines in the study area and on the results of other studies of territorial carnivores. I then used trial values of p_x for the adult age classes until the value for r_s, the exponential rate of increase implied by prevailing survival and fecundity schedules (Caughley 1977:107-110), was essentially zero (stationary population). To do this I used the FORTRAN program provided by Caughley (1977:Appendix 2). The results of this exercise indicated that, under the reproductive rate observed in the study area and the assumed survival rate of kits and yearlings, the adult survival rate must be approximately 0.906 in order for the resident female wolverine population to remain stationary given no emigration. The corresponding estimate of annual loss of adult females (<10% per year) is not unreasonable for the study population since no mortality or emigration of resident females was verified during the study.

Using the survival and fecundity schedules from Table 6-1 as a starting point, I investigated the possible impact of a harvest of 100 wolverines on the projected population of 821 wolverines for GMU 26A. Between 20 and 60 of the harvested wolverines would be females, based on the sex ratio of the reported harvest (Table 5-1) and of the carcasses collected in GMU 26A (Appendix C). The upper limit of 60 females in the harvest will be used in the following discussion, since it represents the most critical scenario in terms of population maintenance. Since there are no data available on the age distribution of the harvest, I derived a value for r_s under four hypothetical situations in order to point out the effect of age distribution of the harvest on population growth. Of an estimated population of 631 resident female wolverines in GMU 26A, 421 were adults, 84 were yearlings, and 126 were kits (p. 155). If the harvest of 60 females came entirely from the kit age class, the yearling age class, or the adult age class, the rate of growth of the population would be negative; if the harvest was distributed evenly over the three age class groups, r_s would be positive (Table 6-2).

In this exercise, loss of wolverines through harvest pressure was considered compensatory rather than additive. Davison (1980) found a compensatory relationship between human harvest and emigration for coyotes (_Canis latrans_), so that as rate of harvest increases, rate of emigration decreases. The yearling age class probably plays a key role in compensating for harvest mortality. If the entire harvest of 60 female wolverines was from the adult age classes, yearling survival (including reduced emigration) would have to increase from 0.500 to

Table 6-2. Changes in the exponential rate of increase (r_s)* of a hypothetical wolverine population in Game Management Unit 26A with a harvest of 60 females in different age distributions.

Age Distribution of the Harvest	r_s
Entire harvest in year class 1 (kits)	-.1054
Entire harvest in year class 2 (yearlings)	-.1560
Entire harvest in year classes 3-13 (adults)	-.0349
Harvest distributed equally among kits, yearlings, and adults	0.0768

*Caughley (1977:107-110).

0.604 to keep the population stationary; if the entire harvest was from the kit year class, the necessary survival rate for yearlings would have to be 0.953.

Though the statistics in Table 6-1 are not unrealistic, they probably do not accurately represent the wolverine population in GMU 26A, especially over the long run. Substantial changes on an annual basis probably occur in fecundity and in the survival schedules of the various age classes. Some of the effects of changes in survival on population growth were discussed above; in Table 6-3, I modified the statistics in Table 6-1 to incorporate some hypothetical fecundity values in order to evaluate their possible effect on the exponential rate of increase of the population. A drop in fecundity of only 0.1 in Table 6-1 produced a negative value for r_s. Either an increase in yearling survival to 0.749 or an increase in adult survival to 1.000 (or a combination of both) would be necessary to reestablish a stationary population (Table 6-3). The highest reproductive rate examined was 1.5 female kits/female/year, which is probably close to the maximum that could be attained in northwestern Alaska. At this reproductive rate, the population level could be maintained at a survival rate of only 0.100 for yearling females or 0.250 for adult females.

I do not wish to imply that the statistics presented in this discussion are necessarily accurate or should be used to establish bag limits for wolverines in northwestern Alaska. Rather, the results should be viewed as only one indicator of the possible impact of harvest pressure on the wolverine population in the region. Perhaps the

Table 6-3. The effect of changes in fecundity in Table 6-1 on the exponential rate of increase (r_s)* of a hypothetical wolverine population and the changes in survival rate for yearling or adult wolverines necessary for $r_s = 0$.

Change in Fecundity from Table 6-1	Resulting Exponential Rate of Increase (r_s)	Change in Yearling Survival Necessary for $r_s = 0$	OR	Change in Adult Survival Necessary for $r_s = 0$
0.2	-0.0677	0.749		1.000
0.5	0.0960	0.300		0.768
1.0	0.2497	0.150		0.501
1.5	0.3550	0.100		0.250

* Caughley (1977:107-110).

greatest value of this analysis lies in emphasizing the importance of accurate harvest records, including sex and age ratios, and the importance of understanding how the biology and behavior of wolverines influence population dynamics.

Conclusions and Management Recommendations

I have found no evidence to indicate that wolverines in northwestern Alaska are overexploited or are being adversely affected by oil and gas exploration activities at this time. In 1952, wolverines were considered "quite abundant" on the Arctic Slope from the head of the Sagavanirktok River to the head of the Etivluk River and "especially abundant" on the northern drainages of the DeLong Mountains toward No Luck Lake (see Figure 1-1) (Burkholder 1952). The fall density estimate for wolverines in the study area (1 wolverine/48 km^2) indicates that the population has remained at relatively high levels into the 1980's despite considerable changes in lifestyles and harvest capabilities of local residents and despite oil- and gas-related activities in NPR-A. Densities in proximity to villages, however, may be considerably lower than in other portions of GMU 26A.

Factors which are probably responsible for long-term wolverine population reductions are:

1. widespread declines in food resources, particularly the demise or range shift of large ungulate populations,
2. widespread habitat destruction, or

3. heavy harvests over large areas of wolverine production.

None of these factors jeopardize wolverine populations in northwestern Alaska at this time. The number of caribou in the WAH is still increasing (approximately 172,000 in 1982-83; Davis and Valkenburg 1983) and the Teshekpuk Lake caribou herd (approximately 4,000; Davis et al. 1982) appears to be increasing as well (P. Valkenburg, pers. commun.). The moose population may be at or near carrying capacity (approximately 600-700; Coady 1981). Large national parks and preserves have been established south of GMU 26A. These large tracts of wolverine habitat will continue to provide transient wolverines to the Arctic Slope. Wolverine harvests in GMU 26A and adjacent areas are likely to remain at reasonable levels as long as human populations remain small and widely scattered.

I believe that successful management of wolverines in GMU 26A is directly related to successful management of the WAH and Teshekpuk Lake caribou and the central Colville River moose population. Sustaining high populations of these ungulates guarantees maximum reproduction and survival for wolverines in the unit. Specific regulations to limit wolverine harvests will be of little value if wolverine food resources diminish to low levels.

Though the wolverine population on the Arctic Slope is generally considered more vulnerable to harvest pressure than the population in interior Alaska due to the ease with which the northern population can be harvested by hunters using snowmobiles or aircraft, the harvest in GMU 26A appears to be within the recruitment capacity of the population at this time. I recommend that obtaining accurate harvest statistics be the primary management goal for wolverines in GMU 26A. This goal can be accomplished to some degree by improving the communication between area biologists and local hunters and trappers and by securing dependable sealing agents in the villages. However, these approaches to improving the accuracy of the sealing program have been recommended in the past, and though efforts to improve compliance with the sealing proram have been successful, the results are often short-lived and inconsistent.

In my analysis of the harvest statistics for GMU 26A, one fact stands out--when a monetary reward was offered, whether a bounty or purchase price for carcasses, the number of wolverines reported increased substantially. The average number of wolverines sealed during the bounty program was 19; during the sealing program, only 9 (Table 5-1). The number of wolverines purchased by Hanson in Anaktuvuk Pass was sometimes four times higher than the reported harvest (pp. 140, 142). Sealing statistics are likely to reflect increasing wolverine harvests by unit nonresidents but will not necessarily reflect increasing harvests by residents (pp. 142, 144).

Wolverine management in GMU 26 would benefit considerably from a program whereby skulls from harvested wolverines are purchased from hunters and trappers:

1. A unit-wide program would provide more accurate estimates of the harvest.
2. Skulls would provide both sex and age ratios of the harvested segment of the population (see below); these ratios would indicate

possible changes in harvest pressure and permit comparisons between different harvest rates and different harvest methods.

3. The proportion of older-aged wolverines in the harvest from the coastal plain would give some indication of the size of the resident population in that area.

The cost and time required to collect and analyze wolverine skulls in GMU 26 must be consistent with the furbearer management priorities of ADF&G. As I pointed out above, the wolverine population in GMU 26A is probably not being adversely affected by human exploitation at this time. However, I believe a skull collection program is justified in order to provide baseline data on the sex and age structure of the harvest in GMU 26A during a period when food resources are relatively good and harvest pressure appears to be within the recruitment capacity of the resident wolverine population.

I have recommended a skull collection program rather than a carcass collection program for several reasons. I believe a greater number of hunters and trappers would be willing to participate in the program if they were not required to provide the entire carcass. Many hunters and trappers travel long distances on snowmobiles or in aircraft and would not be willing to carry the extra weight and bulk of several wolverine carcasses. Moreover, a skull collection program would be less costly because it eliminates the additional time and expense of shipment and carcass necropsy. Loss of data otherwise provided by carcass necropsies would not jeopardize the major objective of the collection program, which is to provide a more accurate harvest record and to determine the sex and age ratio of the harvest. The results from my study indicate that reproductive rate determined from the examination of reproductive tracts from female wolverine carcasses does not necessarily reflect the potential recruitment of juveniles to the population because neonate mortality may be the critical factor determining recruitment rate (see Chapter 1: Reproduction). The proportion of juveniles in the fall harvest is probably a better indicator of recruitment as long as changes in harvest vulnerability for adult females and juveniles are proportional. Moreover, the analysis of stomach contents from carcasses does not necessarily reflect food habits because wolverines are often trapped or shot at baits. Food habits analysis will almost certainly support the general conclusion from other wolverine studies that the main winter food resource is carrion of large ungulates or possibly of marine mammals for wolverines in coastal areas. Of course, if sufficient monies were available, a carcass collection would be preferable, provided it did not interfere with the number of harvested wolverines reported; an accurate harvest record is the primary concern.

The use of skulls for determining sex and age ratios of the harvest is particularly convenient for wolverines because the analysis does not depend upon information on the sex of the animal provided by the hunter and trapper or the sealing agent. Both sex and age of the wolverines can be obtained from the skulls. From an analysis of 535 wolverine skulls from the University of Alaska Mammal Collection, I determined that the condylobasal length measurement can be used to separate males from females (Figure 6-1). Most of the overlap I observed was in skulls

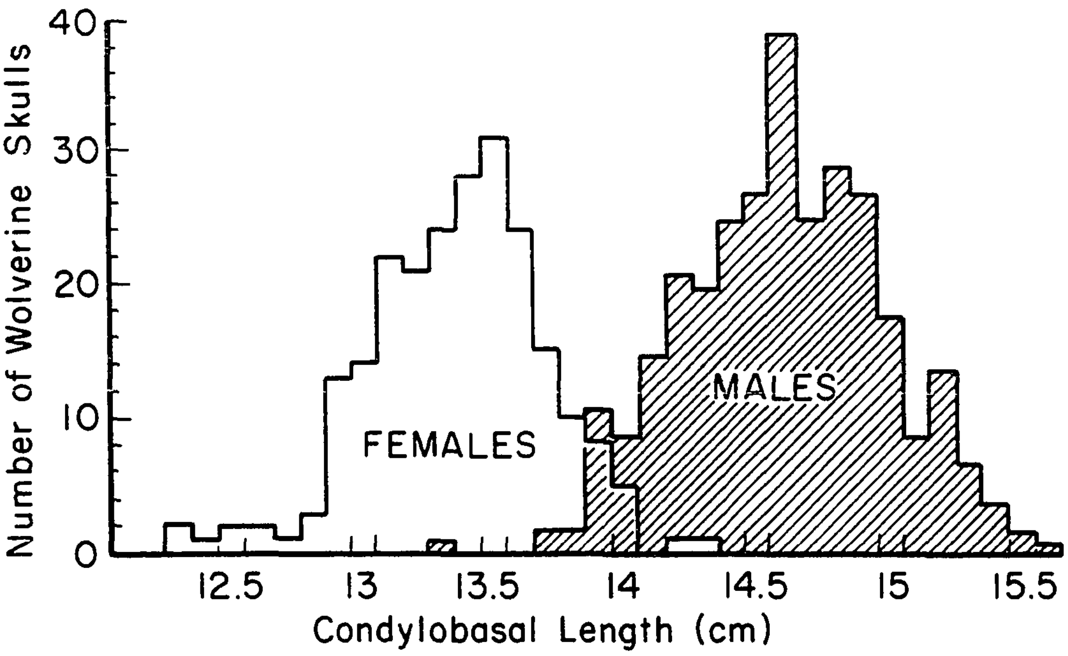


Figure 6-1. Distribution by condylobasal length of 535 Alaskan wolverine skulls showing the difference between males and females.

measuring 13.9 and 14.0 mm and involved only 6% of the sample. An additional five males (1.6%) fell within the female range (12.3-13.8 mm) and two females (0.8%) within the male range (14.1-15.5 mm). The sample of skulls had been collected statewide over several decades which makes the limited amount of overlap between males and females even more striking. Because wolverines have a rapid growth rate (pp. 23-24), it would not be necessary to separate juveniles from the sample. Tooth cementum analysis of the canine teeth will provide age data. With the cooperation of the purchasing agents in the villages, or the hunters and trappers themselves, detailed information could be obtained on the date, method, and location of the harvest which would considerably improve the interpretation of sex and age ratios and evaluation of harvest pressure.

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Appendix A. Seasonal distribution of radiotelemetry locations for wolverines in northwestern Alaska, 1978-1983.

Wolverine	Month	Year	Number of Relocations	Total
F1	Apr	1978	4	
	May	1978	9	
	Jun	1978	4	17
M2	Apr	1978	4	
	May	1978	3	7
M3	Apr	1978	4	
	May	1978	8	
	Jun	1978	17	
	Jul	1978	3	32
F4	Apr	1978	6	
	May	1978	12	
	Jun	1978	8	
	Jul	1978	3	
	Mar	1979	4	
	Apr	1979	1	
	May	1979	3	
	Jun	1979	1	
	Aug	1979	2	
	Mar	1980	3	
	Apr	1980	1	
	May	1980	1	
	Jun	1980	4	
	Jul	1980	3	
	Aug	1980	1	53
M5	Apr	1978	5	
	May	1978	8	
	Jun	1978	8	
	Jul	1978	3	24
M6	Apr	1978	1	1
F7	Jun	1978	2	
	Jul	1978	8	
	Aug	1978	6	
	Sep	1978	15	
	Mar	1979	8	
	Apr	1979	6	

Appendix A. Continued.

Wolverine	Month	Year	Number of Relocations	Total
F7, cont.	May	1979	25	
	Jun	1979	14	
	Jul	1979	3	
	Aug	1979	27	
	Sep	1979	2	
	Oct	1979	2	
	Nov	1979	2	
	Feb	1980	5	
	Mar	1980	9	
	Apr	1980	4	
	May	1980	18	
	Jun	1980	31	
	Jul	1980	13	
	Aug	1980	8	
	Apr	1981	1	209
M8	Jun	1978	2	
	Jul	1978	8	
	Aug	1978	5	
	Sep	1978	19	
	Nov	1978	1	35
F9	Mar	1979	12	
	Apr	1979	5	
	May	1979	18	
	Jun	1979	4	
	Jul	1979	1	
	Aug	1979	15	
	Sep	1979	1	
	Nov	1979	1	57
F10	Mar	1979	9	
	Apr	1979	6	
	May	1979	21	
	Jun	1979	5	
	Jul	1979	1	
	Nov	1979	2	
	Feb	1980	4	
	Mar	1980	11	
	Apr	1980	6	
	May	1980	14	
	Jun	1980	22	

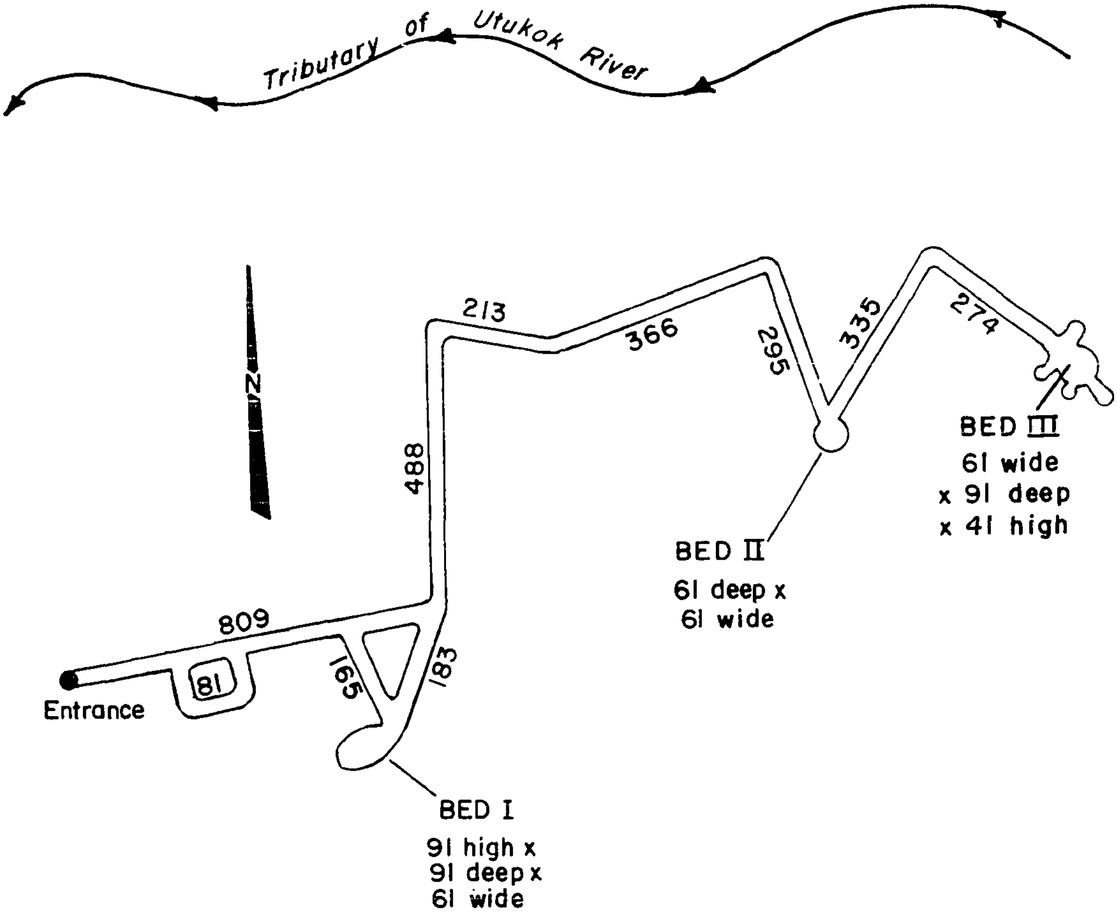
Appendix A. Continued.

Wolverine	Month	Year	Number of Relocations	Total
F10, cont.	Jul	1980	15	
	Aug	1980	9	125
F11	May	1979	11	
	Jun	1979	4	15
M12	May	1979	12	
	Jun	1979	3	
	Jul	1979	1	
	Aug	1979	9	
	Sep	1979	2	27
M13	Jul	1979	1	
	Aug	1979	12	
	Sep	1979	2	
	Oct	1979	2	
	Nov	1979	4	
	Feb	1980	5	
	Mar	1980	7	33
M14	Jul	1979	2	
	Aug	1979	25	
	Sep	1979	2	
	Oct	1979	1	
	Nov	1979	2	32
F15	Feb	1980	3	
	Mar	1980	9	
	Apr	1980	5	
	May	1980	14	
	Jun	1980	20	
	Jul	1980	15	
	Aug	1980	8	
	Apr	1981	2	
	Jun	1981	3	
	Jul	1981	4	83
F16	No locations			
M17	No locations			
F18	No locations			

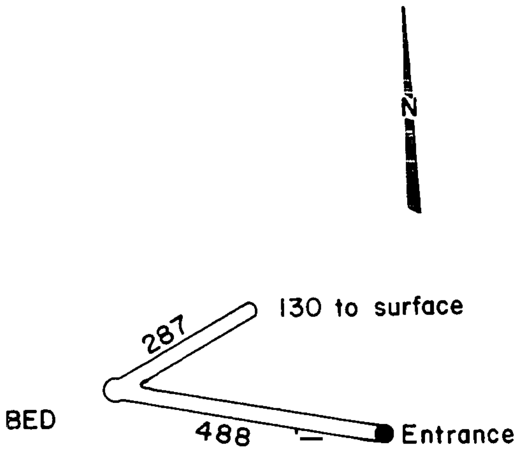
Appendix A. Continued.

Wolverine	Month	Year	Number of Relocations	Total
F19	Nov	1979	2	
	Feb	1980	4	
	Mar	1980	10	
	Apr	1980	5	
	May	1980	2	23
M20	Feb	1980	1	
	Mar	1980	9	
	Apr	1980	1	
	May	1980	12	
	Jun	1980	11	
	Jul	1980	8	
	Aug	1980	9	51
M21	Feb	1980	2	
	Mar	1980	5	7
F22	Mar	1980	4	
	Apr	1980	4	8
F23	No locations			
F24	Apr	1981	4	
	Jun	1981	6	
	Jul	1981	7	
	Sep	1981	1	
	Apr	1982	3	
	Jul	1982	3	
	May	1983	1	25
M25	No locations			
F26	No locations			

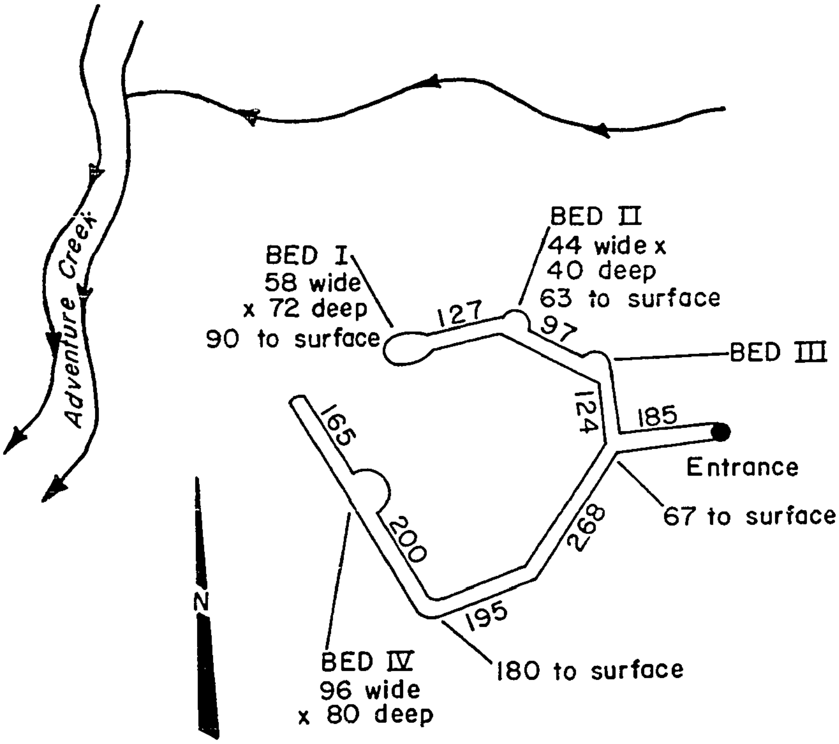
Appendix B. Snow tunnels used by wolverines in the Driftwood area, northwestern Alaska, 1978-1981. All measurements are in centimeters. Curved arrows represent the direction of streamflow for the drainage where the tunnel was located.



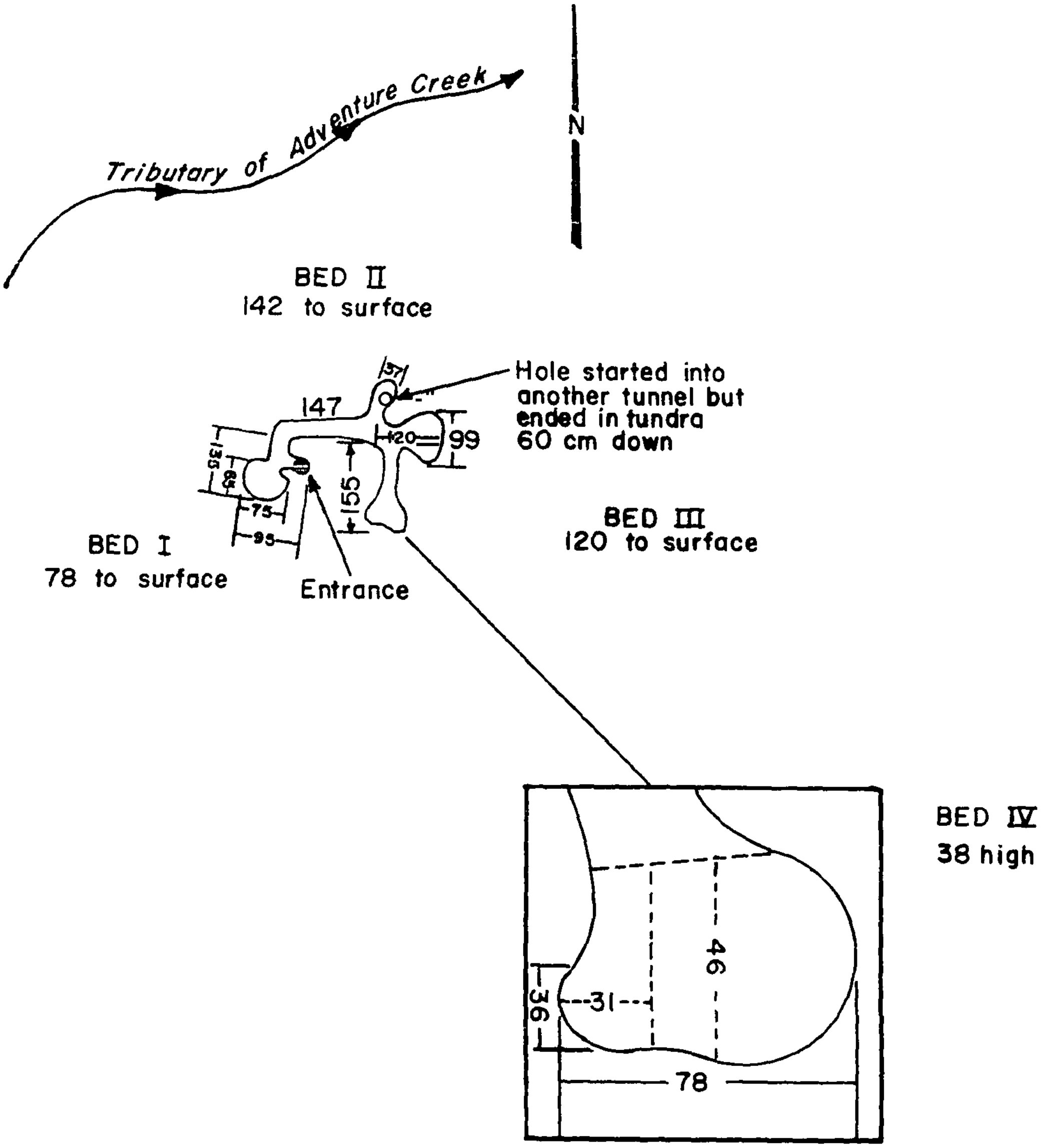
a. Used by unidentified wolverine within the home range of male M3 in 1978; probably a natal den based on the number of wolverine scats found in the area.



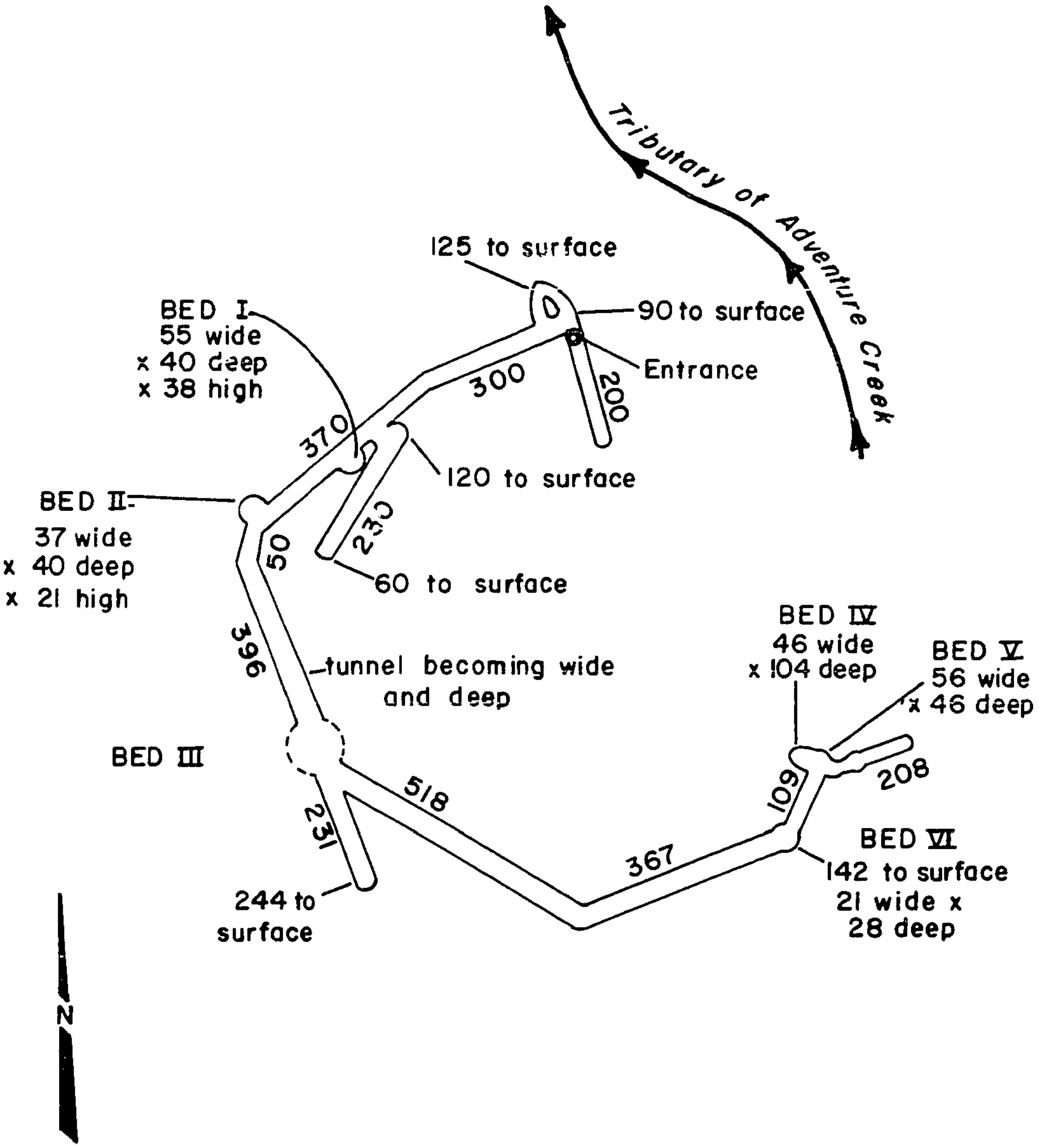
b. Used by male M3 within the home range of female F7 in 1978.



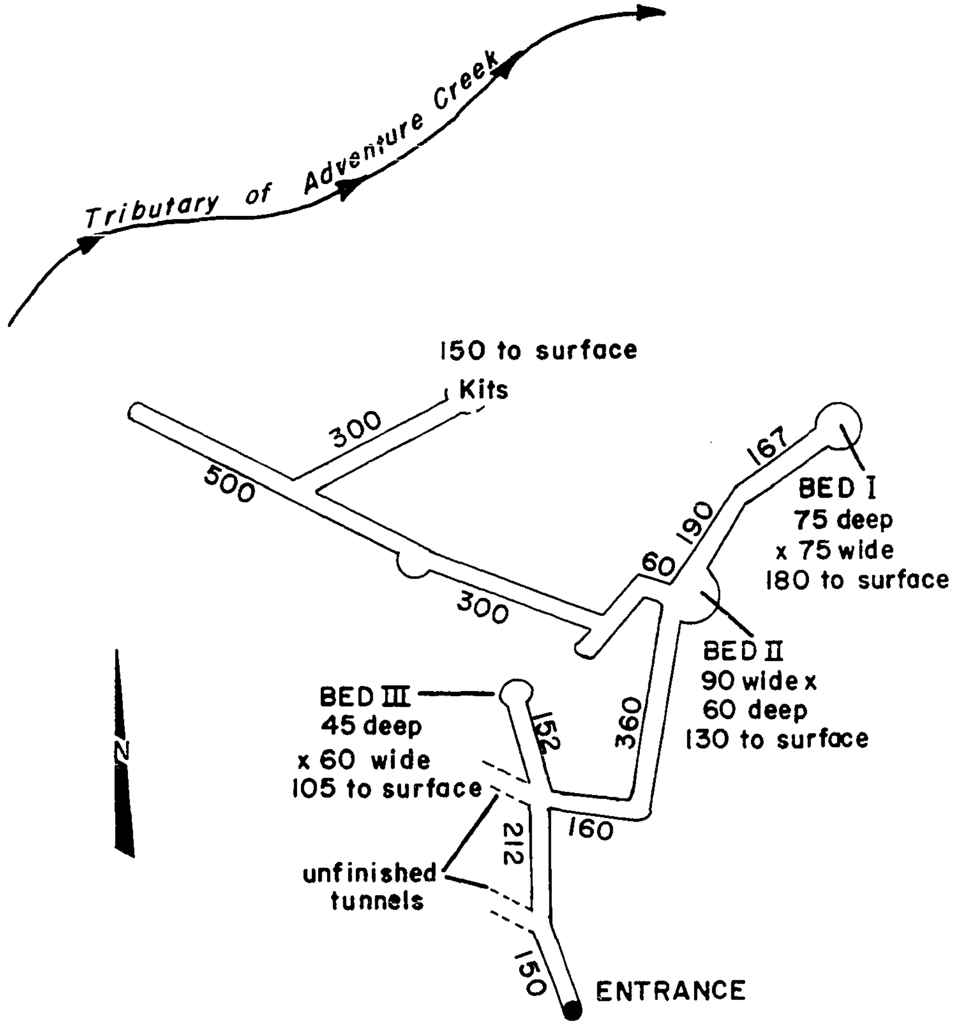
c. Natal den of female F7 in 1979; excavation may not have been complete due to slumping from spring thaw.



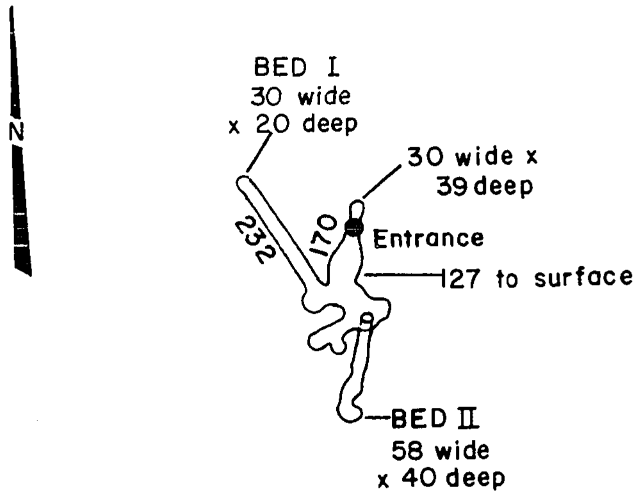
d. Used by female F7 in 1980.



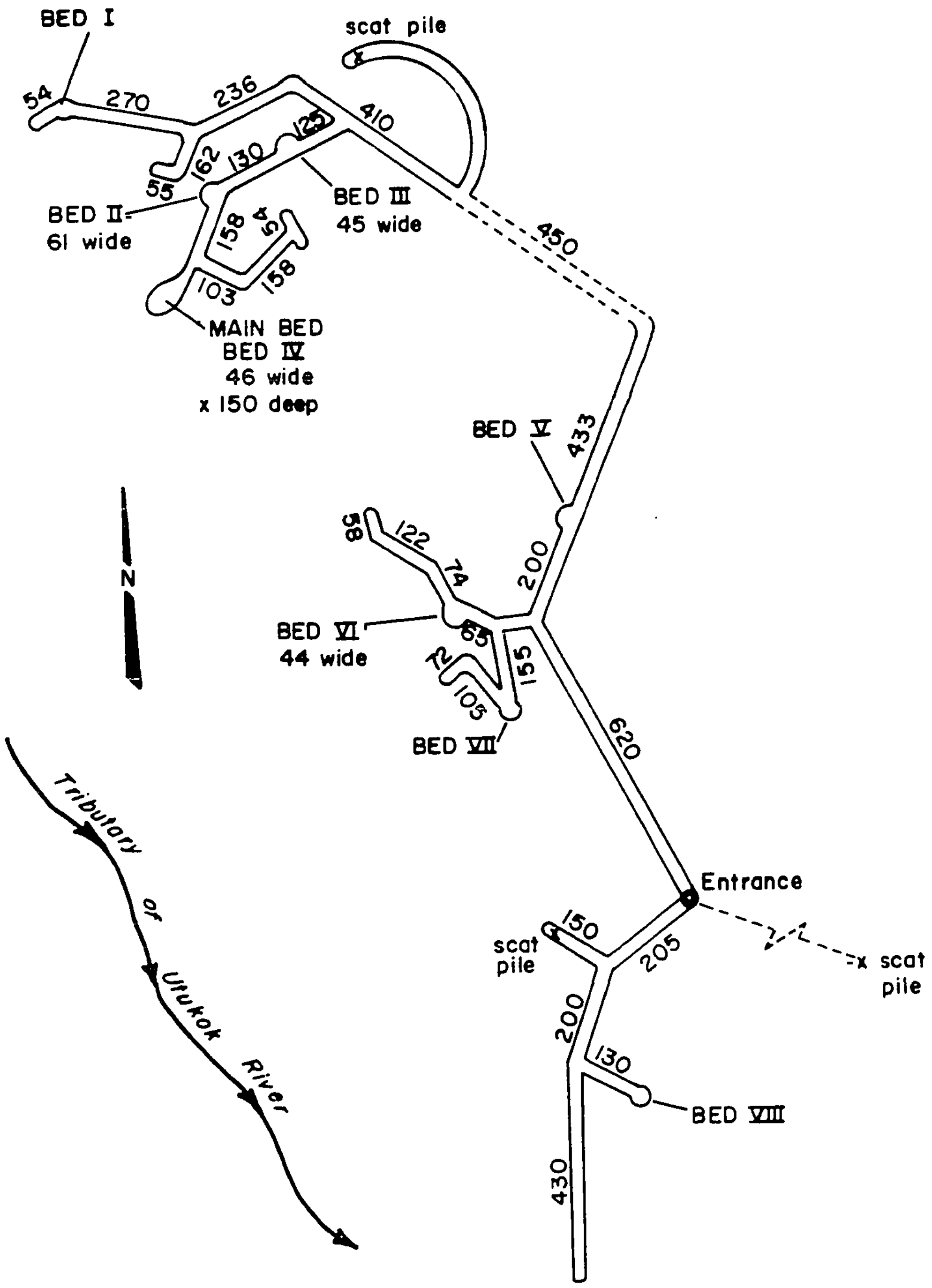
e. Used by female F7 for 10 days in March 1980; also occupied simultaneously by adult male M21 and yearling male M13. The side tunnel near Bed I was flecked with blood.



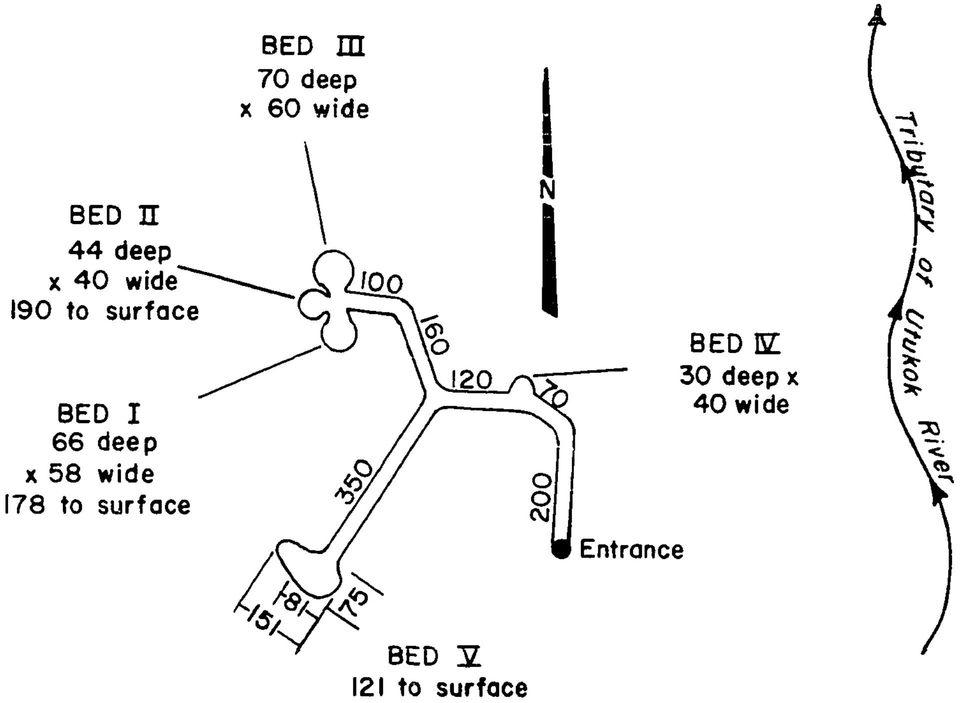
f. Natal den of female F7 in 1981; not fully excavated.



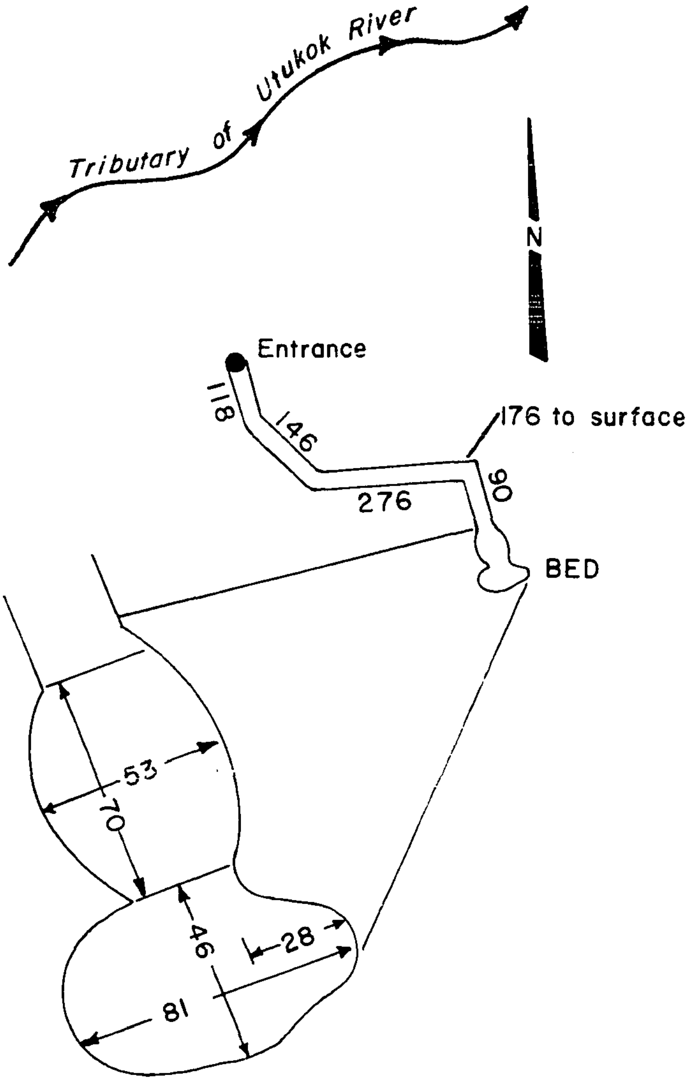
g. Used by female F19 within the boundary of female F7's home range in 1980; also used by M13, F7's male yearling.



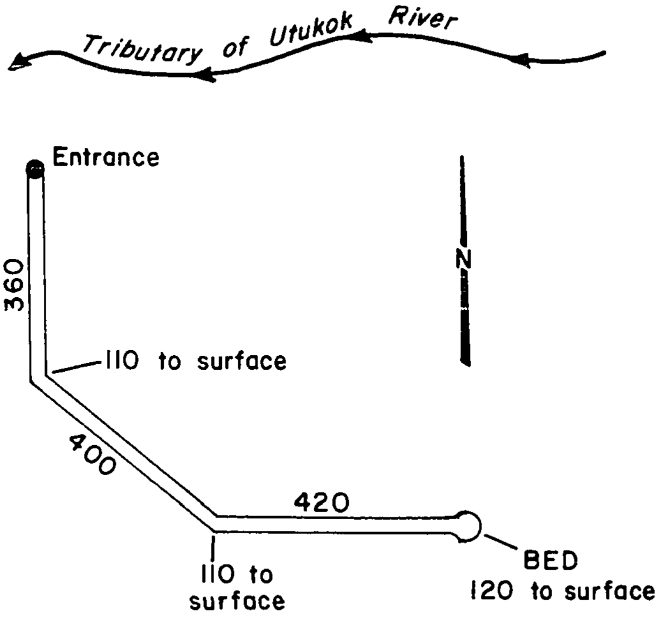
h. Natal den of female F10 in 1979.



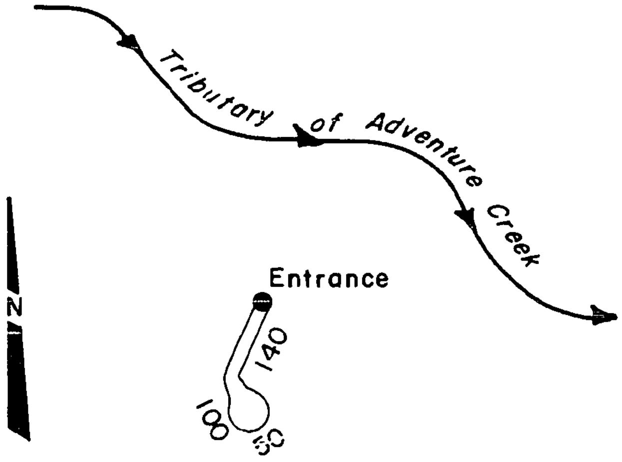
i. Used by female F10 in 1980; also used by F15, F10's female yearling.



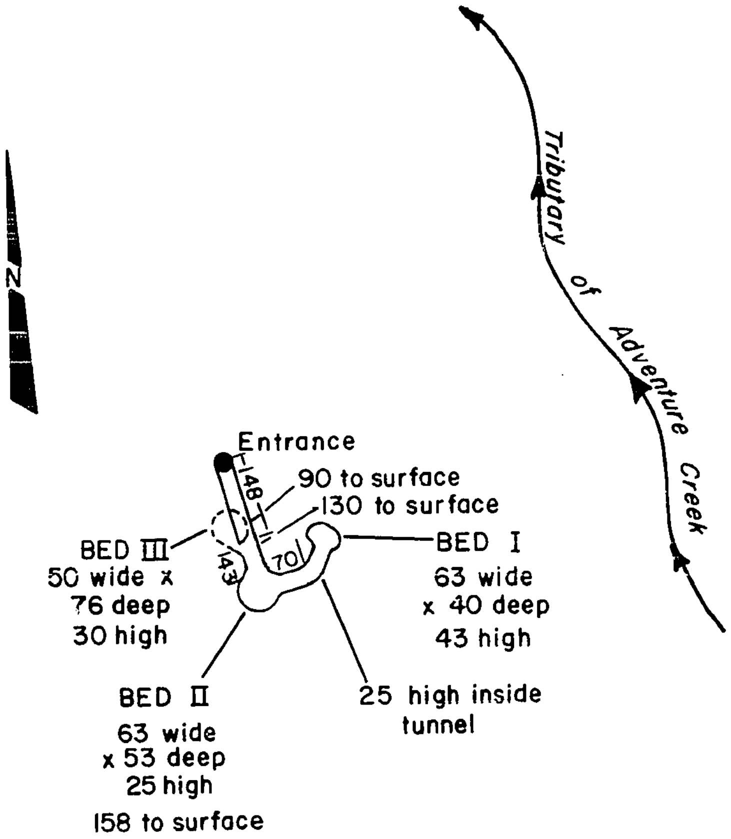
j. Used by female F10 in 1980.



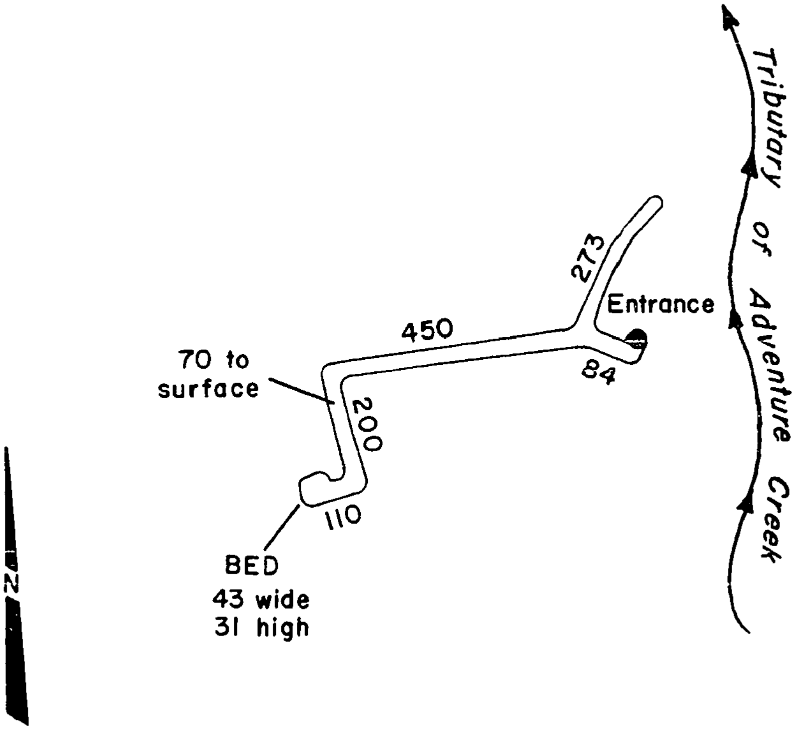
k. Used by female F10 in 1980.



1. Used by female yearling F15 in 1980.



m. Used by an unidentified wolverine in 1980 near the boundaries of F7 and F10's home ranges.



n. Used by an unidentified wolverine in 1980 near the boundaries of F7 and F10's home ranges.

Appendix C. Wolverine carcasses purchased in Game Management Unit 26 during the 1977-78 trapping season.

Accession Number	Reported Kill Date	Location	Est* Age	Cem* Age	Reproductive** Condition
Males					
010	4 Mar 78	112 km from Barrow on Aluktuk River	2-3	1	
011	28 Feb 78	128 km SE of Barrow at Fish Camp	2	3-4	
012	unknown	Probably near Atkasook	1-2	0	
018	-- Mar 78	240 km S of Barrow	3-4	9	
025	18 May 78	146 km from Barrow	2-3	--	
026	4 Apr 78	E of Atkasook	--	--	
027	-- Nov 77	Utukok River area	2-3	4-5	
034	18 Mar 78	32 km SW of Point Lay	3-5	--	
037	unknown	Probably Point Lay or Atkasook	2	1	
041	23 Mar 78	Chipp River	5-6		
Females					
013	28 Feb 78	272 km E of Barrow	3-5	2-4	3 fetuses
014	28 Feb 78	128 km SE of Barrow	1-2	2	--
015	1 Mar 78	240 km S of Barrow	8-9	8-11	UHW=15.0 mm
016	1 Mar 78	240 km S of Barrow	3	5-6	UHW= 3.0 mm
019	unknown	Killik River	4	--	3 placental scars
035	unknown	48 km SE of Atkasook	3-4	2 (9 canine)	UHW= 3.5 mm
036	25 Mar 78	Oumalik River	3-4	2-3	UHW = 4.5 mm
038	26 Feb 78	Cape Beaufort area	5-6	5	4 fetuses
039	-- Mar 78	Headwaters of Meade River	6	9	UHW= 4.0 mm
040	-- Nov 77	Kokolik River area	8-9	9	UHW=10.0 mm
042	-- Nov 77	Kokolik River area	1-2	1	UHW= 2.0 mm
043	23 Mar 78	Price River	2-3	--	UHW= 3.5 mm

* Estimated age was based on tooth wear; cementum age was based on the number of cementum lines. The reason for the large discrepancy in the estimated and the cementum age of 018 is not known. There is also no explanation for the large discrepancy between the cementum age read from the premolar versus the canine tooth for 035.

**UHW refers to the average uterine horn width.