THE ECOLOGY OF WOLVERINES IN SOUTHCENTRAL ALASKA

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A

THESIS

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ABSTRACT

A study of wolverine (*Gulo gulo*) ecology was conducted within the upper Susitna Basin in southcentral Alaska between May 1980 and April 1982. The study was initiated in an attempt to identify potential impacts of hydroelectric development on the wolverine populations. Twelve wolverines (10 males) were fitted with radio transmitters and relocated 153 times. The mean winter and summer home ranges for adult males were 353 km^2 and 385 km^2, respectively. Adult male home ranges were primarily mutually exclusive, having an average overlap of 4.2% between neighbors. On an annual basis, wolverines appeared to select spruce cover types; this selection was strongest during the winter. The most important foods to wolverines were carrion of ungulates (winter) and ground squirrels (summer). The wolverine population in the Susitna Basin during the study period was not heavily exploited by man and was secure.

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INTRODUCTION

Since 1970, there has been an increased focus on resource development in Alaska. Human activities and intensive land use appear to have detrimental effects on resident wolverine populations (van Zyll de Jong 1975, Hornocker and Hash 1981). Stimulated by these concerns, two wolverine projects were initiated in Alaska. The first of the wolverine field studies began in 1978 in the National Petroleum Reserve in northwestern Alaska (Magoun 1979, 1980, in prep.). Magoun's study mainly used radiotelemetry, and efforts were concentrated on collecting data on home range, social habits, food habits, and population characteristics. My study, stimulated by the proposed Susitna Hydroelectric Project, was designed to collect data which could assist in the prediction of probable impacts on the wolverine populations. The majority of the data was collected by following marked individuals by radiotelemetry. My objectives were to:

1. determine home range size and seasonal movement patterns,
2. determine habitat preferences and food habits, and
3. determine the age of harvested wolverines.

In Alaska, prior to these two field studies, data collection dealt predominantly with harvest numbers, which were tallied through bounty payments and then, after 1971, through harvest sealing documents. In addition, information concerning breeding biology, age structure, and food habits was collected from carcasses (Wright and Rausch 1955, Wright 1963, Rausch and Pearson 1972).

There has been a dearth of wolverine research throughout the world. Past studies, mainly in Europe, have utilized snow tracking (Haglund 1966, Pulliainen 1968, Myrberget 1970). In North America, a 5-year (1973-78) study using radiotelemetry was conducted in northwestern Montana (Hornocker and Hash 1981). That study concentrated on population characteristics, home range size, food habits, and habitat utilization.

The present range of wolverines is restricted to the remote mountains in the western United States and northern Canada (Deems and Pursley 1978). In Alaska, wolverines inhabit forests and tundra areas throughout the state except on the Aleutians and on the islands in the southeast (Manville and Young 1965). The wolverine has been classified as a wilderness-dependent species (Schoenfeld and Hendee 1978), and, due to its secretive behavior, solitary life style, and naturally low numbers, little is known about its behavior and status.

The wolverine is North America's largest terrestrial mustelid. It is generally considered a scavenger and its morphological and behavioral characteristics are adapted to the scavenging life style. Wolverine dentition and skull musculature allow feeding on frozen meat and the breaking of large bones (van Zyll de Jong 1975). Also, its extensive movement patterns allow it to search effectively for carcasses. Krott (1959), Haglund (1966), and Hornocker and Hash (1981) have reported that wolverines are not efficient hunters, as they do not possess the stealth or the speed that characterizes the efficient hunters among the Felidae and Canidae. In the summer, wolverines apparently are omnivores, feeding on birds, insects, berries, small mammals, and carrion (Krott 1959).

In Alaska, wolverines breed between May and August (Magoun and Valkenburg 1983). Rausch and Pearson (1972) reported an average of 3.5 fetuses per pregnancy; however, Magoun (in prep.) found average litter sizes for northwest Alaska of only 1.8 kits. Female wolverines are induced ovulators and also have delayed implantation. The blastocysts implant primarily in January or February, with parturition primarily occurring during February and March. The period between nidation and parturition is 30 to 40 days (Rausch and Pearson 1972). Delayed implantation allows kits to be born and breeding to occur during the optimal spring/summer period. Wolverine kits develop rapidly, and by November (at approximately 7 months of age) they are within the adult weight range (Magoun, in prep.).

Wolverines are important furbearers in terms of human income and recreation. During the trapping seasons (November through March) between 1979 and 1982, 534, 610, and 464 wolverines were trapped statewide, grossing $91,314 and $141,660 during the trapping seasons 1980-81 and 1981-82 (Melchior 1982, 1983). No records concerning human income from the wolverine harvest during the 1979-1980 trapping season were collected. Eighty-one, 34, and 63 wolverines were trapped during the trapping seasons between 1979 and 1982 in Game Management Unit 13 (GMU 13) which includes the study area. Game Management Unit 13 ranked number one, six, and one for reported wolverine harvest within Alaska during 1979-1980, 1980-81, and 1981-82, respectively. Alaska ranked number one in wolverine harvest in all of North America during 1977-78 (Deems and Pursley 1978).

STUDY AREA

The study area of approximately 163,000 km^2 lies between 62°30' and 63°00'N and 147°00' and 150°15'W in the upper Susitna Basin in southcentral Alaska (Fig. 1). The area was chosen because, if the Susitna dams are built, it will be directly affected by inundation and indirectly affected through road, power line, and camp construction. The portion of the study area where the instrumented animals resided was monitored the most intensively.

The study area lies within the Coastal Trough Province (Wahrhaftig 1965) and its topography is diverse. The Susitna River flows through a steep-walled canyon that in places is 300 m deep. The canyon gives way to a plateau of rolling uplands which rise into the Talkeetna Mountains on the south and the Alaska Mountain Range to the north. Elevations in the study area range from 275 to 2,100 m. There is a gradual westward decline in elevation across the study area. The area is sparsely populated and relatively inaccessible, as no roads go into the area and there are few improved landing strips for fixed-wing aircraft.

Vegetation types of the area were mapped by a team from the University of Alaska Agricultural Experimental Station, Palmer, Alaska (McKendrick et al. 1982). The primary vegetation types present are forest, shrubland, and tundra. Treeline, although variable, rarely exceeds 975 m for conifers and 700 m for deciduous or mixed deciduous and conifer forests. The most prevalent vegetation types in the study area are mixed low shrub (birch and willow), woodland spruce, sedge

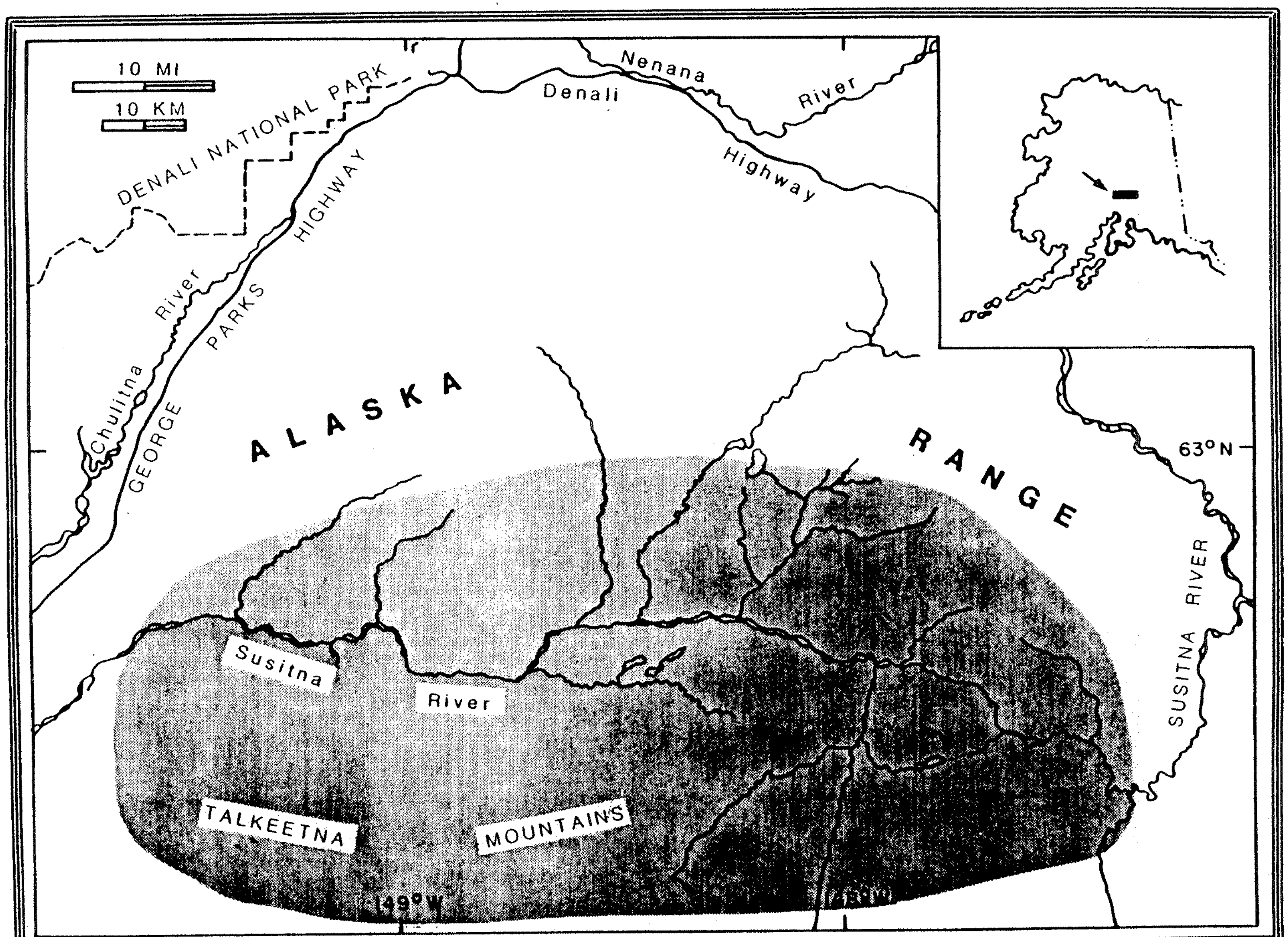


Figure 1. Wolverine study area map. The most intensely monitored area is shaded.

grass tundra, mat and cushion/sedge grass tundra, and open spruce. Within the Susitna River floodplain, deciduous and mixed deciduous and conifer forest types are common. The extent of each of the vegetation types is presented in Table 1.

The study area has cool, rainy summers and cold, dry winters. Snow cover is usually restricted to the period of October to mid-May, although snowfall can occur throughout the year. The best approximation of air temperature and precipitation levels for the study area was recorded at a weather station located at Summit, 40 km northwest. Recorded averages of temperature and precipitation are presented in Table 2. Strong inversions are common in the winter months as high-pressure air masses settle over the area, causing cold, dense air to settle in the steep-walled canyons. Therefore, air temperatures are lowest in the canyon bottoms (Buskirk 1983).

The recorded vertebrate fauna of the area includes 135 species of birds (Kessel et al. 1982), 34 species of mammals, and 1 amphibian species (Buskirk 1983). Six species of large carnivore/scavenger species occur sympatrically in the area: wolf (*Canis lupus*), black bear (*Ursus americanus*), brown bear (*Ursus arctos*), fox (*Vulpes vulpes*), and small numbers of lynx (*Lynx canadensis*) and coyote (*Canis latrans*).

Table 1. Hectares and percentage of total area covered by vegetation/habitat types in the upper Susitna River Basin (above Gold Creek), Alaska. Data from McKendrick et al. (1982).

Vegetation/habitat type[a]	Hectares	Percent of total area
Total vegetation	1,387,607	85.08
Forest	348,232	21.35
Conifer	307,586	18.86
Woodland spruce	188,391	11.55
Open spruce	118,873	7.29
Closed spruce	323	0.02
Deciduous	1,290	0.08
Open birch	968	0.06
Closed birch	323	0.02
Mixed	39,355	2.41
Open	23,387	1.43
Closed	15,968	0.98
Tundra	394,685	24.20
Wet sedge grass	4,839	0.30
(Mesic) sedge grass	184,358	11.30
Herbaceous alpine	807	0.05
Mat and cushion	65,001	3.99
Mat and cushion/sedge grass	139,680	8.56
Shrubland	644,690	39.53
Tall shrub	129,035	7.91
Low shrub	515,655	31.62
Birch	33,549	2.06
Willow	10,645	0.65
Mixed	471,461	28.91
Unvegetated	243,392	14.92
Water	39,840	2.44
Lakes	25,162	1.54
Rivers	14,678	0.90
Rock	113,712	6.97
Snow and ice	89,841	5.51
Total area	1,630,999	100.00

[a] Based on maps produced at a scale of 1:250,000.

Table 2. Recorded average air temperature (C) and precipitation (mm) at Summit, 40 km northwest of the study area, 1951-1975 (Alaska Power Authority 1982).

	Average daily maximum temperature	Average daily minimum temperature	Average daily temperature	Average monthly precipitation
Jan	-14.6	-21.6	-18.1	23
Feb	-10.8	-18.6	-14.7	30
Mar	-7.8	-17.1	-12.4	22
Apr	0.3	-9.8	-4.7	18
May	7.6	-1.5	3.1	15
Jun	11.3	4.3	9.3	55
Jul	15.7	6.3	11.2	75
Aug	13.3	5.1	9.3	78
Sep	8.3	0.1	4.2	65
Oct	-1.4	-8.6	-5.0	40
Nov	-9.1	-15.6	-12.3	33
Dec	-12.7	-19.6	-16.1	28
Annual mean			-3.9	483

METHODS

Wolverines were captured during three periods: April and May 1980, March 1981, and November and December 1981. Helicopter capture techniques (Baer et al. 1978, Ballard et al. 1982a) were used. Wolverines were captured with greater success during periods with good light conditions and fresh snowfall. Wolverines were located initially by fixed-wing aircraft (PA-18 150) and were immobilized by firing a projectile syringe (Cap-chur equipment) from a Bell 206B helicopter. Immobilization of wolverines (Ballard et al. 1982a) was accomplished by using 0.25 cc phencyclidine hydrochloride (100 mg/ml Sernylan, Bioceutic Lab., Inc.) with 0.20 cc xylazine (100 mg/ml Rompun, Barrett Division of Cutter Laboratories, Inc.) or 0.40 to 0.70 etorphine (1 mg/cc M-99, D-M Pharmaceuticals, Inc.) with 0.40 to 0.50 cc xylazine (Rompun, 100 mg/ml).

I tried live traps similar to those used by Hornocker and Hash (1981) and Magoun (in prep.) but failed to capture any wolverines using that method.

Captured wolverines were sexed, weighed, measured, ear tagged with plastic roto tags (Nasco West), their ages estimated, and radio-collared. Measurements taken were total length, neck circumference, chest girth, and skull length and width. Ages were estimated by evaluating the general condition of the teeth and body (apparent trap wounds, scars from fighting), and by length of testes for males and length of teats for females (Magoun, in prep.). The wolverine was considered an adult if it was greater than 1 year old and was apparently sexually mature.

Radio transmitters (Telonics, Inc.) were in the 149.440-153.060 MHz range and had an expected battery life of 1 year. Collars were constructed of butyl rubber and had an inner circumference of 29 to 39 cm. Each collar had a whip antenna which extended 26 cm from the collar. The entire unit weighed 230 g.

The monitoring schedule varied during the study depending on the number of active radios. When possible, instrumented wolverines were located once per 7 days. Inclement weather and other commitments sometimes increased the intervals between sightings. The majority of relocations were from fixed-wing aircraft (Cessna 180 or PA-18 150) equipped with a radio-receiver scanner and three-element Yagi antennas (Telonics, Inc.) mounted to the wing struts. Additional location data came from trappers who harvested the instrumented animals.

Each time a wolverine was located its position was plotted on a 1:63,360 United States Geological Survey (U.S.G.S.) map and date, time, activity, number of associates, topography, and vegetation type were recorded. Vegetation was classified to level 3 of the Viereck and Dyrness (1980) classification system.

Seasonal home ranges (winter period was mid-October through March; summer period was April through mid-October) were determined for wolverines with eight or more locations using the minimum area method of Mohr (1947). Obvious dispersal locations were omitted from the calculations. The enclosed area of the convex polygon was measured by use of a compensating polar planimeter.

Each instrumented wolverine was classified as a resident or a transient. A resident was an adult wolverine that had established tenure in the area. Transients were juveniles and adults that had not yet established residency.

Availability of the different vegetation types within each of the radio-collared wolverine home ranges was determined following procedures outlined by Marcum and Loftsgaarden (1980) using the 1:250,000 scale vegetation maps provided by the Palmer Agricultural Experimental Station (McKendrick et al. 1982). Wolverine use of the available vegetation types was determined by overlaying locations of the radio-collared wolverine onto the vegetation maps. If the location fell on a mapped boundary between different vegetation types, the vegetation type I recorded during the flight was used. I lumped the following vegetation types and considered them as communities due to the fact I could not accurately differentiate between them from fixed-wing aircraft: mat and cushion and sedge grass tundra, white and black spruce, and dwarf birch and shrub willow.

A regression analysis of elevations of wolverine locations and season of the year was conducted using BMDP1R and BMDP6D programs (Dixon et al. 1981). Elevations of radio locations were regressed on Julian date. Elevations were standardized among the instrumented wolverines by determining the mean elevation for all locations for each wolverine, assigning this mean elevation a value of zero, determining the elevational difference between this baseline and each point location, and then pooling these differences for all wolverines by month (Buskirk 1983).

Wolverine tracks were followed on the ground during May and December 1980, February 1981, and April 1982 in an effort to gain information on food habits and habitat use. The route of the animal, its apparent activity, and its interactions with other species were noted.

Wolverine carcasses were purchased from hunters and trappers in GMU 13 for $10 per carcass. Canine teeth and premolars, female reproductive tracts, and gastrointestinal (G.I.) tracts were collected.

Canines and premolars were sectioned at 30μ and 24μ, respectively, using a cryostat (Damon/IEC). Tooth sections were stained and mounted on slides following Goodwin and Ballard (1985) except that the tooth sections were in the hot hemotoxylin stain for 15 minutes and were agitated at 5-minute intervals. Stained sections were removed and rinsed in distilled water for 3 minutes, then dipped in the acid alcohol solution for approximately 20 seconds for canines and 5 to 10 seconds for premolars. The sections were again rinsed in distilled water to stop the stain lightening process of the acid alcohol.

Gastrointestinal tracts were separated into gastric and colonic contents. To decrease the bias associated with the trap bait, gastric contents were not included in the sample unless the wolverine had been shot or had been trapped beside a natural carcass. Scats were removed from the large intestine between the colon and the caecum, accessioned by location and date, and air dried.

Analysis followed standard techniques used for carnivore food habit studies (Korschgen 1980). Dried scat material was weighed and separated by the different prey remains. Food items were identified using a reference collection of vertebrate skins and bones. The different prey items were weighed to the nearest 0.1 g on a top-loading balance. Foods expected to have been taken incidentally during the time the animal was in the trap (vegetation, trap bait) were not included in the analysis.

RESULTS

Between 10 April 1980 and 8 December 1981, 12 wolverines (10 males) were captured a total of 14 times (Table 3). There was one capture-related mortality, probably due to an embolism or toxemia caused by the dart (Albert W. Franzmann, pers. commun.). During the study period, 75 carcasses from GMU 13 were purchased from trappers. Weights and morphometric measurements are presented in Appendix A.

Home Range Characteristics

Instrumented wolverines were located 153 times, primarily from fixed-wing aircraft, between 10 April 1980 and 15 April 1981 and between 18 November 1981 and 1 April 1982 (Table 4). No radio location data were collected between 15 April 1981 and 13 November 1981 due to a lack of functioning radios. Instrumented wolverines were sighted on 54% of the relocations; however, during the snow months (November-April), I sighted the radio-collared wolverines on 73% of the relocations. All locations of the instrumented wolverines are provided in Appendix B. Individual home ranges are presented in Figure 2. Due to dropped collars, trapper harvest, or radio failure, only one wolverine (male 040) was monitored for an entire year. Therefore, other than 040's, the calculated home ranges presented in Table 5 probably are smaller than the actual annual home ranges.

The average winter and summer home ranges for adult males (based on 7 or more radio-locations) were 353 km^2 (n = 5) and 385 km^2 (n = 4),

Table 3. Capture statistics of 12 wolverines in the Susitna River Basin, Alaska, 1980-81.

					Morphometric measurements (mm)								
Wolverine no.	Sex	Age	Date of capture	Capture location	Weight (kg)	Total length	Neck circumference	Chest girth	Skull length	Skull width	Drug type	Initial dosage (cc)	Comments
040	M	6-7 yr	10 Apr 80	Clarence Lk.	14.5	876	330	429	194	116	Sernylan/ Rompun	0.25/ 0.2	Blind in 1 eye; teeth badly worn.
040	M	7-8 yr	25 Mar 81	Clarence Lk.	14.5	--	--	--	--	--	M-99/Rompun	0.5/ 0.4	--
041	M	1 yr	19 Apr 80	Fog Ck.	15.5	877	346	502	166	115	M-99	2.0	Capture mortality.
042	F	Ad	19 Apr 80	Watana Ck.	9.5	806	272	384	147	99	Sernylan/ Rompun	0.25/ 0.5	Lactating; had 2 kits.
043	M	Unk	6 May 80	Standing Bear Lk.	17.7	876	--	451	159	115	M-99/Rompun	0.4/ 0.5	--
044	M	Unk	7 May 80	Susitna R.	--	--	--	--	--	--	M-99/Rompun	0.5/ 0.5	Not fully immobilized; very lively.
050	M	2 yr	6 Mar 81	Clarence Mt.	17.7	960	343	510	138	113	M-99/Rompun	0.5/ 0.4	Dispersed after 1 month.
066	M	Juv	13 Nov 81	Chunilna Hills	14.1	928	--	551	--	--	M-99/Rompun	0.4/ 0.5	Needed additional drug--0.4 cc M-99 and 0.5 cc acepromazine.
067	M	Juv	4 Dec 81	Upper Fog Ck.	14.5	--	--	--	--	--	M-99 Rompun	0.5/ 0.5	--
068	M	Ad	4 Dec 81	Stephan Lk.	16.4	--	--	--	--	--	M-99/Rompun	0.2/ 0.5	All canines and many incisors broken.
068	M	Ad	2 Apr 82	High Lk.	--	--	--	--	--	--	M-99/Rompun	0.7/ 0.5	--
069	F	Ad	5 Dec 81	Chunilna Hills	10.5	794	--	416	152	100	M-99/Rompun	0.7/ 0.5	--
070	M	Unk	6 Dec 81	Upper Coal Ck.	17.3	--	--	--	--	--	M-99/Rompun	0.7/ 0.5	Gave it 7 additional injections--3.5 cc of M-99 before it became immobilized.
071	M	Juv	8 Dec 81	Little Clearwater	15.9	920	378	522	169	110	M-99/Rompun	0.7/ 0.5	--

Table 4. Number of locations for radio-collared wolverines monitored in the Susitna Basin, Alaska, 1980-82. Includes radio, harvest, and dropped collar locations.

Wolverine no.	Sex	Est. age	Year	Locations per month												Totals
				Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
040	M	Ad	1980				4	6	5	1	3	2	4	2	1	
			1981	3	2	6	1									40
041	M	Juv	1980				1									1
042	F	Ad	1980				3	3	8	2	2					18
043	M	Ad	1980					7	6	2	3	3	4	1	1	
			1982		1											28
044	M	Unk	1980					1	2	3	2	2	3			13
050	M	Juv	1981			5										
			1982											1		6
066	M	Juv	1981											4	2	
			1982	2												8
067	M	Juv	1981												4	
			1982	1	1	3	1									10
068	M	Ad	1981												4	
			1982	1	1	3	4									13
069	F	Ad	1981												2	2
070	M	Unk	1981												5	
			1982	1	2	3										11
071															3	3
Totals				8	7	20	14	17	21	8	10	7	11	8	22	153

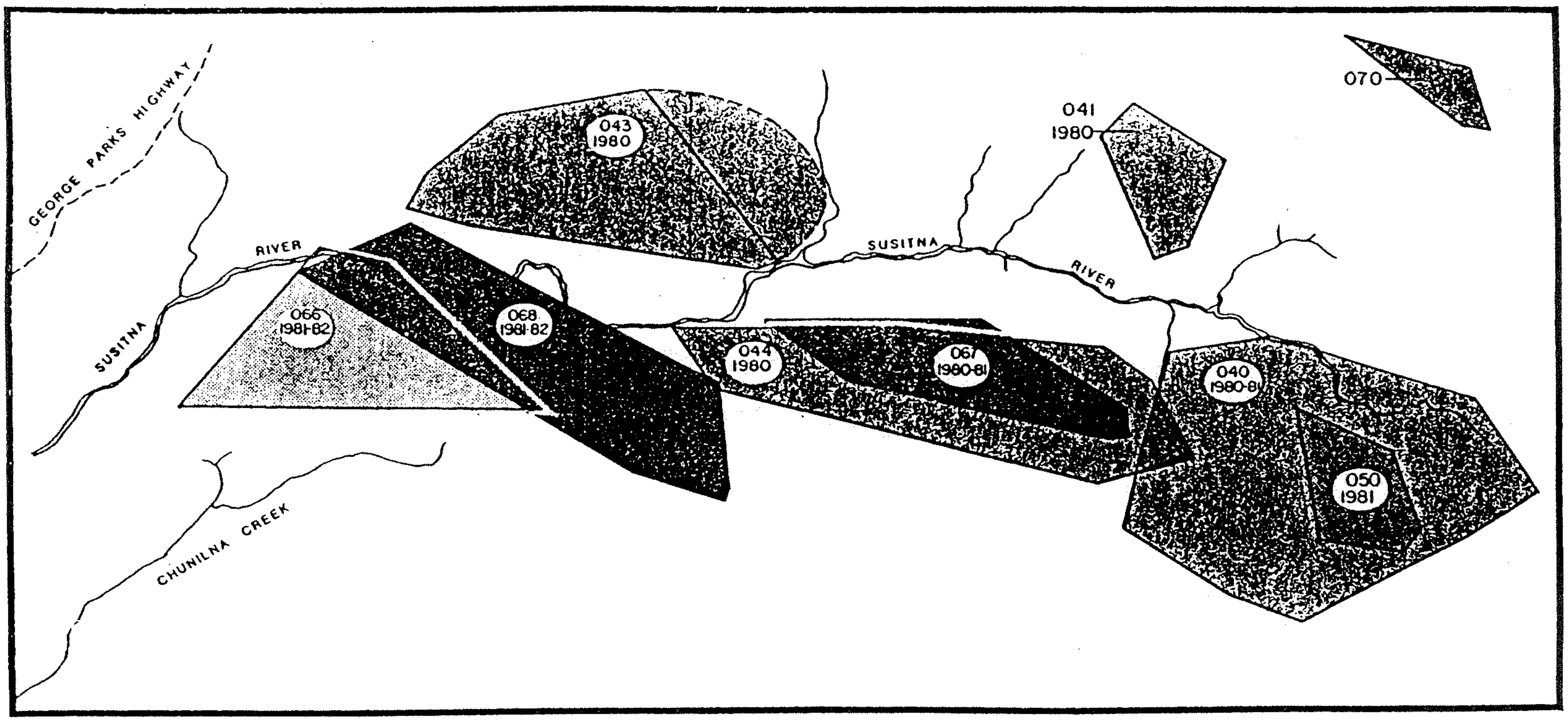


Figure 2. Individual home ranges of the nine radio-collared wolverines monitored between May 1980 and April 1982.

Table 5. Home range size of nine wolverines in the Susitna River Basin, Alaska, 1980-82, as determined by the minimum area method (Mohr 1947).

Wolverine no.	Sex	Age[1]	Period monitored	No. of relocations	Home range size (km^2)	Comments
116040	M	Ad (7)	10 Apr 1980 - 15 Apr 1981	40	637	Died of natural causes.
116042	F	Ad	19 Apr 1980 - 12 Aug 1980	18	92	Lost contact.
116043	M	Unk	6 May 1980 - 4 Dec 1981	27 28	303 405	Lost contact - radio malfunction. Included area in which a trapper had tracked this wolverine before trapping (15 Feb 1980).
116044	M	Unk	7 May 1980 - 9 Oct 1980	13	401	Lost contact.
116050	M	Ad (2)	6 Mar 1981 - 25 Mar 1981	5	89	Harvested.
116066	M	Juv (0)	13 Nov 1981 - 27 Jan 1982	8	238	Harvested. Animal had dispersed out of area prior to trapping.
116067	M	Juv (0)	4 Dec 1981 - 1 Apr 1982	10	179	
116068	M	Ad	4 Dec 1981 - 24 Apr 1982	13	366	

Table 5. Continued.

Wolverine no.	Sex	Age[1]	Period monitored	No. of relocations	Home range size (km^2)	Comments
116070	M	Unk	6 Dec 1981 - 10 Mar 1982	11	69	
116071	M	Juv (0)	8 Dec 1981 - 12 Dec 1981	2	--	Harvested.

[1] The age, in years, is in parentheses.

respectively (Table 6). The size difference was not significant ($p < 0.05$). Male wolverine 040 had an annual home range of 637 km^2 with winter and summer home ranges of 515 km^2 and 451 km^2, respectively. The size difference between male 040's winter and summer ranges was statistically significant ($p < 0.05$).

Only one female was monitored long enough to determine a seasonal home range. Wolverine 042 was lactating with two kits and had a spring/summer home range of 92 km^2.

The general shape of the instrumented wolverines' home ranges indicated that major topographical features such as major waterways and mountains were used as boundaries between home ranges. The Susitna River acted as a home range boundary for six of the seven males. The river itself was not a barrier to travel, however, as wolverines crossed throughout the year and also used it as a travel corridor during the winter.

Movement Patterns

Regression analysis of wolverine elevational use over time showed a significant ($p < 0.05$) upward movement during late winter/early spring and a significant ($p < 0.05$) shift downward during the late fall/winter (Fig. 3). From 31 January to 30 May, the predicted elevational increase based on the regression line was 106 m. The elevational decrease during the fall was more pronounced; from 1 October to 20 December, the predicted decline was 615 m.

Table 6. Seasonal home ranges of the instrumented wolverines in the Susitna Basin, Alaska, 1980-82.

	Accession no.	Sex	Home range (km^2)	No. of Locations	Period monitored
Winter	040	M	515	16	22 Oct - 31 Mar
	066	M	238	7	13 Nov - 4 Jan
	067	M	179	9	4 Dec - 1 Apr
	068	M	366	9	4 Dec - 2 Apr
	070	M	69	11	6 Dec - 22 Mar
		Mean[1] =	353		
Summer	040	M	451	24	10 Apr - 15 Oct
	042	F	92	18	19 Apr - 12 Aug
	043	M	303	23	6 May - 7 Oct
	044	M	401	13	7 May - 9 Oct
		Mean[2] =	385		

[1] Juvenile male 066's and unknown-age male 070's home ranges were not included.
[2] Female 042's home range was not included.

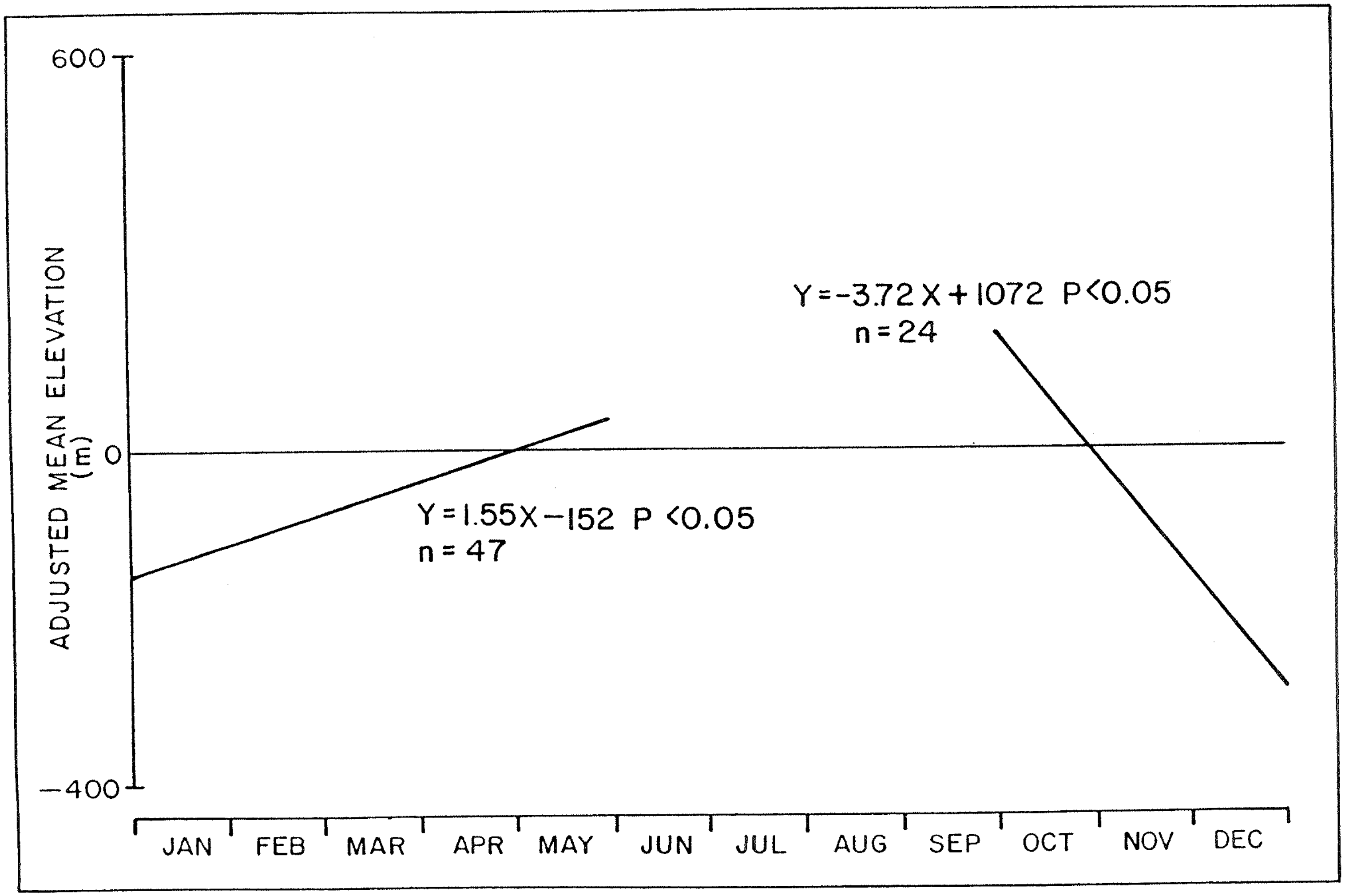


Figure 3. Regression analysis of wolverine elevational use by season.

Related to the elevational shifts during the year, male wolverines 040, 043, and 044 seasonally shifted their primary activity foci within their home ranges. Male wolverine 043 was relocated 10 of 13 (77%) times within the eastern half of its home range between 6 May (capture date) and 27 June 1980 (Fig. 4). Between 8 July and 4 December 1980 (the last of 10 locations before radio failure), 043 was located entirely within the western portion of its home range. Elevations are generally higher in the eastern portion. Wolverine 043 was trapped on the southeastern border of its home range in February 1982 by Roger Smith. Prior to its capture, Mr. Smith had been tracking the wolverine within the eastern half of its suspected home range.

Male wolverine 044 showed a similar fidelity to a portion of its home range (Fig. 5). Between June and mid-September, 044 was found entirely (8 of 8 times) within the eastern portion of its home range, predominantly in the Kosina, Gilbert, and Tsisi Creek drainages. This area is dominated by low shrub habitats, and elevations are generally higher than in the western half. After mid-September, 044 began moving west to the area around Stephan Lake where it had been captured during early May. The western portion of 044's home range is dominated by woodland and open spruce habitats.

Male wolverine 040 did not show as pronounced a seasonal fidelity toward any one area within his home range as did 043 and 044 (Fig. 6). During the winter, 040 was located 10 of 15 times within the eastern half of its home range and showed a fidelity to the Susitna River (54% of the relocations were within 1.6 km of the river), which is a tendency

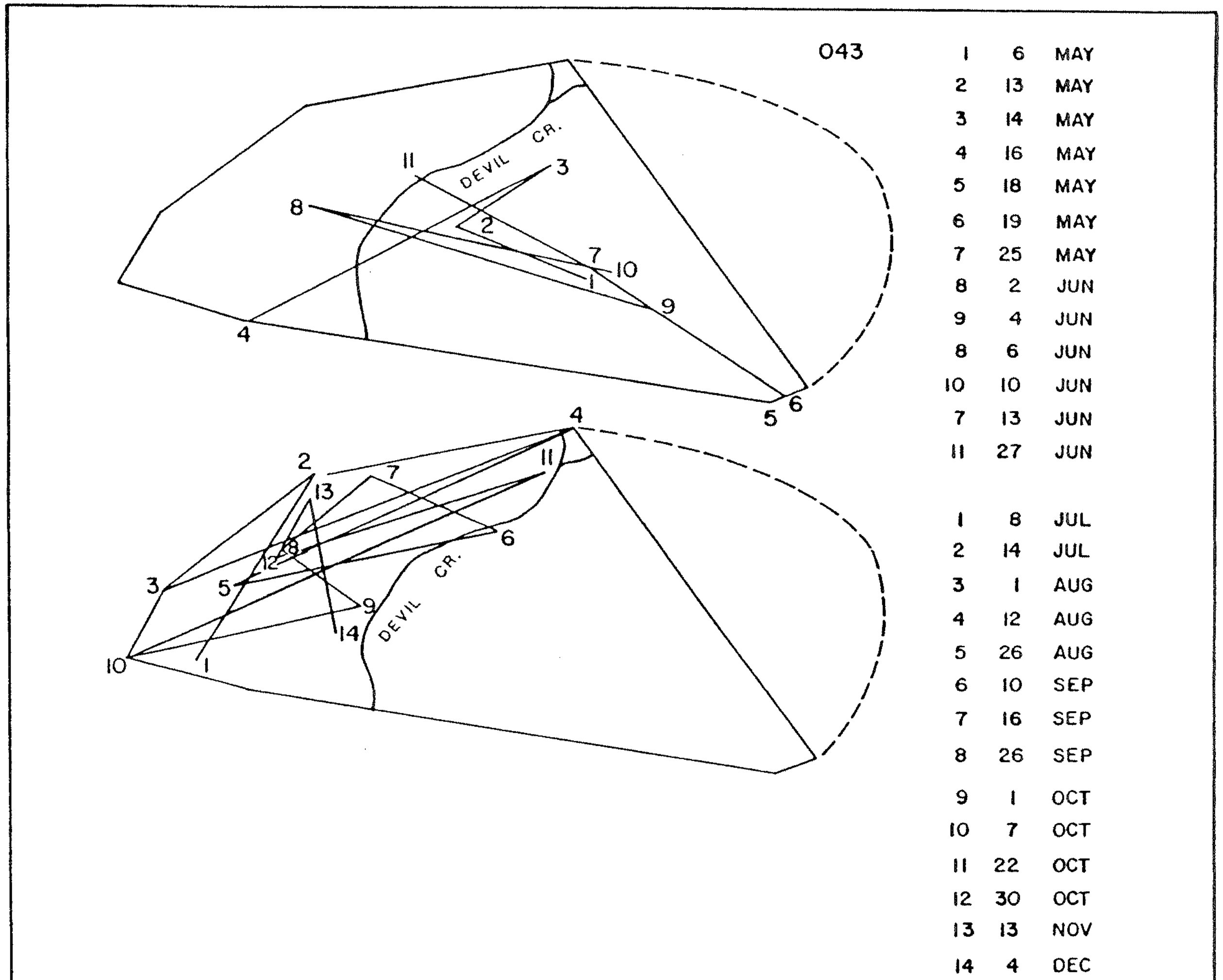


Figure 4. Wolverine 043's seasonal use of its home range. The dotted line encompasses the area 043 utilized during February 1981, just prior to his being trapped. Data were collected by ground tracking.

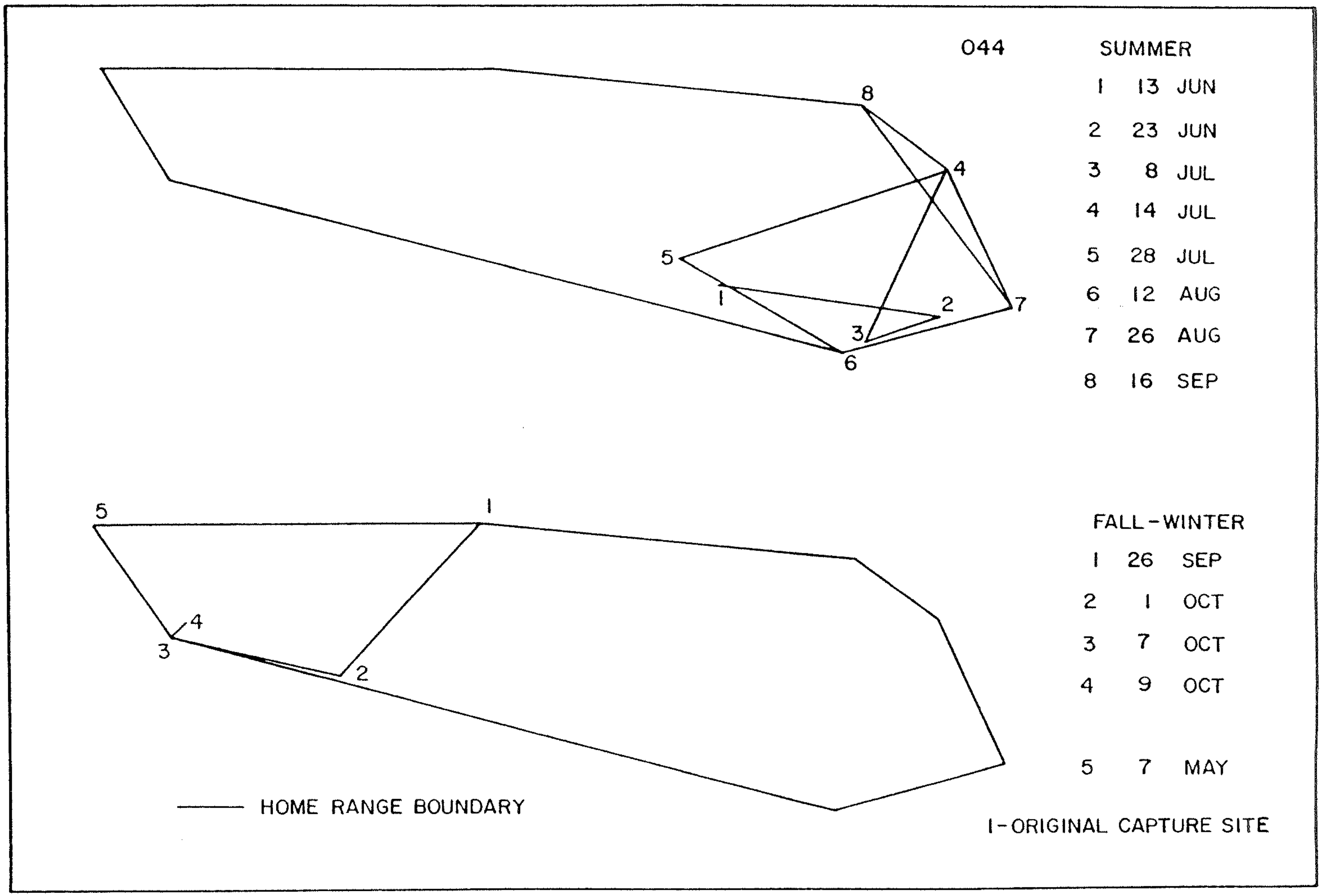


Figure 5. Wolverine 044's seasonal use of its home range.

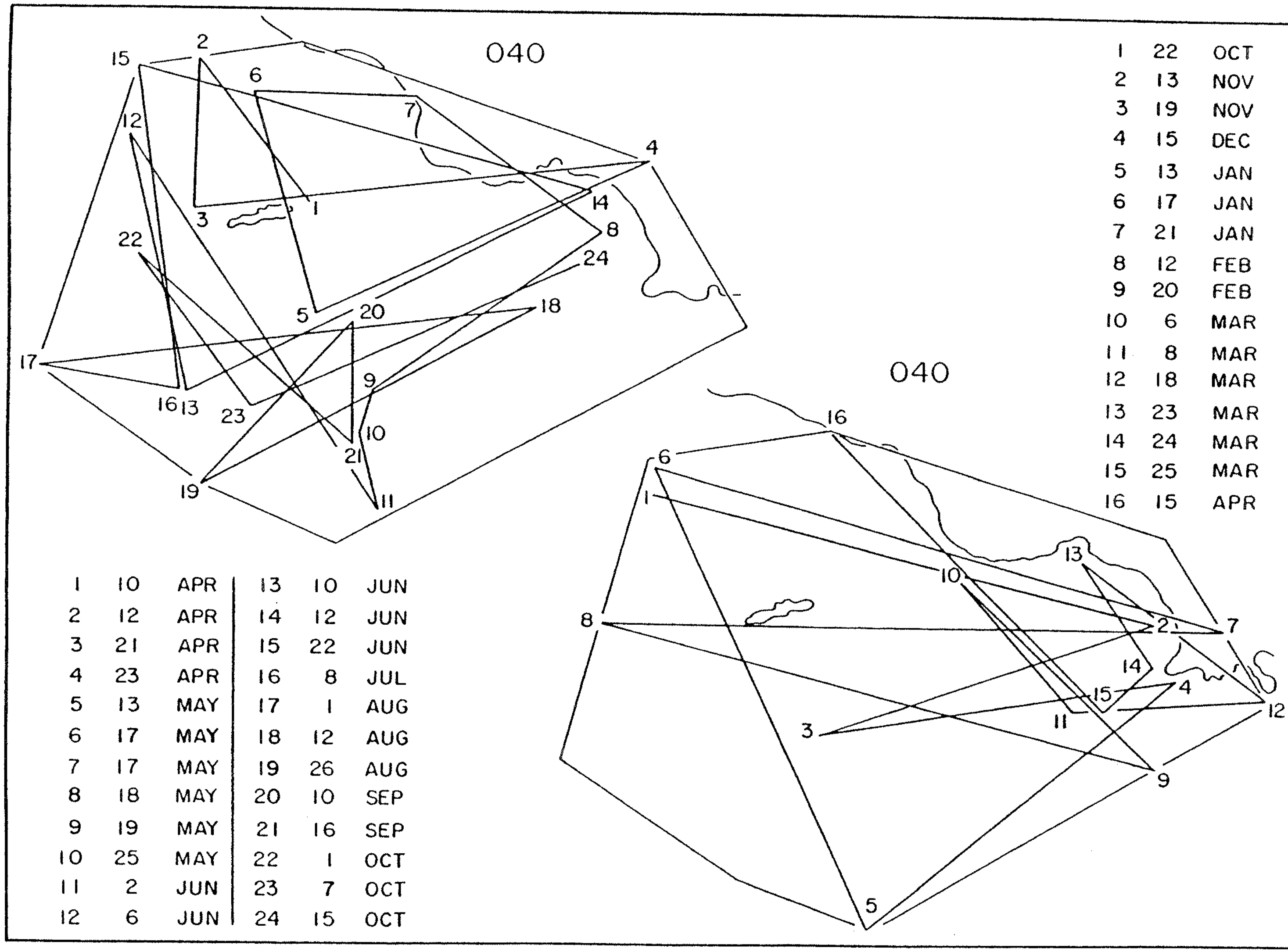


Figure 6. Wolverine 040's seasonal use of its home range.

he did not exhibit during the spring through fall months. During the spring and summer months, 040 traveled throughout its home range except for the far eastern corner (Susitna River). Between 8 July and 8 October, he concentrated his movements (8 of 8 locations) in the southern half of his home range.

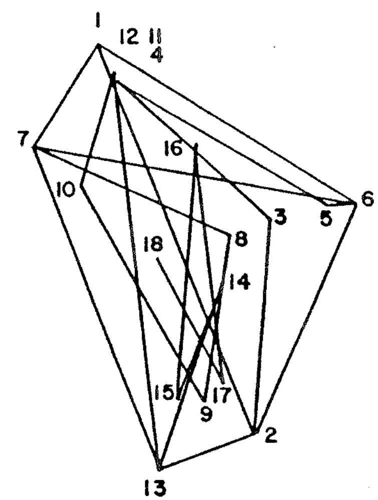
The movements of female wolverine 042 favored a more uniform coverage of her home range and showed little seasonal fidelity toward any one area except for a probable den/rendezvous site (Fig. 7). Her reduced home range size and movements may have been due to the need to return to her kits periodically.

The mean distances traveled between radio locations for male wolverines were 13.0 km with an average interval of 8.5 days in summer and 13.3 km with an interval of 9.9 days in winter. During periods of intensive monitoring of one location per 1.6 days during summer and 1.4 days during winter, the average distance between locations for males was 14.4 km and 4.0 km for the summer and winter periods, respectively. The difference in the average distances between locations during intensive monitoring for the summer and winter periods was significant ($p < 0.05$).

Female wolverine 042 had an average distance between locations of 7.2 km (mean interval of 6.8 days) during the spring/summer months. During an intensive monitoring period (mean interval of 1.7 days), she had an average distance between locations of 6.8 km. Males traveled approximately two times the distance that females did during the summer.

Daily movements of radio-collared wolverines appeared to be restricted due to pairing during the breeding season. Female 042 moved

042



1	19	APR
2	21	APR
3	25	APR
4	12	MAY
5	13	MAY
6	19	MAY
7	2	JUN
8	4	JUN
9	6	JUN
10	10	JUN
11	12	JUN
12	13	JUN
13	23	JUN
14	27	JUN
15	8	JUL
16	14	JUL
17	1	AUG
18	12	AUG

Figure 7. Wolverine 042's seasonal use of its home range.

an average distance of 6.8 km within a 1.7-day interval. However, between 12 and 13 June, she moved only 0.8 km. She was observed with an uncollared wolverine, suspected to be a male because of its size, during this period. They restricted their movements to an alder thicket which bordered a rock slide.

Male wolverines moved an average of 4.0 km per 1.4 days during the winter. However, juvenile male 066 was relocated three of three times on the same moose carcass. He restricted his movements to an area around the carcass for 27 days. This carcass was used concurrently by adult male 068.

Home Range Overlap

Three instances of home range overlap between instrumented males were observed during the study period. Male 040 (6-7 years old at collaring) and male 044 (age unknown) shared 17.4 km^2 which was 3.9 and 4.3% of 040's and 044's summer home range, respectively. They were separated by an average of 20.8 km when the other wolverine was in the overlap area. After 16 September, 044 shifted his use area westward away from the overlap area.

Male 050 was monitored during March 1981, and his use area was entirely within 040's annual home range. At that time, 050 was 2 years old and 040 was 7 or 8 and was the resident male. During March, I located each animal six times and during that period found their use areas to be almost entirely exclusive (Fig. 8) and comparable in size, 80 and 89 km^2 for 040 and 050, respectively. The two wolverines shared

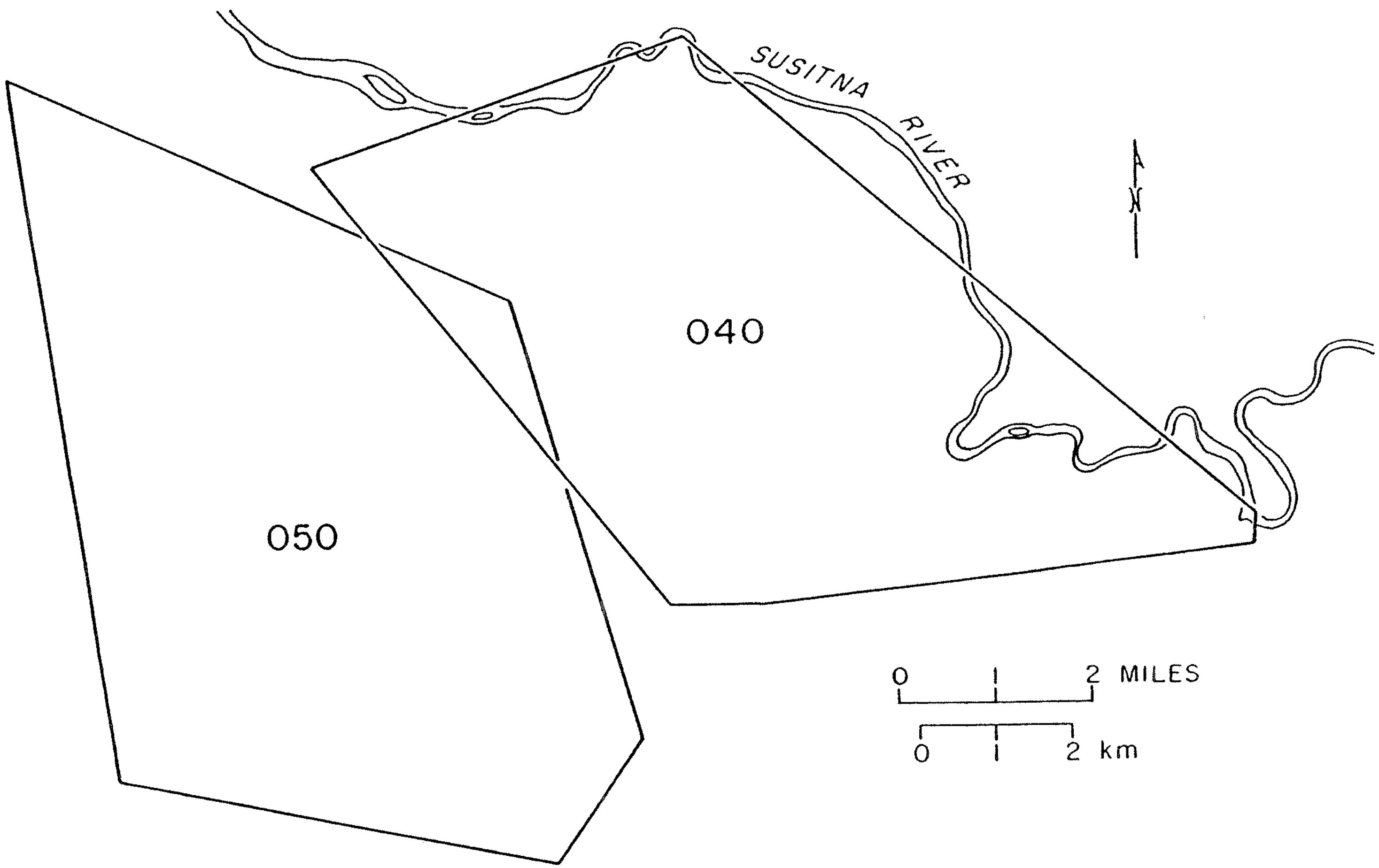


Figure 8. Overlap in the March home ranges of transient adult male 050 and resident adult male 040.

3.4 km^2 which was 4.3% of 040's and 3.8% of 050's March use area. They were separated by 5 to 11 km when located on the same day. During the first week of April, I found 040 dead and lost contact with 050 as he had left the area. The cause of 040's death is unknown. The carcass had been fed upon and cached by another wolverine.

Juvenile male 066 and resident adult male 068 shared 66 km^2 of their winter home ranges. This constituted 27.7% of 066's range and 18.0% of 068's range. Within the overlap area there was a calf moose carcass which both wolverines were utilizing between 8 December and 4 January. They were together on the carcass on 19 December. Between 5 and 12 January, 066 left the study area.

Long-Distance Movements and Dispersal

During the study period, male 050 and male 066 left the study area after 1 month and 1-1/2 months of monitoring, respectively. Male 050 was a 2-year-old transient that resided within resident male 040's annual home range during March 1981. I lost contact with 050 after 25 March 1981. For 19 months, its status was not known until it was trapped on 29 November 1982 along the White River in the Yukon Territory, Canada, a straight-line distance of 378 km from its collaring location. At the time of harvest, 050 was 3-1/2 years old and was in good physical health, showing no excessive tooth wear and possessing a high degree of kidney fat (R. Harvey Jessup, pers. commun.).

Male 066 was a juvenile wolverine who dispersed from his natal home range between 5 and 12 January. His last radio location within his home range was on 4 January at the moose carcass which he had been sharing with the resident adult male 068. Prior to 066's dispersal, 068 overlapped 066's range by 27.7%. Within 2-1/2 months after 066's dispersal, 068 utilized 70% of the vacated range. Male 066 was trapped 30 km northwest of his home range.

Habitat Use

Instrumented wolverines did not use the vegetation types within their home ranges in proportion to their availability ($p < 0.001$). The utilization availability analysis of Neu et al. (1974) indicated that on an annual basis (Table 7) spruce communities and ecotonal areas were used significantly more ($p < 0.05$) than expected in relation to their availability, while tundra communities were used significantly less ($p < 0.05$).

During summer (Table 8), it appeared that wolverines were selecting rock outcrops or ridges (ecotonal areas) and avoiding tundra communities. However, when the vegetation type which surrounded the small rocky areas was included, on the assumption that the wolverines ran into the rocks due to the airplane's presence, then all available vegetation types were used in proportion to their availability.

Spruce communities were preferred and tundra communities were avoided during the winter ($p < 0.05$). All other vegetation types were used in proportion to their availability (Table 9).

Throughout the year, wolverines utilized all aspects, showing no apparent preferences ($p > 0.05$).

Table 7. Wolverine occurrence in vegetation types within the Susitna Basin, Alaska, 1980-82.

Vegetation type	Area (km^2)	Proportion of total area	No. of locations observed	No. of locations expected	Proportion observed in each area	Confidence interval in proportion of occurrence (95% family confidence interval)
Tundra[1]	927	0.395	15	55	0.109	$0.042 \le p \le 0.168$[3]
Low shrub	755	0.322	40	44	0.290	$0.203 \le p \le 0.377$
Spruce	260	0.111	29	15	0.210	$0.133 \le p \le 0.288$[4]
Spruce-deciduous	192	0.082	19	11	0.138	$0.072 \le p \le 0.204$
Tall shrub	151	0.064	14	9	0.101	$0.044 \le p \le 0.158$
Ecotonal[2]	63	0.027	21	4	0.152	$0.084 \le p \le 0.220$[4]
Totals	2,348		138	138		

1 This is a combination of sedge grass tundra, mat and cushion tundra, and sedge grass/mat and cushion tundra.

2 Includes talus, rock outcrops, and water.

3 This vegetation type was used significantly less ($p = 0.05$) than expected.

4 This vegetation type was used significantly more ($p = 0.05$) than expected.

Table 8. Wolverine summer use of vegetation types within the Susitna Basin, Alaska, 1980-82.

Vegetation type	Area (km^2)	Proportion of total area	No. of locations observed	No. of locations expected	Proportion observed in each area	Confidence interval in proportion of occurrence (95% family confidence interval)
Tundra[1]	491	0.393	14	33	0.165	$0.075 \leq p \leq 0.255$[3]
Low shrub	484	0.388	29	33	0.341	$0.226 \leq p \leq 0.456$
Spruce	99	0.079	9	7	0.106	$0.031 \leq p \leq 0.181$
Spruce-deciduous	39	0.031	7	3	0.082	$0.015 \leq p \leq 0.149$
Tall shrub	97	0.075	11	6	0.129	$0.048 \leq p \leq 0.210$
Ecotonal[2]	40	0.032	15	3	0.176	$0.083 \leq p \leq 0.269$[4]
Totals	1,247		85	85		

1 This is a combination of sedge grass tundra, mat and cushion tundra, and sedge grass/mat and cushion tundra.

2 Includes talus, rock outcrops, and water.

3 This vegetation type was used significantly less ($p = 0.05$) than expected.

4 This vegetation type was used significantly more ($p = 0.05$) than expected.

Table 9. Wolverine winter use of vegetation types within the Susitna Basin, Alaska, 1980-82.

Vegetation type	Area (km^2)	Proportion of total area	No. of locations observed	No. of locations expected	Proportion observed in each area	Confidence interval in proportion of occurrence (95% family confidence interval)
Tundra[1]	484	0.340	6	21	0.098	$0.013 \le p \le 0.183$[3]
Low shrub	508	0.357	15	22	0.246	$0.122 \le p \le 0.370$
Spruce	174	0.122	20	7	0.328	$0.193 \le p \le 0.463$[4]
Spruce-deciduous	160	0.112	11	7	0.180	$0.070 \le p \le 0.290$
Tall shrub	57	0.040	2	2	0.033	$0.018 \le p \le 0.084$
Ecotonal[2]	41	0.029	7	2	0.115	$0.024 \le p \le 0.206$
Totals	1,424		61	61		

1 This is a combination of sedge grass tundra, mat and cushion tundra, and sedge grass/mat and cushion tundra.
2 Includes talus, rock outcrops, and water.
3 This vegetation type was used significantly less ($p = 0.05$) than expected.
4 This vegetation type was used significantly more ($p = 0.05$) than expected.

Snow tracking during early summer (14-16 May 1980) and winter (27 November-1 December 1981 and 29 March-1 April 1982) gave me an indication of how wolverines were using the different vegetation types and communities. During May, I followed two different wolverines which traveled through low shrub and tundra communities and investigated rock outcrops, apparently searching for arctic ground squirrels (Spermophilus parryii). Along the trail of what I believed was a female, the wolverine had excavated two ground squirrel dens. Four additional holes were dug into the snow along 5.2 km of the trail. Three of these were dug down into rock outcrops which I couldn't completely excavate, and one was dug into a snow drift within a tundra community. None of these snow holes were caches.

From 30 November to 1 December, I surveyed by air and on the ground the high-elevation, predominantly tundra communities which 042 utilized during the summer months, but I found no wolverine tracks. I did find a set of wolverine tracks in 042's home range in a mixed spruce/alder community. I followed this track for 5 km. No coursing or obvious hunting behavior was observed in the alder thickets. In a white spruce community, the wolverine was apparently hunting red squirrels (Tamiasciurus hudsonicus) and possibly porcupine (Erethizon dorsatum). The wolverine had partially excavated a squirrel midden.

Between 30 March and 1 April, I followed a wolverine for 13 km through low shrub and spruce communities. Signs of hunting and resting were seen in both types. It appeared that the travel route was mostly coursing and that more time was spent hunting in the spruce communities than in the low shrub areas. Two kills were observed along this route: a ptarmigan (*Lagopus* sp.) in low shrub and a *Microtus* sp. in spruce. Also, the wolverine dug up a cache within a white spruce stand which contained a golden eagle (*Aquila chrysaetos*).

Food Habits

Contents of the colons of 35 harvested wolverines were collected and analyzed. This sample only represented the winter period between 1 December and 29 March. Supplemental food habits information was collected by aerial and ground tracking. Wolverines were seen digging or hunting for prey or feeding on 27 occasions. The results of the food habit analysis are presented in Tables 10 and 11.

Ungulates were the most important food types during the winter period, using either frequency of occurrence (50.4%), percent weight (61.5%), or aerial observations (57.1%). In the Susitna Basin, moose were the most important ungulate in the wolverines' diet, as the majority of the caribou migrate out of the study area prior to the winter period. All the moose being utilized by wolverines observed during aerial monitoring were carrion. Ungulate mortality was caused by either wolf predation or starvation. Other important food items during the winter were microtines, squirrels, and gallinaceous birds. A female wolverine was observed carrying an arctic ground squirrel in December, indicating that she had dug it up from the squirrel's hibernaculum or from a summer cache.

Table 10. Wolverine colonic contents (N=35) collected between December and April expressed by percent dry weight and percent frequency of occurrence.

Food item	Percent dry weight	Percent frequency of occurrence	Importance value[1]
Moose	41.1	24.7	10.2
Caribou	20.4	20.0	4.1
Microtines	6.7	20.0	1.3
Bird	1.7	11.4	0.2
Squirrel	1.7	8.6	0.1
Snowshoe hare	0.8	5.7	0.1
Porcupine	1.7	2.9	0.1
Beaver/muskrat	10.6	2.9	0.3
Soil	15.4	20.0	3.1
Unidentified ungulate	--	5.7	

[1] Importance value = (% occurrence x % dry weight)/0.01 (Hugie 1982).

Table 11. Observations of wolverines digging, hunting, or utilizing prey items during radio-tracking flights or through ground tracking within the Susitna Basin, Alaska.

Prey item	Mid-October - March	April - mid-October
Moose	8	3
Ground squirrels	1	3
Birds	2	1
Microtines	2	1
Porcupines	1	--
Beaver	--	1
Identified	14	9
Not identified	4	0
Grand total	18	9
Total aerial sightings	63	70

The importance of moose to the wolverine diet appears to decrease during the summer months. Of the three moose utilized during the summer, two were adults which had been killed by bears (Ursus spp.), and the other was a 6-week-old calf which had died of unknown causes that did not appear to be predator related. The most important food types during the summer appear to be ground squirrels, birds, and microtines. Ground and aerial tracking during early summer indicated the importance of ground squirrels to the wolverine diet.

The presence of soil within the colon contents was high in both frequency of occurrence (20.0%) and by percent weight (15.4%). Of the seven colons that contained soil, three also contained ungulate remains. The other four colons contained a combination of several food remains and soil. Soil occurred in the colon contents between 15 January and 21 March.

Wolverine foraging behavior was also investigated through ground tracking. During winter, I tracked one wolverine that had coursed through a white spruce stand investigating red squirrel and porcupine tracks. Often the wolverine would stand up on its hind legs with its forepaws on a tree, apparently investigating for possible prey. If a fox track was encountered, the wolverine often investigated it and followed it from 10 m to approximately 2 km. The reciprocal was also true; foxes which came across a wolverine track would often follow that track.

In both instances that I observed wolverines killing ptarmigan, the capture appeared to be incidental as the wolverine was traveling a relatively straight course and came upon the ptarmigan while the bird was bedded. Evidence of wolverines pouncing and digging after microtines was noted.

During late April and early May wolverines were hunting ground squirrels extensively. They had success in capturing male ground squirrels which were setting up breeding territories. If the chase was unsuccessful, burrows were often excavated. The wolverine would dig on two ends of the burrow, apparently trying to scare the squirrel from the burrow. Magoun (in prep.) observed similar behavior in her study area.

I found only two caches during the study period. One cache found on 1 April contained remains of an immature golden eagle. The eagle was under 46 cm of snow and 15 cm of soil. Prior to the wolverine's arrival at the cache, the wolverine had traveled 2 km with very little deviation, then turned sharply and traveled 50 m to the cache location. The wolverine excavated a trench 2.4 m long and 0.25 m wide before locating the eagle. The eagle was apparently cached during the previous summer.

I found the other cache on 17 April, and that cache contained the remains of wolverine 040. All that remained was the head and most of the hide. The wolverine that had made the cache had apparently eaten all the musculature, internal organs, and genitalia. The remains were buried under approximately 20 cm of snow.

Harvest

The harvest of wolverines was documented through the State's sealing program, which requires the hide of each harvested wolverine to be presented to a representative of the ADF&G. A metal locking tag is attached to the hide and the sex, the harvest location, and the date and method of capture of the animal are recorded.

During the study period, the most common methods of harvest in GMU 13 were trapping and ground shooting, accounting for 84.7% and 14.2% of the take, respectively. Ground shooting can be an effective harvest method when snow and light conditions allow wolverine tracking from an airplane. Table 12 presents the chronology and the sex ratio of harvest for the three trapping seasons during the study period. The wolverine harvest was greatest during the months of February and March, accounting for 24.4% and 32.4%, respectively. The harvest during the three trapping seasons combined comprised 103 males (58.2%) and 73 females (41.5%), which does differ from a 1:1 sex ratio ($p < 0.05$). Harvest sex ratios differed significantly from 1:1 only in December, which significantly favored males ($p < 0.05$).

Harvest method may affect the sex ratio. During the denning period between mid-February and May, fewer female wolverines were taken in comparison to the rest of the trapping season by either ground shooting by trappers or by helicopter capture techniques used by me to radio collar. The difference was not significant ($0.05 < p < 0.10$); however, information concerning breeding status of the harvested female

Table 12. The chronology, sex ratio, and method of harvest of wolverines in GMU 13, Alaska between 1979 and 1982.

	November		December		January		February		March		Total	
	M	F	M	F	M	F	M	F	M	F	M	F
1979-1980												
Trap	4	2	8	3	4	5	13	12	11	7	40	29
Ground shooting	0	0	0	0	1	0	1	0	3	3	5	3
Snare	0	0	0	1	0	0	0	0	0	0	0	1
Total	4	2	8	4	5	5	14	12	14	10	45	33
1980-81												
Trap	5	2	6	0	1	6	4	2	5	3	19	13
Ground shooting	0	1	0	0	0	0	4	0	1	0	5	1
Snare	0	0	0	0	0	0	0	0	0	1	0	1
Total	3	3	6	0	1	6	4	2	6	4	24	15
1981-82												
Trap	3	2	6	1	10	5	2	2	8	9	29	19
Ground shooting	1	0	0	0	0	1	1	2	3	3	5	6
Snare	0	0	0	0	0	0	0	0	0	0	0	0
Total	4	2	6	1	10	6	3	4	11	12	34	25
Totals												
Trap	10	6	20	4	15	16	19	16	24	19	88	61
Ground shooting	1	1	0	0	1	1	6	2	7	6	15	10
Snare	0	0	0	1	0	0	0	0	0	1	0	2
Total	11	7	20	5	16	17	25	18	31	26	103	73

wolverines was not collected, and the inclusion of non-breeders would mask the effect of denning on harvest method.

During the study period, data concerning sex, age, and timing of the harvest were collected from 51 purchased wolverine carcasses: 28 males (54.9%) and 23 females (45.1%). The chronology of the harvest is tabulated by age and sex in Table 13. Appendix C presents the sex, harvest date, and estimated age of the wolverines purchased from trappers.

The harvested population consisted of 22 (43%) young-of-the-year, 15 (29%) yearlings, and 14 (28%) adults. During December, when a greater proportion of males was harvested, five of the seven wolverines for which ages were determined were juvenile or yearling males.

The first incremental line can develop in the wolverine's canine or premolar by at least February. Wolverine 066 (male), which was estimated to be a juvenile by tooth wear and testes size, was trapped on 27 January and did not have a cementum annulus. However, 051 (male) had one incremental line at the time of capture on 4 February and also an open root tip which characterizes a 0- to 15-month-old wolverine (Rausch and Pearson 1972). By the end of March, not all juvenile wolverines have laid their first annulus, for on 29 March neither of the two males 083 or 086 had an incremental line.

I compared the apparent ages of canines and premolars collected from 13 wolverines by counting cementum annuli on both the canine and the premolar from each individual. The age determined from the canine agreed with the age determined from the corresponding premolar for 12 of

Table 13. Chronology of harvest tabulated by age and sex of wolverines purchased from trappers in GMU 13, Alaska between 1979 and 1982.

	Age in years and sex							
	0		1		2 or older		Totals	
Month	M	F	M	F	M	F	M	F
November	0	3	0	0	2	1	2	4
December	3	0	2	0	1	1	6	1
January	2	2	2	2	0	1	4	5
February	5	0	2	2	1	3	8	5
March	4	3	2	3	2	2	8	8
Totals	14	8	8	7	6	8	28	23

the 13 wolverines. The canine/premolar pair that did not agree was collected from an older wolverine. The cementum annuli counts for the canine and premolar were seven and four, respectively. Because of the clarity of the cementum lines, I believe the canine gives the more accurate age.

DISCUSSION

Home Range Size and Movements

Differences in data collection methods and in techniques employed to calculate home ranges make it difficult to compare wolverine home range sizes based on this study with those determined in other North American studies. Magoun (in prep.) and I used the same methods of collecting and analyzing home range data, but our timing and frequency of data collection differed. Hornocker and Hash (1981) included home ranges of individual wolverines of unknown resident status and of juveniles in their home range estimate. Also, they combined all locations from an individual wolverine to obtain a yearly range estimate even if the animal was monitored for more than 1 year.

During my study, only one male wolverine was monitored for an entire year. Its home range of 637 km^2 was larger than ranges of males in Montana (Hornocker and Hash 1981) but comparable to male home ranges in northwestern Alaska (Magoun, in prep.). Whitman and Ballard (1984) estimated by a logarithmic extrapolation that the annual home range for male wolverines in the Susitna Basin is 535 $\pm$ 189 km^2. I believe their estimate is a more accurate estimate of the average male home range size in the Susitna Basin as their method incorporated the number of relocations of each animal, length of time each wolverine was monitored, and their known seasonal home ranges. The average home range size of males in the Susitna study area is probably greater than the average range size of adult males in Montana but less than that of adult males in northwestern Alaska.

Harestad and Bunnell (1979) derived an annual home range estimate based on a (ha)/body weight (g) regression equation of $H = 0.11W^{1.36}$ for carnivores. Using the mean weight of the adult male wolverines (16 kg) I captured, the estimated home range would be 574 km^2. However, if I use Harestad and Bunnell's (1979) equation on Magoun's (in prep.) male weight data, the estimated home range in her study area would be 483 km^2, which is much smaller than her calculated 666 km^2 area. It would appear that wolverine home range size is not simply a function of body size.

Gittleman and Harvey (1982) reported several cases in which differences in home range size between populations of the same species were found to be influenced by food availability. Magoun (in prep.) has found very low food availability during the winter period, while in the Susitna area there were stable ungulate (moose and/or caribou) populations throughout the year. A more plausible explanation of wolverine home range size would be that it is a function of the variety of habitats and topography of an area and the prey number and availability to wolverines. Wolverines, as scavengers, primarily depend on ungulate carrion during the winter, as most small game are hibernating or have migrated out of the area. It is therefore important that there are suitable areas to support ungulates within each home range. As Magoun found, that is largely not the case in her study area. The tendency for a species to have larger home ranges at higher latitudes regardless of trophic status or the weight of the species (Harestad and Bunnell 1979) may be due to the lower diversity of habitats and prey available.

Male wolverines in my study area had significantly smaller ($p < 0.05$) summer home ranges than did males in northern Alaska (Magoun, in prep.). Since Magoun and I used the same methods in data collection and in calculating home range, I would have expected to find comparable home range sizes during summer since food availability during that period is probably plentiful in both areas. However, the Susitna Basin has a greater elevational range and also more diversified habitats which support a more stable and varied prey base than does northern Alaska and therefore could have supported a greater number of wolverines. There appears to be little overlap of home ranges between resident males in my study area so smaller home ranges due to a greater wolverine density may be expected.

Home range size of lactating females appears to be similar among the three North American studies. However, these ranges are much smaller than the average range of three lactating females (170 km^2) studied by Bjarvall (in prep.) in Sweden. This difference may be due to actual biological differences between the wolverine populations or to the different sampling methods (Magoun, in prep.). Bjarvall snow tracked the female's movements on a daily basis. This technique would always detect short-term forays by the female to the extremities of her range, while periodical radio-tracking flights could possibly miss these movements.

The summer ranges of male wolverines in my study area appeared to be larger than their winter ranges. However, the sampling intensity was not equal due to inclement weather, radio failure, and mortality during the winter period. I compared 040's seasonal home ranges, as sampling intensity for each season was equal, to see if there were differences in size. Its winter range was 515 km^2, 114% the size of its summer range, which was significantly larger ($p < 0.05$). Harestad and Bunnell (1979) reported that winter home ranges of carnivores are 130 $\pm$ 30% of the non-winter home ranges. The size of the carnivores is a factor in this estimate. Seasonal home range sizes of large carnivores (*Lynx* and *Felis*) appear to change little, while smaller carnivores may increase their home range during winter (Harestad and Bunnell 1979). A larger home range during the winter period seems likely if a greater search area is required as the availability and vulnerability of prey decrease. However, increased movement during winter would not be advantageous if long movements through areas of low prey availability were unavoidable. During the winter, within the Susitna Basin there are concentration areas of ungulates (Ballard et al. 1982b) and small mammals (Kessel et al. 1982). Wolverine 040 did restrict a majority of its movements to an area of high ungulate densities. Factors other than foraging may have governed the few movements away from the area of high ungulate density.

There are seasonal shifts of activity within stable home ranges. These shifts coincide with elevational changes during winter and spring seasons and can be explained in terms of food availability. Early in summer (mid-April) male ground squirrels, which generally inhabit areas above treeline, emerge and set up territories. During this period the squirrels are very susceptible to predation, and wolverines appear to select for these areas. The importance of ground squirrels to wolverines during the spring has been documented previously (Hornocker and Hash 1981; Gardner and Ballard 1982; Whitman and Ballard 1983; Magoun, in prep.).

After mid-October, available food resources at higher elevations decrease due to hibernation and migration. At this time, wolverines move to lower elevations and rely more heavily on carrion (mainly moose), caches made during the summer, grouse (Canachites canadensis) and ptarmigan, microtines, and possibly red squirrels and porcupine. Moose in the Susitna Basin also selected lower elevations during the winter months (Ballard et al. 1982b) and were found primarily between 600 and 850 m. Whitman and Ballard (1984) found that wolverines in the Susitna Basin selected for areas between 305 and 914 m.

Vegetation types associated with the higher elevations used during the spring and summer months were upland shrub, tundra, and rock outcrops. During the winter, wolverines were found predominantly in spruce dominated communities.

In the Susitna Basin, male wolverines move greater distances during the summer than during the winter and also move greater distances during summer than do female wolverines. Magoun (in prep.) and Hornocker and Hash (1981) reported that movements by males during the summer are influenced by breeding activity. Magoun found that males traveled four times the distance at a rate of two times that of females. She believed the greater distance traveled by males was to monitor the four to six females which could reside within the resident male's home range. The data I collected support these findings.

Two factors which restricted wolverine movements were identified: the pairing of a male and female for breeding, and the presence of carrion during winter. In my area, pairing lasted for at least 2 days, during which the pairs moved between 2 and 4 km. Magoun and Valkenburg (1983) also observed restricted movements during the 2 to 3 days that pairs were together.

The presence of carrion during the winter also appeared to restrict wolverine movements. Once a carcass was located, it was more efficient for the wolverine to center its activities around that known food source.

Home Range Overlap

There is disagreement among the North American studies concerning home range overlap. Hornocker and Hash (1981) reported that wolverine home ranges overlapped between individuals of the same and opposite sex. They believed that male wolverines have home ranges much too large to actively defend and that scent marking by individual males is to maintain temporal spacing (cited Koehler et al. 1980). Strict territorialism does not seem beneficial to a species that relies to a large extent on carrion. A system which allows flexibility of movement to areas of carrion abundance would be more successful (Hornocker et al. 1983). However, Hornocker and Hash (1981) did not establish the residency or the familial relationships of their instrumented wolverines. This knowledge may be vital, for Magoun (in prep.) found exclusive use of summer home ranges by resident adult female wolverines but also found that mother and daughter combinations may have overlapping home ranges and that adult resident male home ranges may overlap those of juvenile males which had not yet dispersed.

In my area, there was a varying amount of range overlap for males between two resident adults, between a juvenile and a resident adult, and between a transient adult and a resident adult. The percentage of overlap was smallest between the adults, irrespective of residency. The transient was within the annual home range of the resident for at least 1 month prior to its movement from the area; however, during the month-long monitoring period, the ranges of the two wolverines overlapped very little. It appears that residency and familial relationships should be known for a wolverine population in order to interpret the amount of home range overlap.

Hornocker et al. (1983) reported that the degree of overlap can be influenced by human exploitation. In areas of high wolverine mortality, there may be a breakdown in the social organization, keeping it in a state of flux. Magoun's (in prep.) instrumented animals suffered no natural mortality and only one of the 26 was trapped. In my area, five of the nine instrumented males died during the study period, yet male ranges appeared to be exclusive. The most important mortality factor in my area appeared to be harvest by humans, which removed a higher proportion of juveniles. The harvest of resident animals may have been low enough not to affect the social organization or maybe harvest does not affect social organization.

Long-Distance Movement and Dispersal

The 376-km movement by the 2-year-old male represents the longest recorded movement by a wolverine. The age of the wolverine makes the movement somewhat unique, as dispersal in mammals most often occurs at puberty (Storm et al. 1976). Little is known about the movement patterns of transient wolverines, the mechanisms that initiate the movements, or factors that can terminate a wolverine's travel and the subsequent establishment of residency.

Juvenile male 066's dispersal falls within the time period in which Magoun (in prep.) observed juveniles to be dispersing in northwestern Alaska. As with other carnivores (Storm et al. 1976, Messick and Hornocker 1981), the factors which initiate wolverine dispersal are not known. Magoun found that a food shortage, confrontations with the resident adults, and/or hormonal changes due to the approach of the breeding season may have influenced dispersal of one of her instrumented juveniles. In my study, juvenile 066 dispersed away from known carcasses. Food abundance probably has little to do with dispersal as most juvenile males, at least, disperse regardless of food levels within their natal range.

Habitat Use

There are problems associated with the interpretation of habitat use based solely on aerial location data overlaid on vegetation maps. One major shortcoming of this type of analysis is that only the vegetative component of habitat is being analyzed. In addition, aerial location data are only an estimator of habitat use because the relocation points are based strictly on wolverine movements. There are a number of activities conducted by a wolverine during its travels such as foraging, exploration, reproductive behavior, and dispersal or migration which have varying degrees of association with vegetation type. Also, the vegetation maps were made from high-altitude infrared photographs which could not delineate vegetative types smaller than 1.5 ha. For these reasons, the aerial location data used in conjunction with vegetation maps are considered only indicators of wolverine habitat use.

By snow tracking, I could separate out some of the wolverine activity-vegetation type associations. Snow-tracking data used in conjunction with the aerial data gave additional insight into wolverine-habitat relationships.

Food availability by season was probably the primary factor determining use of vegetation types. The significantly higher use of spruce communities and lower elevations during the winter probably was influenced by a more plentiful food supply of carrion and small mammals. Snow-tracking and food habits data during the winter identified the importance of carrion, microtines, red squirrels, and possibly porcupines. Kessel et al. (1982) found that within the spruce communities in the Susitna Basin, abundant populations existed of tundra and meadow voles, and red squirrels, with porcupines locally abundant. Tracks indicated that wolverines coursed through the spruce communities, apparently foraging for food. Snow tracking through tall shrub or deciduous forest communities indicated that wolverines made more straight-line movements, indicating the animal was just traveling through. These observations agree with Bjarvall (in prep.), who found that denning females during March and April used all the available vegetation types in the proportion they occurred for traveling; however, almost all food was obtained in the coniferous forests. In my study area, tundra communities were avoided during the winter, probably due to the very low food resources during that time.

Radio and ground tracking indicated that wolverines spent considerable time during spring and summer in the higher elevations of their home ranges, in the low shrub and tundra communities. They were engaged in foraging for arctic ground squirrels and possibly searching for mates.

The apparent affinity of wolverines for rock outcrops during the summer was confounded by the possibility that wolverines may have been using the rocks for escape cover. Hornocker and Hash (1981) noted the apparent reluctance of wolverines to cross large openings and that timber was important for cover. Within the tundra communities there is very little available escape cover for a wolverine except for rocks. Potential prey within these rock outcrops are marmot (*Marmota caligata*) and pika (Ochotona collaris). Hornocker and Hash (1981) and Magoun (in prep.) have found that wolverines had preyed upon marmot; however, the importance of marmot to the wolverine's diet is not known.

Food Habits

Several similarities in the diet of North American wolverines have been observed at all the sites that have been studied. These include the importance of ground squirrels during the spring and ungulates, normally in the form of carrion, during the winter. Also, wolverines appear to be opportunistic and respond to seasonal and locally abundant prey.

In my study area, starting in late April and continuing to October, a plentiful and varied food supply was available for wolverines. Ground squirrels emerged during late April (Kessel et al. 1982) and microtines became more available as their nest sites and runways were exposed by melting snow. Caribou and moose calving began during late May and peaked between 25 May and 5 June (Ballard et al. 1982b, Pitcher 1982). Peak egg laying for ground-nesting birds occurred in June (Kessel et al. 1982). Ground squirrel dispersal occurred during August. Ground squirrels were available to wolverines until the squirrels went into hibernacula during the first part of October.

The importance of these species to the wolverines' spring/summer diet was evident from aerial and ground tracking. The timing of wolverine movements to higher elevations which were inhabited by ground squirrels coincided closely with the squirrels' emergence from hibernacula. Also, there appeared to be a change in wolverine movements, at least for male wolverine 040, due to caribou calving. During peak calving, I observed 040 disproportionately more often in the calving area. Brown bears also appeared to make directional movements to the caribou calving grounds (Miller and McAllister 1982). A disproportionate number of brown bears and wolverines have been observed on other caribou calving grounds in Canada (Arthur T. Bergerud, pers. commun.).

By mid-October food availability had declined. Ground squirrels had gone into hibernation and most birds and caribou had migrated out of the study area. Wolverines moved to lower elevations and were searching for small mammals, gallinaceous birds, and carrion. Magoun (in prep.) found that during the early winter period wolverines in northwestern Alaska were apparently relying on caches made during the summer, and on microtines.

During the study I never observed a wolverine cache any prey remains; however, it was apparent by ground tracking and the presence of soil in the colonic contents that wolverines were utilizing caches during the winter. Not all the caches utilized by a wolverine were necessarily constructed by that wolverine. Foxes and grizzly bears also make caches (Magoun, in prep.). A wolverine that intercepted a fox trail often followed the track, perhaps in search of the fox's food caches.

While Magoun (in prep.) observed that caching behavior by wolverines during summer in northwestern Alaska was fairly common, Hornocker and Hash (1981) found little evidence of caching by wolverines in Montana. They believed that caching by wolverines in Montana would be a wasted effort as the other numerous scavengers present would quickly discover and consume the cache's contents. Also, food cached during the summer or fall that was not quickly utilized would decompose. Other possible reasons why Hornocker and Hash (1981) and I did not observe much caching behavior compared to that observed by Magoun are our less intensive monitoring schedules and the larger, more stable winter food bases in our respective study areas. The death rate of moose due to natural mortality in the Susitna area during winter may have been great enough so wolverines did not need to depend greatly on caches. In Magoun's area, there were no stable winter ungulate populations nor was there a normally high ungulate carcass population remaining from the summer.

In my study area, moose were the major source of winter food, as caribou mostly migrated out of the area. During the winter, all the wolverines I monitored resided in areas of medium to high moose densities. The three males that I monitored through the summer and winter periods shifted their activity centers during the winter to areas of higher moose densities. This concurs with van Zyll de Jong (1975) that wolverine distribution appears to be related to the biomass and turnover of large herbivore populations.

The presence of two wolf packs within the study area had an effect on the abundance of carrion available to wolverines during the winter. During March 1981 there were three carcasses of moose known to have been killed by wolves within an area of approximately 100 km^2. This area supported at least two wolverines. I observed the two wolverines utilizing the kills on three occasions, and tracks indicated that these carcasses were being used intensively by wolverines. Winter predation rates for the two wolf packs ranged from one ungulate kill every 4 to 5 days (Ballard et al. 1982c), which should have increased the availability of food for wolverines with home ranges that overlapped the home ranges of the wolf packs.

It appears that, at present wolverine densities, there is an adequate food supply in the Susitna Basin. There are healthy ungulate and ground squirrel populations present. However, if adverse effects to these prey species occur due to human disturbance, they could prove detrimental to the resident wolverine population. Magoun (in prep.) found that a restricted winter diet can drastically decrease wolverine productivity.

Harvest

In Alaska, mandatory sealing of the pelts of furbearers, including wolverine, was initiated in 1971. Wolverine management is dependent primarily upon the results of this sealing program. The manager uses the information to determine total harvest, sex ratio, harvest chronology, and harvest methods in order to evaluate the current harvest level and to recognize population trends. The appropriate harvest rate for an area is dependent upon the population's density and productivity, degree of natural mortality, and the population status of adjacent areas. At this time, little is known about wolverine densities in most areas of the state. There are wolverine population estimates from only two areas, the upper Susitna River Basin (Gardner and Ballard 1982; Whitman and Ballard 1983) and northwestern Alaska (Magoun, in prep.). Presently, there is no technique available to estimate wolverine population size for large areas such as a game management unit, nor is it likely that resources will be available to develop such techniques in the near future. Therefore, the sealing program is the only tool the manager has to monitor the harvest. However, the problem with this management technique is that any changes in the population will only be recognized after the fact.

The actual sex and age structure of a wolverine population cannot be discerned by trapping records, as unequal catchability biases the estimate toward males and younger age classes. Therefore, only between-year comparisons of harvest can give an indication of trapping pressure. For example, if females equaled or exceeded males in the harvest, the indication may be that trapping has become exhaustive.

However, other factors that are not readily apparent from the sealing documents that could affect the sex ratio are the method and the timing of harvest (Magoun, in prep.). During December a disproportionately greater number of males was harvested in GMU 13. Males have larger home ranges and greater movement patterns than do females, and therefore have a greater probability of being captured. Also, it appears that a large number of the males captured in December are juveniles, which could indicate that dispersal may be initiated at this time. Banci (1984) also found that a higher proportion of juvenile males was captured during the early trapping season.

During the late season (February-March) pregnant females den, probably making them less susceptible to ground shooting. Bjarvall (in prep.), while observing denning behavior of three females, found that their active period away from the den was predominantly at night. However, denning females would not be less susceptible to traps as they would still be searching for food during their nightly travels.

To further assist the manager in monitoring the harvest from year to year, a canine (preferably) or premolar from the harvested wolverine could be collected. The age structure of the harvest may be a function of trapping intensity, as found by Archibald and Jessup (in prep.) for marten. If the average age of the harvested animals is low, it could indicate a heavily exploited population. The loss of a resident adult allows a transient animal to take up residence, therefore decreasing the average age of the population. If the population is in such a high state of flux, its productivity could be lower, as the yearling females which have immigrated into the area during the trapping season and taken up residency could not have bred as kits the previous summer. In lightly harvested areas, the average age of the harvested animals, the productivity of the area, and emigration of the juveniles should be higher (Archibald and Jessup, in prep.). Davidson (1980) found that in a lightly harvested coyote population emigration was significantly higher. This may explain the high number of juvenile male wolverines trapped during early winter in GMU 13.

Within GMU 13, using the small sample of ages I collected, the percentage of juveniles:yearlings:adults does not indicate a heavily harvested population. In addition, 6 of the 10 wolverines I captured were adults, indicating an older and less harvested population.

SUMMARY

A study of wolverine ecology within the upper Susitna Basin in southcentral Alaska was conducted between May 1980 and April 1982. The majority of the data on wolverine ranges and movements, seasonal habitat preference, and seasonal food habits was collected by following marked individuals by radiotelemetry. Additional data concerning the human harvest of wolverines were collected in GMU 13 through the use of sealing documents and the purchase of wolverine carcasses from trappers.

Twelve wolverines (10 males) were captured 14 times. The instrumented wolverines were located 153 times between 10 April 1980 and 15 April 1981 and between November 1981 and 1 April 1982. I purchased 75 wolverine carcasses from GMU 13 trappers.

The mean winter and summer home ranges for adult males were 353 km^2 and 385 km^2, respectively. Only one male was monitored for an entire year, and his annual home range was 637 km^2 with a winter and summer home range of 515 km^2 and 451 km^2, respectively. The mean summer home range for a lactating female with two kits was 92 km^2. It appeared that major topographical features such as rivers and mountains were used as boundaries between home ranges, even when these did not form barriers to wolverine movement. Adult male home ranges were primarily mutually exclusive, having an average overlap of only 4.2% between neighbors. An adult male's range overlapped a juvenile male's range by 27.7%. After the juvenile male dispersed, the adult male utilized 70% of the vacated range.

Wolverines shift their primary activity areas within their home ranges between summer and winter. During the summer, wolverines moved to higher elevations. Throughout the year, wolverines are highly mobile but appear to restrict their movements during the breeding season due to pairing and also during the winter when a locally abundant food source was located (e.g., ungulate carcasses).

During the study, two male wolverines departed the area. One was a 2-year-old male, which had resided within the known resident's annual home range for at least 1 month prior to leaving the area. This wolverine departed in March 1981 and was trapped 19 months later, 378 km from its collaring location, in Yukon Territory, Canada. The other was a juvenile male which had a winter range that was partially overlapped (27.7%) by a resident adult male. The juvenile dispersed from its range between 5 and 12 January and was trapped 30 km from its natal range.

Wolverine habitat use was studied by superimposing 138 point locations onto vegetation maps. On an annual basis, spruce communities and rock outcrops were used significantly more ($p < 0.05$) than expected.

Winter food habits were studied by collecting and analyzing colon contents. Thirty-five specimens were examined. In addition, summer food habits data were collected by aerial and ground tracking. During the winter, ungulates were the most important food type using either frequency of occurrence (51.4%), percent weight (61.5%), or aerial observation (57.1%). Moose were the most important ungulate in the diet, as the majority of the caribou migrated out of the study area prior to winter. Other important food types during winter were microtines, gallinaceous birds, and red squirrels. During summer, arctic ground squirrels were an important food item to wolverines. Wolverine movements to higher elevations which were inhabited by ground squirrels coincided closely with the squirrels' emergence from hibernacula.

The most common methods for harvesting wolverines in GMU 13 were trapping and ground shooting, accounting for 84.7 and 14.2% of the take, respectively. The combined harvest for the three trapping seasons was 103 males and 73 females, which does differ from a 1:1 sex ratio. Harvest sex ratios did not differ significantly by month from 1:1 except for December, which favored males ($p < 0.05$). The wolverine harvest was greatest during the months of February and March, accounting for 24.4% and 32.4% of the total harvest, respectively. The harvested population of GMU 13 during these trapping seasons consisted of 43% young-of-the-year, 29% yearlings, and 28% adults, which does not indicate a heavily harvested population.

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APPENDIX A. Morphological data collected from skinned wolverine carcasses harvested during the trapping seasons between 1979 and 1982 in GMU 13, Alaska.

Accession no.	Age[1] (yr)	Weight (kg)	Measurements in cm Chest girth	Neck girth	Nose to base of tail	Base of tail to last vertebrae	Skull length	Skull width
MALES								
005	0	9.8	39.7	33.5	81.8	18.4	16.4	11.8
010	0	12.7	46.7	34.7	86.0	24.0	15.1	10.5
012	0	9.8	39.7	31.7	85.8	19.0	16.5	10.4
013	1	9.5	36.8	29.5	82.6	19.4	15.8	10.8
014	--	8.4	38.3	31.5	84.1	17.5	16.0	10.6
017	1	9.3	41.1	28.7	83.0	20.6	16.8	10.6
019	--	9.5	38.9	29.9	84.4	20.5	16.3	11.1
020	1	11.8	37.9	30.9	84.0	20.5	15.8	11.9
021	1	11.1	35.7	28.9	83.8	17.8	15.5	10.7
022	--	8.6	34.0	26.2	75.4	18.1	14.4	9.8
024	2	11.4	40.2	31.2	84.0	19.0	15.4	9.9
026	3	11.1	40.6	30.1	83.0	22.9	15.6	10.9
027	--	9.8	39.7	33.3	81.7	23.9	16.5	11.0
029	--	9.5	38.5	29.6	80.5	19.2	16.7	10.7
031	1	9.1	36.7	31.1	80.0	22.6	16.5	11.2
034	3	9.5	37.8	30.1	85.4	21.8	--	--
037	0	7.0	35.4	25.6	75.0	19.4	15.6	10.0
039	0	9.5	38.0	27.5	83.8	21.1	16.4	9.9
051	1	--	39.2	32.5	82.5	23.0	--	--
054	1	11.0	39.9	27.0	83.5	19.5	--	--
055	0	12.0	43.0	31.7	85.7	20.6	--	--

APPENDIX A. Continued.

Accession no.	Age[1] (yr)	Weight (kg)	Measurements in cm					
			Chest girth	Neck girth	Nose to base of tail	Base of tail to last vertebrae	Skull length	Skull width
MALES, cont.								
056	0-1	10.0	41.2	31.7	79.5	21.0	--	--
058	2	10.5	39.9	33.7	84.2	20.4	16.4	11.1
059	4	3.0	26.4	21.5	78.1	20.5	16.1	10.1
060	1	9.5	39.1	31.7	79.0	20.3	15.1	10.8
063	1	--	35.2	28.9	79.4	19.0	14.5	10.4
065	1	9.5	36.2	31.6	78.6	--	16.0	10.7
066	0	9.5	35.5	30.0	85.0	--	16.6	12.2
067	--	8.6	--	28.0	--	--	16.1	11.6
073	0	8.6	41.5	30.5	80.3	22.0	16.1	9.8
074	3	6.8	36.2	28.9	76.0	21.5	15.5	10.2
075	0	8.6	37.0	30.7	81.2	22.5	16.2	9.7
077	4	11.4	45.5	36.3	87.5	20.2	16.6	10.9
081	7	10.5	40.5	33.5	90.5	22.2	17.4	10.8
083	0	6.8	35.5	26.8	76.5	20.9	15.0	9.3
085	1	9.1	37.8	31.5	84.5	17.1	16.0	9.8
086	0	8.4	35.9	30.6	80.5	--	15.8	9.5
087	--	11.4	50.2	32.2	88.0	22.9	16.2	10.6
n	29	35	36	38	37	34	33	33
MIN	0	3.0	50.2	21.5	78.1	17.1	14.4	9.3
MAX	7	12.0	26.4	36.3	88.0	24.0	17.4	12.2
MEAN	1.3	9.5	38.6	30.4	82.3	20.6	16.0	10.6
STDEV	1.6	1.78	3.91	2.76	3.58	1.81	0.66	0.70

APPENDIX A. Continued.

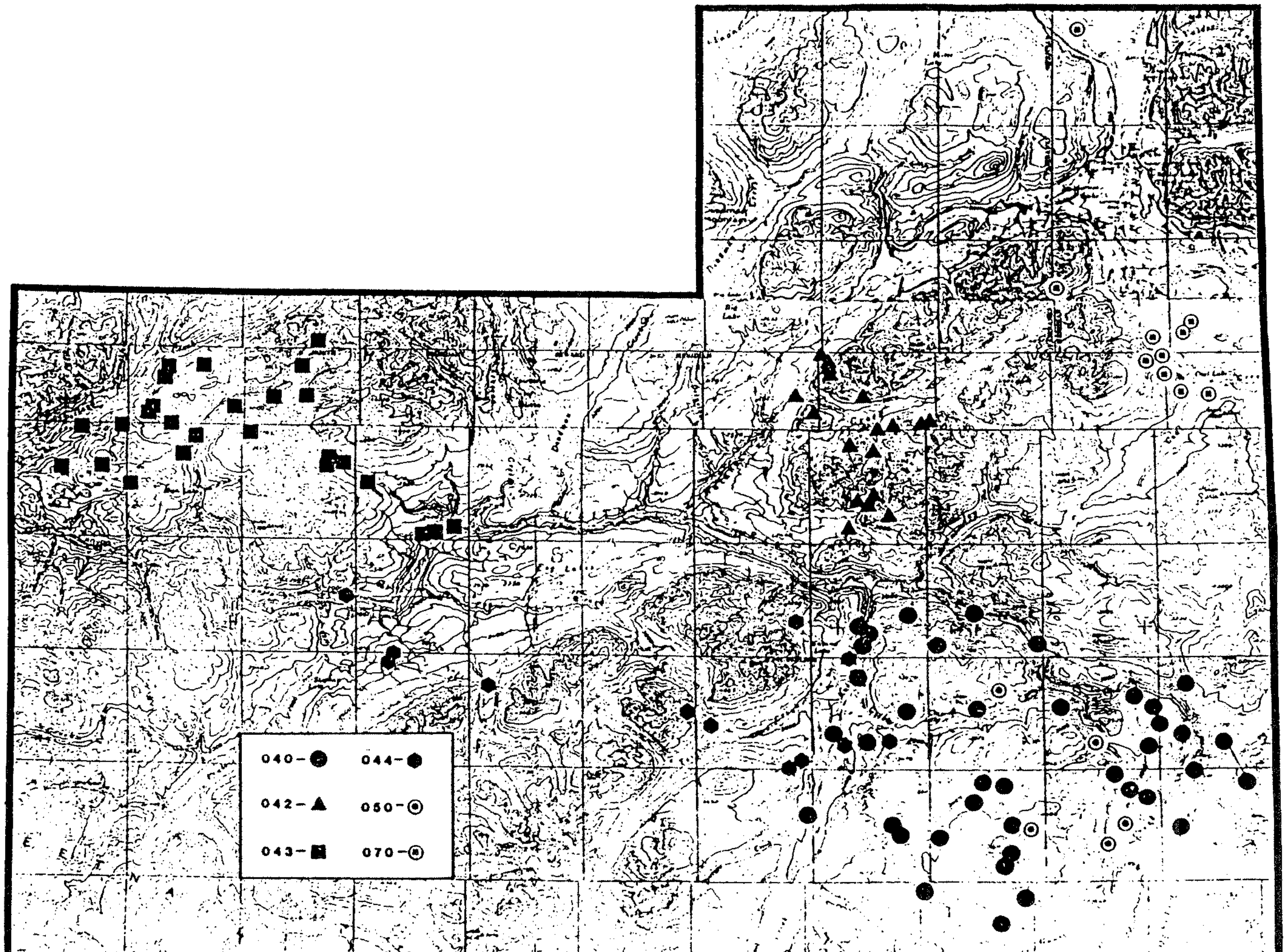
Accession no.	Age[1] (yr)	Weight (kg)	Measurements in cm					
			Chest girth	Neck girth	Nose to base of tail	Base of tail to last vertebrae	Skull length	Skull width
FEMALES								
001	1	6.1	34.0	26.2	77.0	18.8	14.9	9.1
003	1	6.4	32.4	26.4	73.0	22.0	14.9	9.6
004	2	7.3	33.9	32.1	76.5	20.5	15.2	10.1
006	--	5.9	35.7	27.9	73.0	19.8	15.4	9.6
008	--	4.1	25.7	21.8	75.8	19.4	15.3	9.2
009	0	4.8	28.1	23.6	75.0	18.4	14.6	9.3
011	--	7.5	35.9	26.8	74.3	19.9	14.8	9.9
015	1	4.1	30.9	20.4	71.0	20.0	14.1	9.6
016	--	5.9	--	24.7	72.0	17.7	12.8	9.0
018	--	6.1	39.0	24.1	67.0	19.1	14.1	9.4
023	--	10.5	34.7	27.9	81.0	20.7	14.6	9.6
025	--	7.3	35.7	28.5	75.8	17.2	14.6	9.7
028	9	7.0	33.9	24.6	68.5	21.2	13.8	9.3
030	--	6.4	33.8	25.6	69.9	16.7	14.1	8.7
032	2	7.0	28.9	24.9	74.3	21.0	14.2	9.4
033	--	7.5	26.1	--	70.0	17.3	14.0	9.0
035	0	6.5	32.5	23.4	77.0	17.6	14.1	9.4
036	1	8.0	38.2	28.2	76.0	20.9	15.0	10.0
038	6	5.5	29.1	25.6	71.1	19.0	14.4	9.2
046	2	6.0	31.9	25.7	78.5	21.0	--	--

APPENDIX A. Continued.

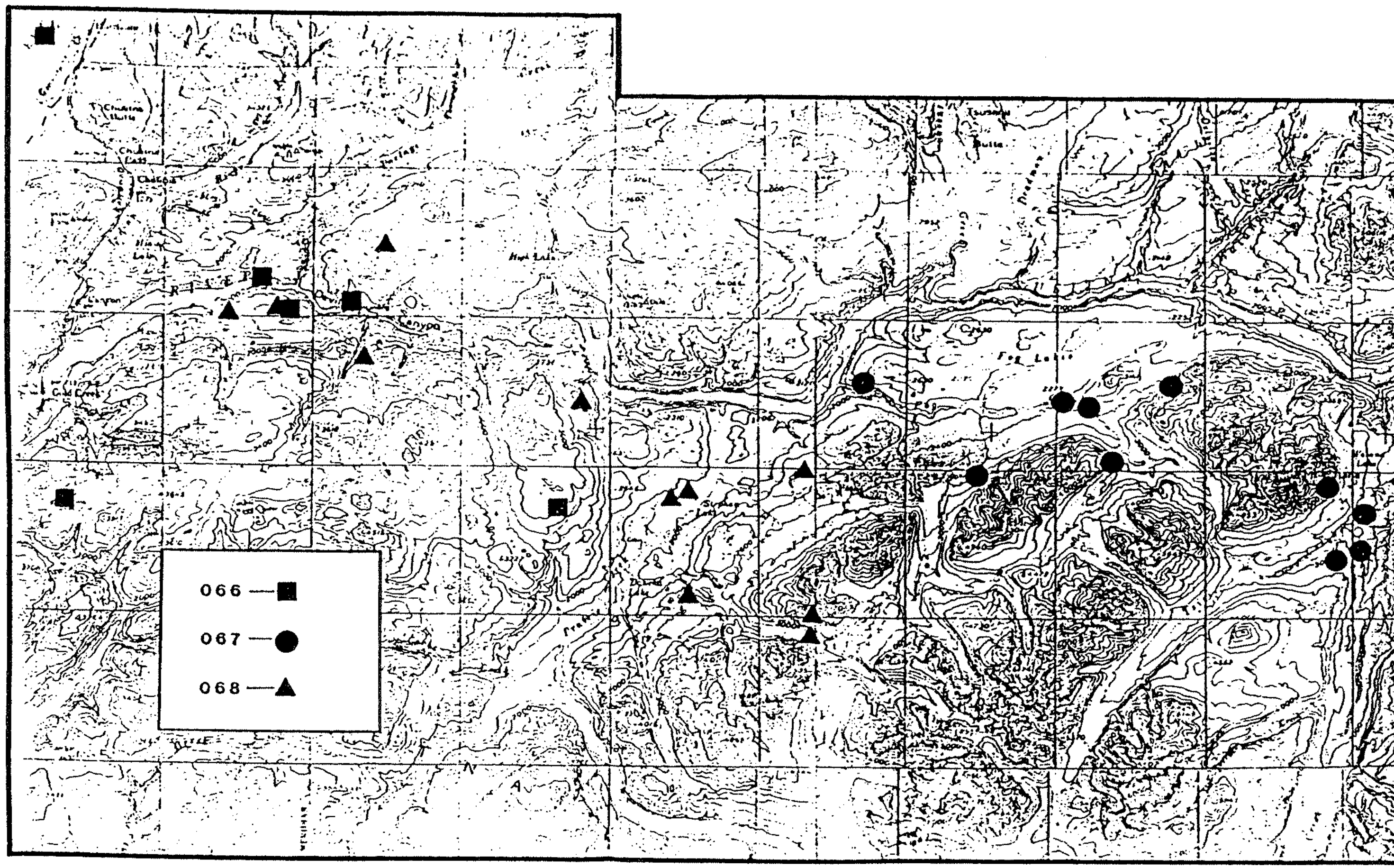
Accession no.	Age[1] (yr)	Weight (kg)	Measurements in cm: Chest girth	Neck girth	Nose to base of tail	Base of tail to last vertebrae	Skull length	Skull width
FEMALES, cont.								
049	6	7.5	36.1	25.6	74.1	21.1	13.3	9.2
052	3	--	36.8	27.0	75.0	19.0	--	--
053	0	--	31.8	25.7	72.5	18.0	--	--
061	0	5.5	33.0	24.0	71.1	19.5	14.4	9.3
062	3	6.0	34.2	27.0	70.2	21.6	15.0	9.6
064	5	9.0	37.1	25.7	77.4	18.0	13.7	8.9
072	0	6.8	36.2	27.9	74.5	18.0	14.9	9.4
076	7	--	34.2	27.4	77.8	17.9	13.1	10.5
078	1	6.8	35.1	30.5	82.0	19.3	14.2	9.2
079	1	8.2	34.6	31.0	75.2	21.4	14.9	10.4
080	0	6.6	35.0	25.5	74.3	19.6	14.4	9.3
082	1	5.0	34.3	29.5	75.5	21.2	15.2	9.2
084	1	8.2	41.0	28.9	83.0	18.9	15.3	9.6
n	23	29	32	32	33	33	30	30
MIN	0	4.1	25.7	20.4	67.0	16.7	12.8	8.9
MAX	9	10.5	41.0	32.1	83.0	22.0	15.4	10.5
MEAN	2.3	6.6	33.7	26.4	74.5	19.4	14.4	9.5
STDEV	2.5	1.39	3.45	2.54	3.68	1.47	0.66	0.41

[1] Ages determined by cementum analysis.

APPENDIX B. Plotted locations of radio-collared wolverines in the upper Susitna Basin, Alaska between May 1980 and April 1982.



Locations for six radio-collared wolverines in the upper Susitna Basin, Alaska between May 1980 and April 1982.



Locations for three radio-collared wolverines in the upper Susitna Basin, Alaska between November 1981 and April 1982.

APPENDIX C. Ages, determined by cementum analysis, of male and female wolverines harvested during the trapping seasons between 1979 and 1982 in GMU 13, Alaska.

Accession no.	Sex	Capture date	Estimated age (years)	
			Canine	Premolar
001	F	02/04/80	1	-
003	F	01/21/80	1	-
004	F	02/11/80	2	-
005	M	01/15/80	0	-
007	F	01/11/80	1	-
009	F	02/05/80	0	-
010	M	02/26/80	0	-
012	M	12/07/79	0	-
013	M	03/02/80	1	-
015	F	03/23/80	1	-
017	M	03/06/80	1	-
020	M	02/15/80	1	-
021	M	01/15/80	1	-
024	M	Spring 1980	2	-
026	M	Spring 1980	3	-
028	F	Spring 1980	9	-
031	M	Fall 1980	1	-
032	F	Fall 1980	2	-
034	M	11/27/80	3	-
035	F	11/30/80	0	-
036	F	11/16/80	1	-
037	M	12/27/80	0	-
038	F	01/09/81	6	-
039	M	12/07/80	0	-
040	M	04/15/81	7	-
041	M	04/19/80	1	-
046	F	Spring 1981	2	-
049	F	02/16/81	6	-
050	M	11/29/82	3	-
051	M	02/14/81	1	-
052	F	02/23/81	3	-
053	F	03/05/81	0	-
054	M	--	1	-

APPENDIX C. Continued.

Accession no.	Sex	Capture date	Estimated age (years)	
			Canine	Premolar
055	M	02/20/81	0	-
056	M	02/20/81	1	-
058	M	02/15/81	2	-
059	M	03/06/81	4	-
060	M	02/20/81	1	-
061	F	01/09/81	0	-
062	F	11/15/80	3	-
063	M	--	1	-
064	F	02/01/81	5	-
065	M	03/16/81	1	-
066	M	01/27/82	0	-
071	M	12/81	1	-
072	F	11/22/81	0	0
073	M	12/01/81	0	-
074	M	12/14/81	3	3
075	M	02/03/82	0	0
076	F	03/26/82	7	4
077	M	03/26/82	4	4
078	F	03/26/82	1	1
079	F	03/15/82	1	1
080	F	03/03/82	0	0
081	M	--	7	-
082	F	03/14/82	1	1
083	M	03/29/82	0	0
084	F	02/27/82	1	1
085	M	11/14/81	1	1
086	M	03/29/82	0	0