THE ECOLOGY OF MARTEN IN SOUTHCENTRAL ALASKA

A
Thesis

Doctor of Philosophy

By
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University of Alaska
Fairbanks, Alaska

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DOCTOR OF PHILOSOPHY

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ABSTRACT

The ecology of marten in the upper Susitna Basin, southcentral Alaska was studied from January 1980 to June 1982. Data were gathered on home range and movements, seasonal food habits, habitat use and winter energetic strategies. Radio telemetry was used to obtain a total of 560 locations for 17 marten. Mean home range sizes of marten along the Susitna River were 3.71 km^2 for females, 6.82 km^2 for males and 6.75 km^2 for adult males (2 + years). Marten were found to be nocturnal in autumn and to show strong variability in their diel activity patterns in late winter. Marten tended to move upward in elevation during spring and downward in autumn, contrary to the prevailing views of trappers.

Analyses of marten scats and colon contents collected during four seasons showed the most important foods to be microtine rodents, squirrels, fruits and birds. Major foods showed strong seasonal variation in utilization. Microtines were most important in autumn and showed declining use over winter. Northern red-backed voles were the most important microtine species. Sciurids were most important in spring and appeared to be a nonpreferred alternative food. Marten made little use of shrews, snowshoe hares, porcupines or insects. Carrion and human foods were highly preferred and consumed when available.

Habitat utilization was studied through the use of aerial transects and snow tracking and by identifying resting sites. Marten foraged for microtines more frequently than expected in vegetation types dominated by black spruce. Marten rested in winter primarily in active red squirrel middens in stands dominated by old-growth white spruce. Fat depot and organ weights and total body fat of marten were measured to find an indicator to total body fat. Marten were found to have extremely low body fat ratios which did not show a significant change over winter.

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INTRODUCTION

The American marten (*Martes americana*) is distributed in boreal and forested montane habitats across North America. In Alaska, marten occur in forest and woodland habitats from the southern end of southeast Alaska to the northern and western limit of trees (Manville and Young 1965). Because of their keen senses, elusive behavior and forested habitat, marten are seldom seen and are largely unfamiliar to the lay public, except through their pelts. Marten are weasels with slender torsos, long legs, bushy tails and well-developed facial and pelage markings (Figure 1). They are primarily solitary animals. Although they have excellent climbing skills and are athletic and enthusiastic tree climbers, marten forage mostly on the ground or snow surface. Their diet consists primarily of mammals smaller than themselves. The denning or resting habits of marten are very poorly documented. Only a few natal densites have been described for North America (e.g., O'Neil 1980) and none for Alaska.

Marten breed in late summer. The zygote develops to the blastocyst stage, which is dormant in the uterus until spring. After implantation, the embryo develops rapidly. Parturition probably occurs in Alaska in March or April, depending upon geographic latitude. General treatments of the life history of the species have been presented by Banfield (1974) and Strickland et al. (1982).

Marten are among the most important Alaskan furbearers from standpoints of income and recreation. During the 1980-81 trapping season an estimated 36,053 marten were trapped in Alaska with a mean value of

Figure 1. Radiocollared marten on Watana Creek, March 1981.

$38 per pelt (Melchior 1982). Total value of the pelts was estimated to be $1,370,014; the highest amount for any Alaskan furbearer. Alaska ranked first in marten pelt harvest in the United States from 1970-71 to 1975-76 and second only to Ontario among the 62 United States and Canadian provinces and territories (Deems and Pursley 1978). The recreational values associated with marten trapping in Alaska have not been quantified, but it is apparent that marten trapping is an important form of winter recreation for many Alaskans.

Scientific research on Alaskan marten has not kept pace with harvest levels. No journal articles or graduate theses dealing with Alaskan marten ecology have come forth since 1955 (Lensink et al. 1955). A large body of knowledge and lore concerning marten passes among Alaskan trappers, but this information varies in value and reliability and has not been compiled or published. The late Fabian Carey (1979), one of Alaska's most renowned and articulate trappers, summarized the state of knowledge of marten as follows:

> The life history of the marten has been little known and misunderstood. Knowledge of feeding habits and habitats was developed by trappers in order to catch the animal successfully. Population dynamics, reproductive biology, population fluctuations, dispersal and activity patterns were only observed casually and usually misinterpreted. Myths and misconceptions were commonplace. (p. 5).

The present study was conceived for the purpose of gathering data which would permit the prediction of the impacts of the proposed Susitna Hydroelectric Project upon mustelid carnivores, particularly marten. Data were required on the habitat needs, diet, seasonal distribution and population density of marten. These data served as the basis for the assessment of impacts originating from a variety of project components. As ecological data on marten were gathered, fundamental questions regarding the life strategy of marten in winter were raised. A great deal of research has been done on thermoregulatory and energetic strategies of such tundra carnivores as arctic fox (*Alopex lagopus*), wolf (*Canis lupus*) and red fox (*Vulpes vulpes*). Yet, practically no comparable information exists for marten, which, because of small body size and foraging syle, must experience comparable or more severe energetic stresses. Objectives of the study were as follows:

1. To determine the home range and movements of marten in the Susitna Basin;
2. To determine the seasonal food habits of marten, and relate them to movements and habitat use;
3. To describe the habitat preferences of marten with respect to major activity types, particularly foraging and resting; and
4. To describe the energetic strategy employed by marten during winter.

STUDY AREA

The study area was located in the upper basin of the Susitna River in southcentral Alaska (Figure 2). This area was chosen because it held the impoundment zones of the proposed Susitna Hydroelectric Project. It was chosen also because of the availability of detailed data for the area on climate, vegetation and vertebrate populations. Intensive field work was conducted at two sites, one near the mouth of

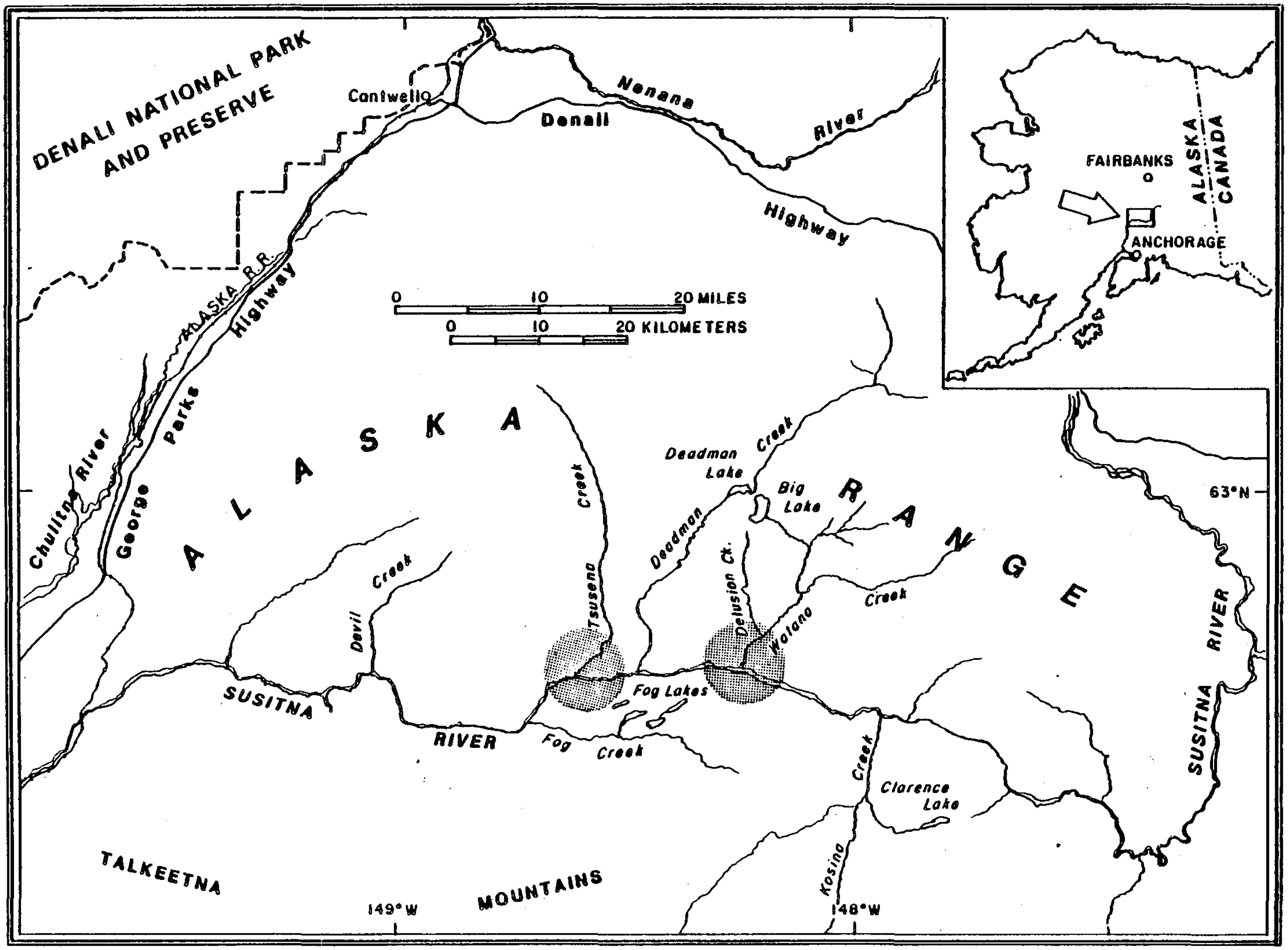

Figure 2. Study area map. Intensive study areas are shaded.

Tsusena Creek and the other along lower Watana Creek. The topography of the area is complex. The Susitna River and most of its tributary streams between the Indian and Oshetna rivers flow through steep-walled canyons up to 300 m deep. Above the Susitna River and separating the tributary creeks are flat or rolling benches which rise to become the Talkeetna Mountains to the south and the Alaska Range to the north. These benches consist of mosaics of weathered glacial till, exposed bedrock and acidic, wet, peaty soils. The area is remote and roadless. Transportation during the study was by helicopter, snowmobile or foot.

Vegetation of the study area is a mosaic of forest and shrubland vegetation types. Treeline, although quite irregular, occurs at 850-1000 m elevation. Vegetation of the study area was described and mapped by a team from the University of Alaska Agricultural Experimental Station, Palmer, Alaska (University of Alaska 1982). The most widespread vegetation types in the upper Susitna basin were found to be low mixed shrub, woodland and open black spruce, sedge-grass tundra, mat and cushion tundra and birch shrub. Forest and woodland vegetation types were dominated by white spruce (*Picea glauca*) or black spruce (*P. mariana*). Other tree species which occurred with spruce or in other associations were paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*) and quaking aspen (*P. tremuloides*).

Two vegetation types, white spruce and black spruce woodlands, were of particular importance to marten, and warrant detailed description. Stands of white spruce woodland are dominated by white spruce with total tree canopy cover over 10% but less than 60% (Figure 3).

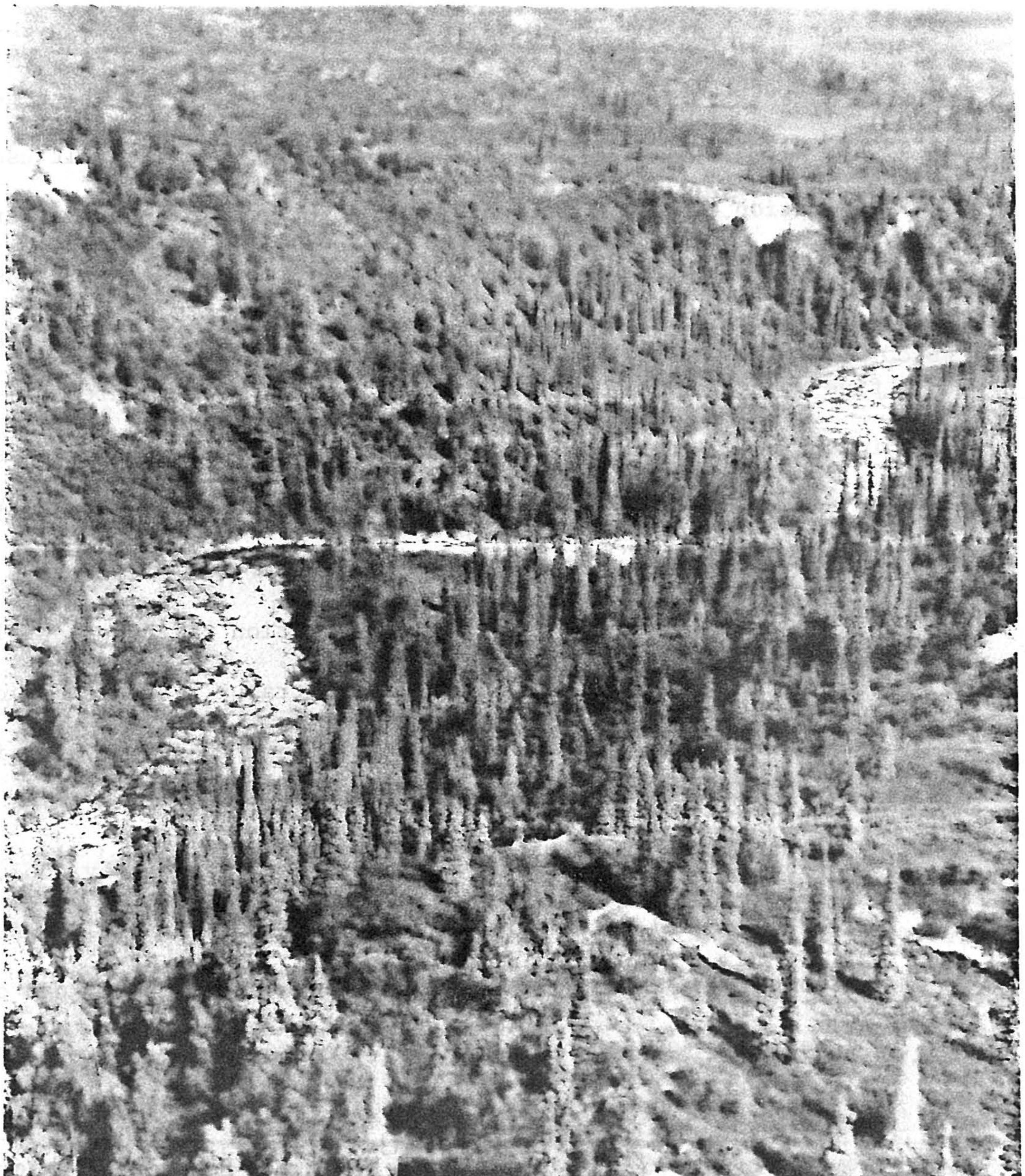

Figure 3. White spruce woodland at the 650 m elevation level along Deadman Creek. White spruce cover varies from 10 to 60 percent. Treeless areas in background are dominated by shrub birch (*Betula glandulosa*).

Paper birch is often present as a secondary tree species. This type intergrades with white spruce forest (canopy >60%), which generally occurs in patches smaller than the smallest mapping unit used in the vegetation mapping effort. Ground cover consists of feather moss (*Hylocomium* sp.), horsetail (*Equisetum* sp.), shrubs and subshrubs. Cover percentages of vertical strata and individual plant species for five woodland white spruce stands within the study area are presented in Table 1. Black spruce woodland includes most cover types dominated by black spruce and is generally found on poorly drained soils, frequently underlain by permafrost. White spruce often occurs at less than 25% of total canopy cover. Total vegetation cover is near 100%, most of it contributed by the ground cover stratum. A description of cover for six woodland black spruce stands within the study area is presented in Table 2.

The climate of the study area is characterized by cool, rainy summers and cold, dry winters. Snow cover is generally restricted to the months of October through April, although snowfall can occur even at the lowest elevations in the study area (450 m) during any month of the year. At Summit, 66 km northwest of the study area and at 773 m elevation, annual precipitation is 480 mm. Recorded air temperatures and precipitation at Summit are presented in Table 3 and are probably the best approximation available for long-term climatic conditions in the study area. High-pressure air masses settle over the area in winter and permit the formation of low level temperature inversions, which have important micro-climatic effects. Cold dense air pools in the

Table 1. Cover percentages for total vegetation, vertical strata, and plant species in woodland white spruce vegetation/habitat type on 5 sample sites in the upper Susitna Basin during summer 1980. Data from University of Alaska (1982), p. 38.

Category		Average Cover (%)[a]
Total Vegetation		100
Overstory (>100 mm dbh)		35
Picea glauca	White spruce	35
Understory (25-100 mm dbh)		11
Picea glauca	White spruce	3
Alnus sinuata	Sitka alder	6
Shrub layer (>0.5 m tall, <25 mm dbh)		4
Picea glauca	White spruce	1
Alnus crispa	American green alder	4
Rosa acicularis	Prickly rose	3
Ground layer (<0.5 m tall)		94
Feather mosses	Feather moss	30
Ptilium spp.		24
Equisetum arvense	Meadow horsetail	11
Equisetum silvaticum	Woodland horsetail	6
Linnaea borealis	Twinflower	15
Betula glandulosa	Resin Birch	6
Rosa acicularis	Prickly rose	5
Calamagrostis canadensis	Bluejoint	23

[a] Included only those species with at least 5% cover in any one area sampled.

Table 2. Cover percentages for total vegetation, vertical strata and plant species in woodland black spruce vegetation/habitat type on 6 sample plots in the upper Susitna River Basin during summer 1980. Data from University of Alaska (1982), p. 36.

Category		Average Cover (%)[a]
Total vegetation		99
Overstory (>100 mm dbh)		1
Picea glauca	White spruce	
Understory (25-100 mm dbh)		12
Picea mariana	Black spruce	11
Shrub layer (>0.5 m tall, <25 mm dbh)		17
Picea mariana	Black spruce	15
Ground layer (<0.5 m tall)		93
Feather mosses	Feather moss	5
Sphagnum spp.	Sphagnum moss	62
Empetrum nigrum	Crowberry	8
Ledum decumbens	Northern Labrador tea	5
Ledum groenlandicum	Labrador tea	5
Vaccinium uliginosum	Bog blueberry	23
Equisetum silvaticum	Woodland horsetail	10
Rubus arcticus	Nagoonberry	15
Rubus chamaemorus	Cloudberry	5
Picea mariana	Black spruce	3
Carex bigelowii	Bigelow sedge	7
Carex spp.	Sedge	6

[a] Included only those species with at least 5% cover in any one area sampled.

Table 3. Recorded average air temperatures (C) and precipitation (mm) at Summit, 66 km northwest of the study area, 1951-1975 (Alaska Power Authority 1982*a*).

	Daily Maximum Temperature	Daily Minimum Temperature	Daily Average Temperature	Monthly Average 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

steep-walled canyons so that air temperatures are lowest near the canyon bottoms. Wendler and Nicpon (1975) reported that from November to February inversions are found more than 95% of the time in interior Alaska and commonly reach a strength of 20 C over 200 m altitude differences. Such inversions also occur within the study area, although data on their strength and frequency have not been reported.

Fires appear to have occurred infrequently in the past, perhaps because of the relatively high summer precipitation in the study area. Fire scars were observed in the upper Susitna Basin and appear to increase in frequency from Devil Canyon eastward toward the Oshetna River. Fire scars were noted in many places on the intensive study site along Watana Creek. Mr. William Collins (University of Alaska Agricultural Experimental Station, Palmer, Alaska) estimated the age of one such scar to be 56 years. It is clear from the distribution of old spruce trees that this fire left most of the forest in the lower Watana Creek valley unburned.

The recorded vertebrate fauna of the study area includes 34 species of mammals, 135 of birds and 1 of amphibian. Six species of mustelids occur sympatrically in the area; marten, mink (*Mustela vison*), short-tailed weasel (*M. erminea*), least weasel (*M. nivalis*), land otter (*Lutra canadensis*) and wolverine (*Gulo gulo*) (Alaska Power Authority 1982*b*).

The trapping history of the area is not well documented. There is evidence that the study area has been trapped intermittently during the past half-century. Several old trappers' cabins were found within the study area, some of them with traps, suitable for marten, stored nearby. My assistants and I also found old, rusted marten-sized (No. 0 or No. 1) leghold traps hanging from trees along lower Tsusena and Watana Creeks. Some areas of the upper Susitna Basin were trapped during the course of this study by four groups of trappers. Groups based at Fog Lakes and upper Tsusena Creek trapped during the winters of 1980-81 and 1981-82. A third group trapped near Stephan Lake during the first winter. A fourth individual trapped on Watana Creek during the winter of 1981-82. Due to difficult access to and within the upper Basin, the area has received fairly light trapping pressure in historic times. It is my impression that the intensive study sites on Tsusena and Watana Creeks had not been trapped for at least several years preceding our field work.

MARTEN HOME RANGES AND MOVEMENTS

Information on marten home ranges and movements has come through a variety of investigative methods. During the first half of the century biologists relied upon snow tracking, casual observations and the beliefs of trappers for their information (Seton 1929, Marshall 1942). Newby (1951) and Lensink (1953) were among the earliest workers to use mark-recapture techniques to study marten movements. By the early 1970's radio transmitters had become sufficiently miniaturized and reliable to be used on marten. There are now available a number of reports, primarily unpublished theses (e.g., Spencer 1981, Major 1979, Mech and Rogers 1977), which provide telemetry-based depictions of the home ranges and movements of marten in a variety of ecological settings. Major (1979) has shown that telemetry-based home range sizes are larger than those determined by mark-recapture techniques on the same study site. Considering movement and physiological data which can now be obtained through the use of telemetry, Mech's (1974) claim that telemetry has "revolutionized the study of elusive wilderness carnivores" seems particularly true of marten.

Data gathered before this study suggest that the spatial organization of marten is similar in many respects to a pattern typical of terrestrial mustelids (Powell 1979). Adult home ranges show little intrasex overlap, male ranges are larger than those of females, and male ranges overlap those of females or young animals of either sex (Hawley and Newby 1957, Lensink et al. 1955, Francis and Stephenson 1972, Major 1979, Spencer 1981). Sexual differences in home range size have been observed by most workers. Male marten home ranges have been reported to range between 7% smaller (Simon 1980) and 760% larger (Major 1979) than female home ranges.

The objectives for this segment of the study follow:

1. Delineate the home ranges of male and female marten in the study area using radiotelemetry techniques;
2. Seek evidence to evaluate seasonal/elevational movements of marten; and
3. Determine the diel activity patterns of marten on a seasonal basis.

MATERIALS AND METHODS

Marten were live trapped during three periods: August-September 1980, February-March 1981 and September-October 1981. Traps were placed not on grids, but to optimize capture success (e.g., along trails, at ungulate carcasses). Traps used were models 203, 205 and 206 manufactured by Tomahawk Live Trap Co., Tomahawk, Wisconsin 54487. A variety of baits and lures were used, most commonly canned sardines and oil of anise or oil of wintergreen. The floors of traps were covered with polyethylene padding to prevent injury to trapped animals' claws. In wet or windy weather, traps were covered with various materials to protect captured animals. Traps were checked once per day (in morning) at air temperatures above 0 C. Between temperatures of 0 C and -15 C traps were checked twice daily. Traps were sprung at temperatures below -15 C in order to minimize trap mortality.

Captured animals were maneuvered into a wire holding cone and immobilized with a mixture of ketamine hydrochloride (6 mg kg B.W.$^{-1}$), xylazine (0.5 mg kg B.W.$^{-1}$) and atropine sulfate (0.3 mg kg B.W.$^{-1}$). The animals were examined, measured and outfitted with radiocollars supplied by AVM Instrument Co., Dublin, California 94566 and Advanced Telemetry Systems, Bethel, Minnesota 55005. AVM radio collars with mercury batteries weighed approximately 29 g, with lithium batteries approximately 27 g. Advanced Telemetry System radiocollars weighed approximately 34 g. All radiocollars had antennas enclosed within the collar and transmitted in the 164-166 MHz frequency band. Marten were held until ambulatory and released at the capture site.

Radio locations of marten were obtained as often as aircraft support and available manpower would permit. An intensive effort was made in the weeks following collaring to gather data because of the relatively short life of these small transmitters. Radiotracking was conducted from helicopters and from the ground using AVM LA-12 and Telonics TR-2 receivers (Telonics, Mesa, Arizona 85201). Three-element and four-element AVM yagi antennas were used for aerial and ground radiotracking. A few locations of radiocollared animals were obtained from live trap captures and returns of carcasses of collared animals by local trappers.

Locations of marten were recorded on 1:63,360 topographic maps. For each marten location, date, time, vegetation type and elevation were recorded. Seasonal home range sizes were calculated for each animal for which at least 8 locations had been obtained, using the minimum area method of Mohr (1947). I examined the effect of the number of locations on size of corresponding home range by regressing home range size on number of locations for 19 seasonal home ranges. Home range maps were plotted on paper, cut out and compared with replicate paper weight standards. A regression analysis of marten elevations over time was conducted using the BMDP1R and BMDP6D programs (Dixon et al. 1981). Elevation of marten locations was regressed on Julian date. Data were standardized among individuals by assigning each marten a seasonal mean elevation of zero and pooling data for all marten for one season.

Patterns of activity of free-ranging marten were monitored using telemetry signals and the system of signal interpretation employed by More (1978), Burnett (1981) and Zielinski (1981). Activity was sampled at 15 minute intervals. Observers listened to a signal for one minute and classified the animal as active, inactive or unknown. Animals which showed an abrupt change in signal strength during the sample period were classfied as active. Activity data were grouped into one-hour segments and tabulated using a contingency table program from the Statistical Package for Social Sciences (Nie et al. 1975).

Radiocollared marten which died and were recovered were aged using tooth cementum annuli. Lower canine teeth were sectioned and interpreted by Matson Commercial Microtechnique, Milltown, Montana 59851. Ms. Diane Preston, Alaska Department of Fish and Game, Fairbanks, Alaska 99701 confirmed age interpretations.

RESULTS

A total of 16 marten were captured in live traps 22 times and equipped with 20 radio collars. Five animals received replacement collars. None of the captured marten died or were seriously injured in the traps and no mortality or injury associated with the wearing of collars was observed. Measurements and other characteristics of radiolocated marten are presented in Table 4. Radiocollar life varied from 71 days to 189 days.

Marten were radiolocated a total of 560 times during 4 major data collection seasons (Table 5). Plotted locations are presented in Appendix A. Plotted marten home ranges are presented in Figures 4-7. Regression of home range area on number of locations for 19 seasonal home ranges showed that over the range of sample sizes considered, the regression coefficient did not differ significantly from zero (Figure 8). Thus, the relationship of home range size to number of locations did not appear significant above the cut-off point of 7 locations which I used.

Areas of seasonal home ranges are presented in Table 6. The mean home range area for male marten was 6.82 km^2. Mean home range area for females was 3.71 km^2, 54% that of males. Male marten, particularly those known or believed to have been adults, possessed mutually exclusive home ranges. Intersexual overlap of home ranges was common (e.g., Figure 7). Telemetry data in no case indicated that marten had crossed a body of water which required them to swim. Creeks and the Susitna River formed home range boundaries in many cases. On 28 November 1980,

Table 4. Characteristics of marten captured on the Susitna study area. Linear dimensions are in mm.

Number	Sex	Age	Date of Capture	Weight (g)	Length	Tail Length	Hind foot Length	Ear Length	Front foot width	Neck Girth	Chest Girth
044	M	Adult*	12 Nov 81	1280	771	274	95	48	37	132	192
045	F	Juv	12 Sep 81 27 Oct 81	760 790	595	228	88	38	–	108	140
126	M	Juv	28 Mar 81	1200	680	240	100	42	40	135	185
127	F	Adult	28 Mar 81	840	612	234	86	41	35	130	163
128	M	Adult	6 Mar 81 9 Sep 81	1300 1300	696	252	97	47	47	150	180
200	M	Adult	17 Sep 81 29 Oct 81	1180 1200	722	270	100	46	40	130	190
512	M	Adult	2 Mar 81 7 Sep 81	1130 1450	710	262	110	48	40	135	191
514	M	Juv	24 Feb 81 28 Apr 81	1020 1150	660	230	92	40	36	150	164
515	F	Unknown	20 Feb 81	1080	720	265	93	40	35	140	164
516	M	3	2 Nov 81	1260	723	252	102	48	–	–	–
517	M	Adult	21 Mar 81	1470	734	265	100	42	43	140	197

Table 4. Continued

Number	Sex	Age	Date of Capture	Weight (g)	Length	Tail Length	Hind foot Length	Ear Length	Front foot width	Neck Girth	Chest Girth
518	M	3	9 Sep 80	1380	703	265	94	46	-	-	-
			25 Nov 80	1120							
519	M	Adult	22 Aug 80	1440	720	281	102	42	-	-	-
			23 Aug 80								
			25 Sep 80								
520	M	Adult	27 Aug 80	1370	705	240	102	41	-	-	-
654	F	Unknown	12 Sep 81	950	610	210	80	40	40	132	160
655	F	Unknown	6 Sep 81	860	620	220	85	39	30	-	160

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*Adult classification indicates animals 2+ years old based upon tooth wear or sagittal crest development.

Table 5. Number of locations for each marten during seasons monitored. Numbers in parentheses are number of aerial radiolocations, number of ground radiolocations and number of trap locations.

Animal Number	Autumn 1980	Spring 1981	Summer 1981	Autumn 1981	Totals
Males					
044				8 (5/2/1)	8 (5/2/1)
126		27 (11/15/1)	13 (9/4/0)		40 (20/19/1)
128		39 (18/20/1)	6 (5/1/0)	46 (40/5/1)	91 (63/26/2)
200				42 (37/3/2)	42 (37/3/2)
512		37 (21/15/1)	11 (11/0/0)	49 (46/2/1)	97 (78/17/2)
514		46 (14/29/3)			46 (14/29/3)
516	5 (4/0/1)				5 (4/0/1)
517		23 (14/8/1)	12 (12/0/0)		35 (26/8/1)
518	22 (18/2/2)				22 (18/2/2)
519	18 (7/8/3)				18 (7/8/3)
520	32 (23/8/1)				32 (23/8/1)
Females					
045				11 (6/3/2)	11 (6/3/2)
515		40 (34/5/1)	3 (3/0/0)		43 (37/5/1)
654				34 (28/5/1)	34 (28/5/1)
655				36 (31/4/1)	36 (31/4/1)
Totals	77 (52/18/7)	212 (112/92/8)	45 (40/5/0)	226 (193/24/9)	560 (397/139/24)

Table 6. Seasonal home range sizes ($km^2 \pm SD (n)$) of radio-collared marten.

Number (sex)	Autumn 80	Spring 81	Summer 81	Autumn 81	$\bar{x}$
044 (male)	-	-	-	5.98	5.98
045 (female)	-	-	-	2.15	2.15
126 (male)	-	4.74	9.69	-	7.22
128 (male)	-	4.48	-	2.46	3.47
200 (male)	-	-	-	13.42	13.42
512 (male)	-	12.04	7.49	8.57	9.37
514 (male)	-	9.95	-	-	9.95
515 (female)	-	20.56	-	-	20.56
517 (male)	-	7.64	3.86	-	5.66
518 (male)	4.74	-	-	-	4.74
519 (male)	5.44	-	-	-	5.44
520 (male)	4.87	-	-	-	4.87
654 (female)	-	-	-	1.09	1.09
655 (female)	-	-	-	7.90	7.90
Females	-	20.56	-	3.71 ± 3.66 (3)	7.93 ± 8.93 (4)
Males	5.02 ± 0.37 (3)	7.77 ± 3.28 (5)	7.01 ± 2.94 (3)	7.61 ± 4.61 (4)	7.02 ± 3.17 (15)
Females[a]	-	-	-	3.71 ± 3.66 (3)	3.71 ± 3.66 (3)
Males[a]	5.02 ± 0.37 (3)	7.23 ± 3.51 (4)	7.01 ± 2.94 (3)	7.61 ± 4.61 (4)	6.82 ± 3.18 (14)
Adult males[b]	5.02 ± 0.37 (3)	8.05 ± 3.80 (3)	5.68 ± 2.57 (2)	7.61 ± 4.61 (4)	6.75 ± 3.29 (12)

[a] Excluding numbers 514 and 515, animals with more than one intense use areas.

[b] Adults are 2+ years of age.

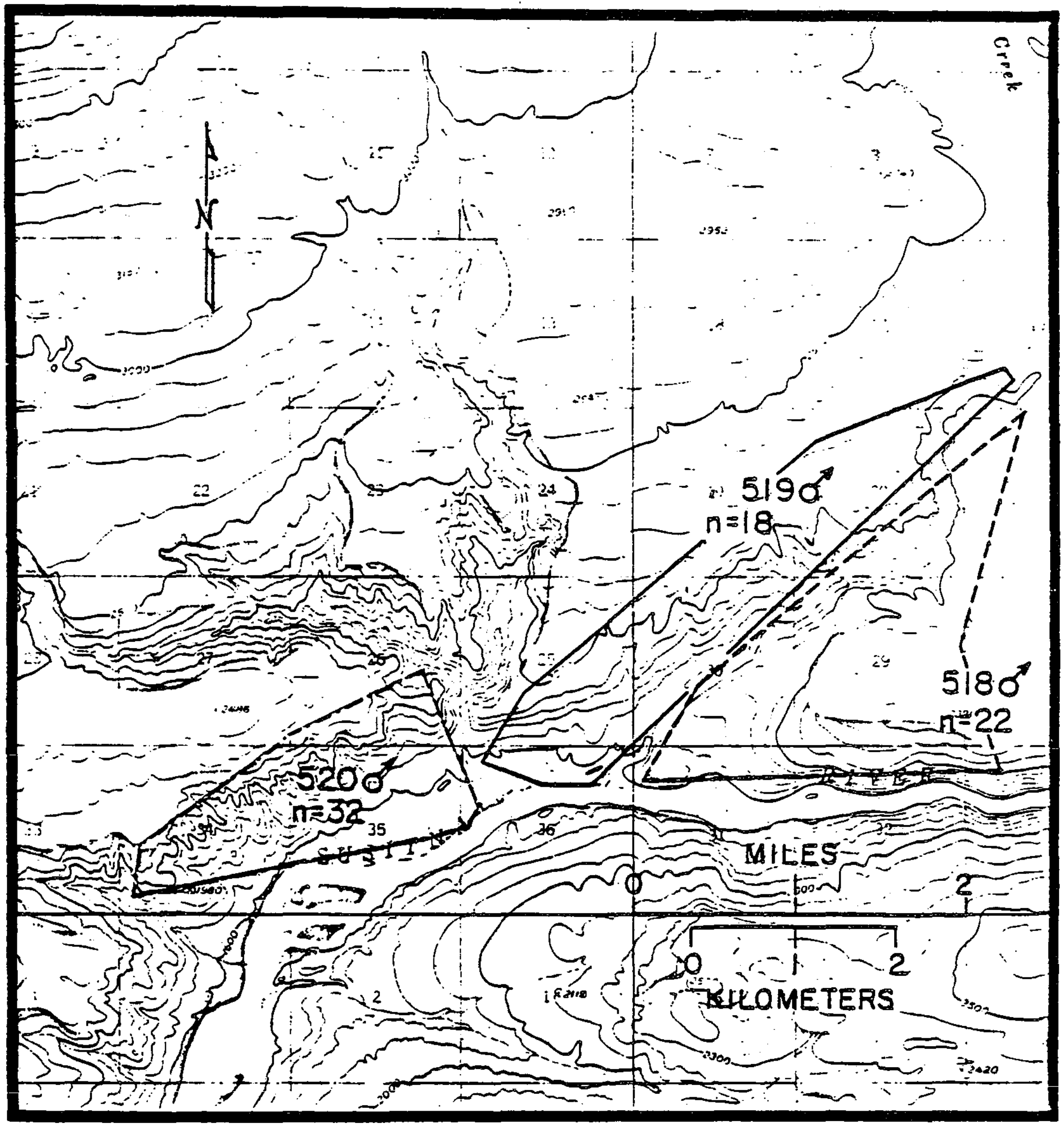

Figure 4. Home range perimeters of 3 radiocollared marten on the Susitna study area in autumn 1980. n = number of locations.

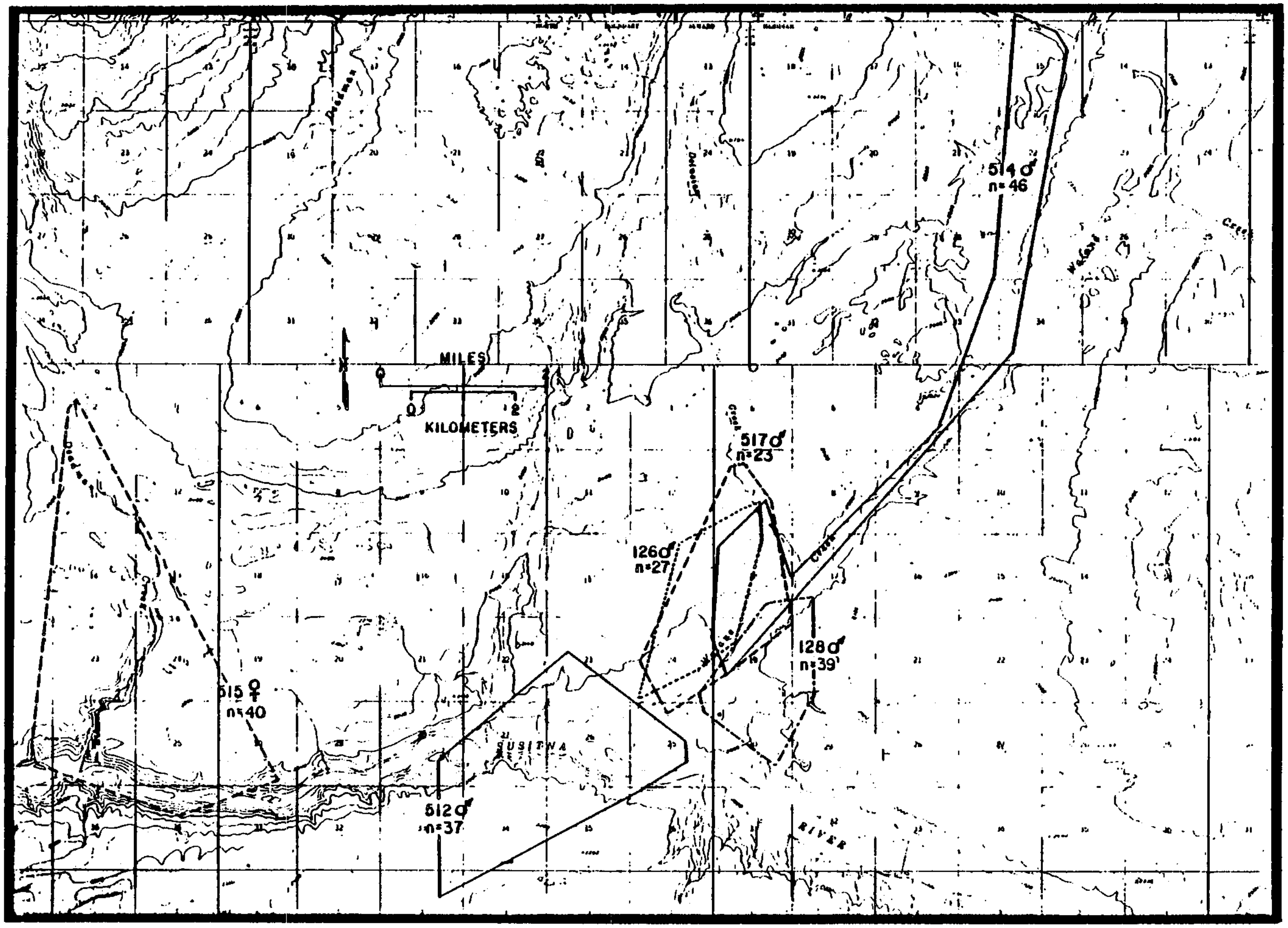

Figure 5. Home range perimeters of 6 radiocollared marten on the Susitna study area in spring 1981. n = number of locations.

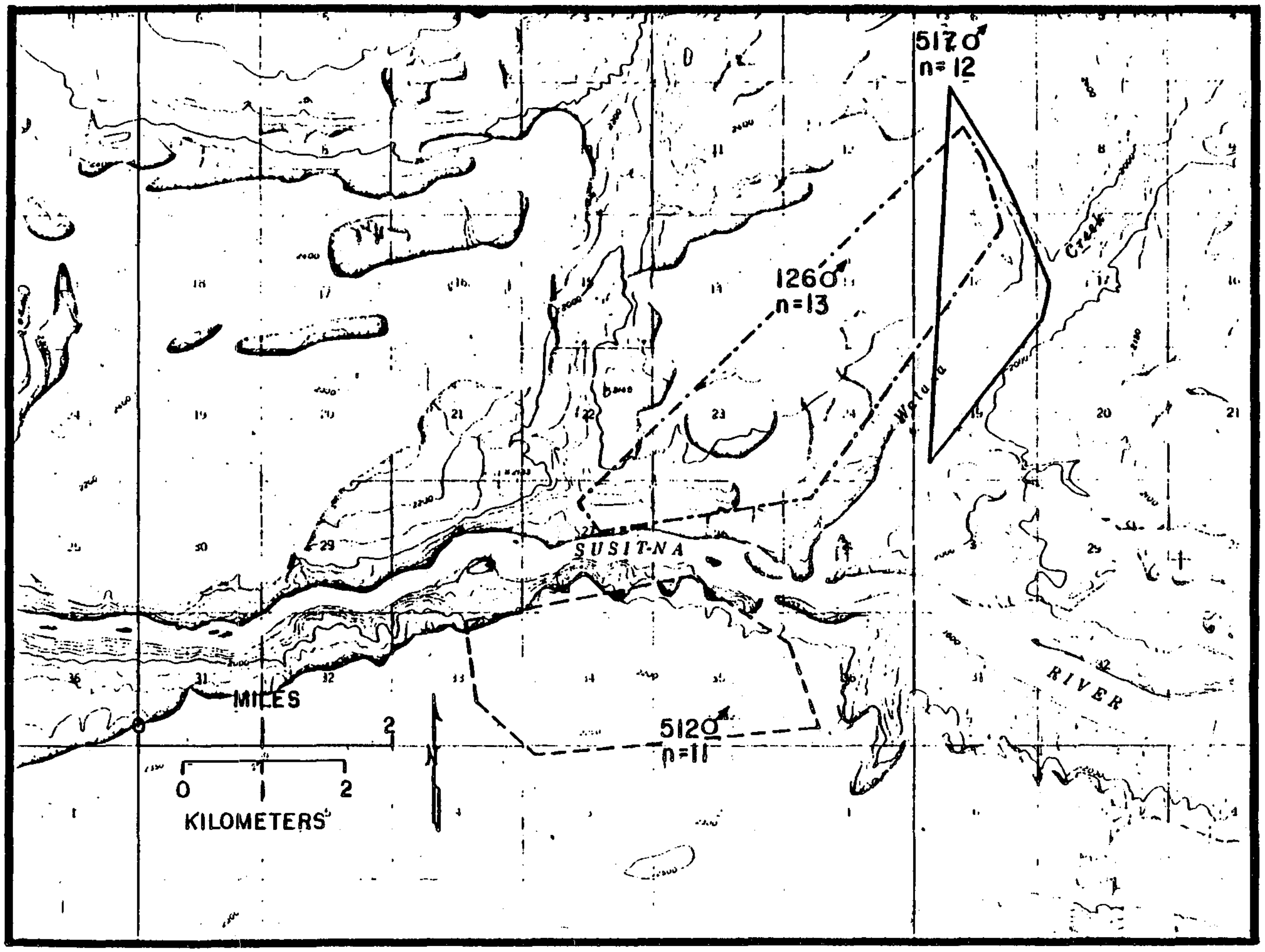

Figure 6. Home range perimeters of 3 radiocollared marten on the Susitna study area in summer 1981. n = number of locations.

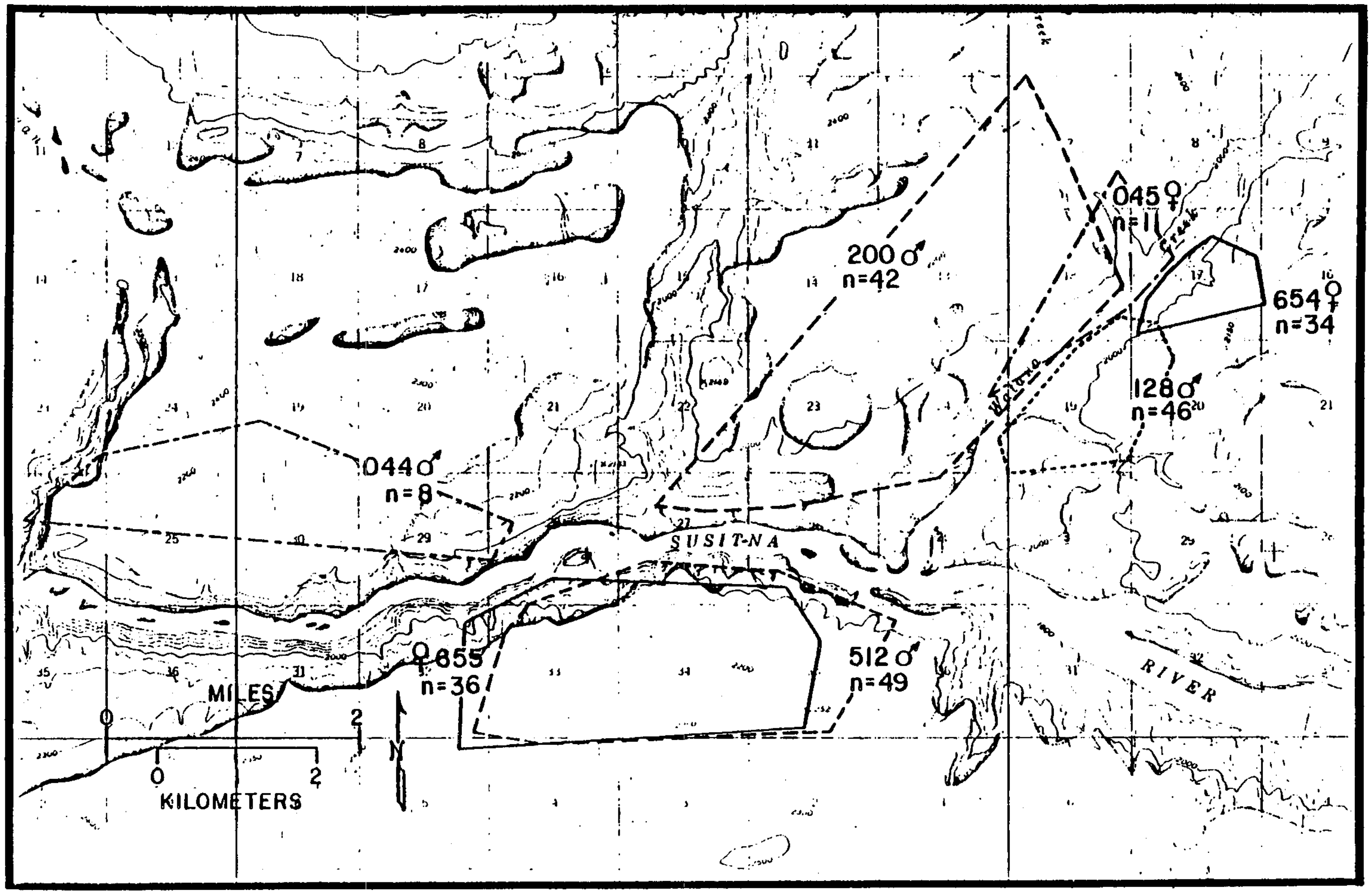

Figure 7. Home range perimeters of 7 radiocollared marten on the Susitna study area in autumn 1981. n = number of locations.

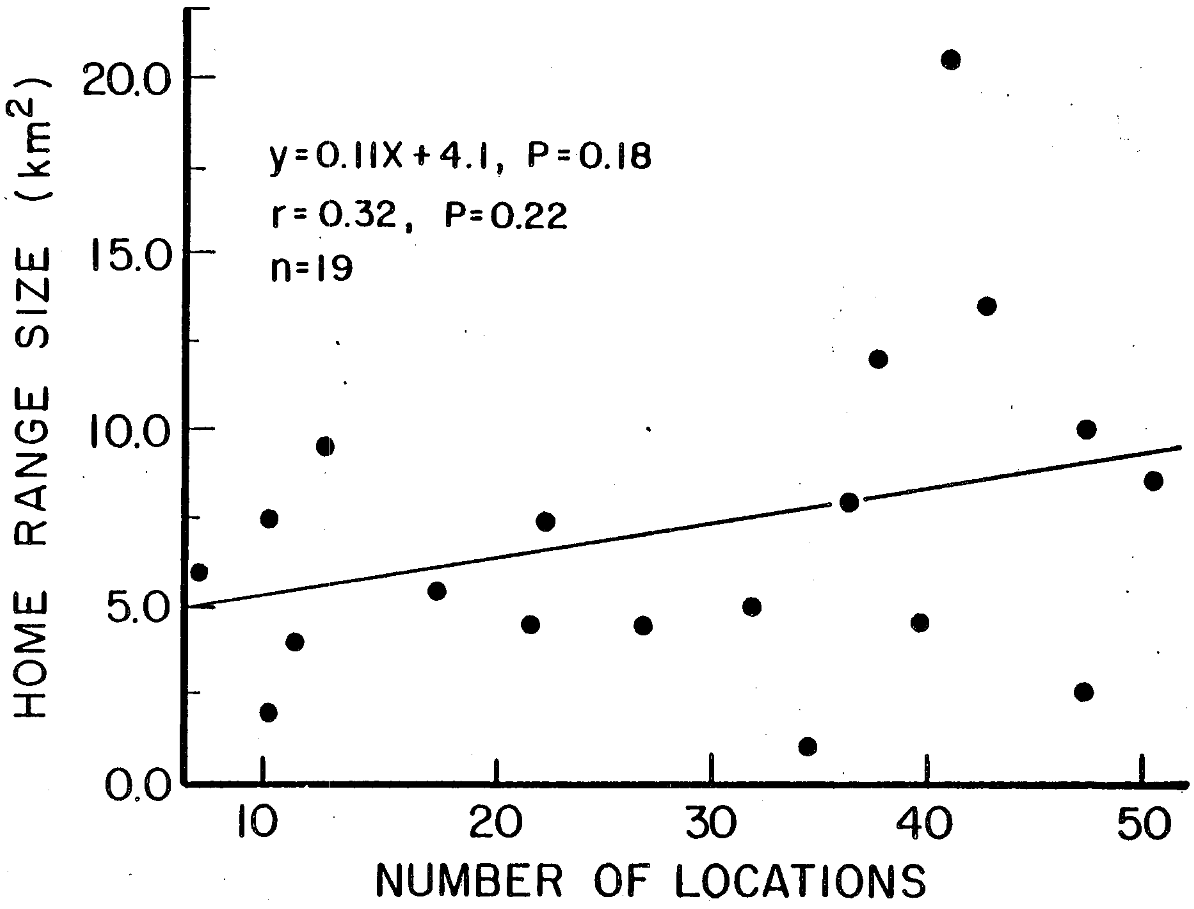

Figure 8. Regression of home range size (km^2) on number of locations for marten in the upper Susitna Basin.

I recorded that the first ice of the season had covered the mouth of Tsusena Creek. This ice provided the first dry crossing of Tsusena Creek for the winter and, when only a day or two old, showed heavy marten travel in both directions.

Regression analysis of marten elevations on time during spring 1981 and autumn 1981 showed that marten underwent a significant upward elevation shift between 20 February and 25 June. Three out of six marten underwent upward elevation shifts which were significant ($P < 0.05$) (Table 7). Pooled data for all six marten (5 males, 1 female) produced a regression line with a highly significant slope ($P < 0.001$). The increase in elevation from 20 February to 25 June predicted by the regression equation was 91 m. Regression analysis of data from autumn are not as conclusive as those from late winter and spring. None of the five marten exhibited regression slopes which differed significantly from zero. Pooled data for all five marten produced a regression line which did not differ significantly from zero, however, the slopes of 4 out of 5 autumn regression lines and the pooled data regression line were negative (Table 7). The regressions of adjusted mean elevation on time for these two seasons in 1981 are presented in Figure 9. I examined plotted residuals for the pooled data regressions and could find no departure from linearity. To determine whether elevation shifts were due to home range shifts or to the use of higher elevation areas within a stable home range, I examined the distribution of locations for individual animals within a season. The results varied considerably. Numbers 126, 512 and 514 displayed home range shifts to

Table 7. Regression analyses, elevations (m) of marten locations on time during two seasons in 1981. Probability values refer to regression coefficient.

Marten Number	Season	Earliest	Latest	Minimum Elevation	Maximum Elevation	Elevation Range	Mean Elevation	N	r	P
126♂	Spring	28 Mar	25 Jun	503	701	199	594	33	0.71	<0.001
128♂	Spring	6 Mar	20 Jun	495	648	153	570	42	0.22	0.17
512♂	Spring	2 Mar	25 Jun	473	702	229	558	43	0.64	<0.001
514♂	Spring	24 Feb	2 May	503	786	283	573	36	0.31	0.06
515♀	Spring	20 Feb	10 Jun	458	732	274	603	41	0.25	0.11
517♂	Spring	21 Mar	25 Jun	503	701	198	596	29	0.38	0.04
	Spring*	20 Feb	25 Jun	458	786	328	581	224	0.36	<0.001
128♂	Autumn	9 Sep	28 Nov	487	640	153	590	44	-0.21	0.18
200♂	Autumn	17 Sep	4 Dec	488	701	213	592	34	-0.16	0.37
512♂	Autumn	4 Sep	4 Dec	473	717	244	637	47	-0.03	0.85
654♀	Autumn	12 Sep	18 Oct	533	663	130	602	31	0.11	0.56
655♀	Autumn	6 Sep	24 Oct	518	732	214	637	34	-0.15	0.38
	Autumn*	4 Sep	4 Dec	473	732	259	612	190	-0.09	0.20

*Regression of pooled values for all marten for the season.

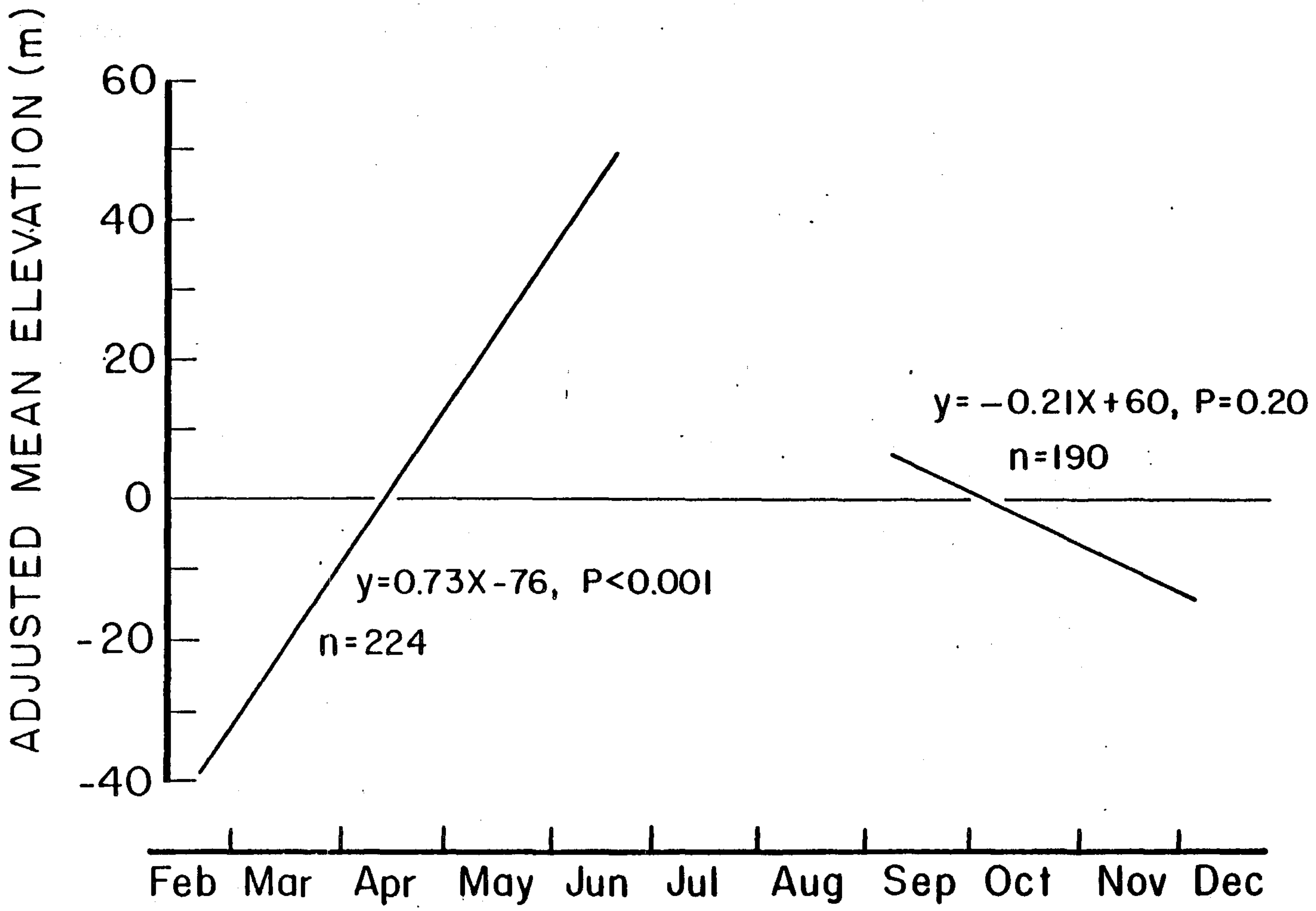

Figure 9. Regression of adjusted mean elevations of marten locations on Julian Date 1981.

higher-elevation areas in spring 1981. Number 128 displayed a home range contraction from early spring to late spring 1981, but used higher elevation areas late in the spring. Early spring and late spring plotted locations are presented for numbers 126 and 128 in Figures 10-11.

An adult male (512) shifted his home range from the north side of the Susitna River to the south side (Figure 12). This shift appeared to be a permanent one not associated with seasonal environmental fluctuations. In the course of making this range shift, he made what appeared to be a series of exploratory trips, returning each time to his old home range. By 1 May 1981, the Susitna River had broken up at the mouth of Watana Creek. He remained on the south side and established the home range depicted in Figure 7.

Two marten (male 514, female 515) occupied home ranges during spring 1981 which differed from most of the home ranges observed. Both had home ranges characterized by two foci of activity, a primary one at a low elevation near the Susitna River, the other at a much higher elevation several kilometers from the primary use area. In these cases, few or no radiolocations were obtained for the area between the two foci; the animals tended to be near either the lower focus or the higher one. Usually, the distance between the two foci was travelled overnight, which, in the case of 514, was a distance of 11-14 km (Figure 5). I suspect that the routes travelled by these marten between foci were narrow corridors along their respective creeks. The areas between foci appear to have been used little, except

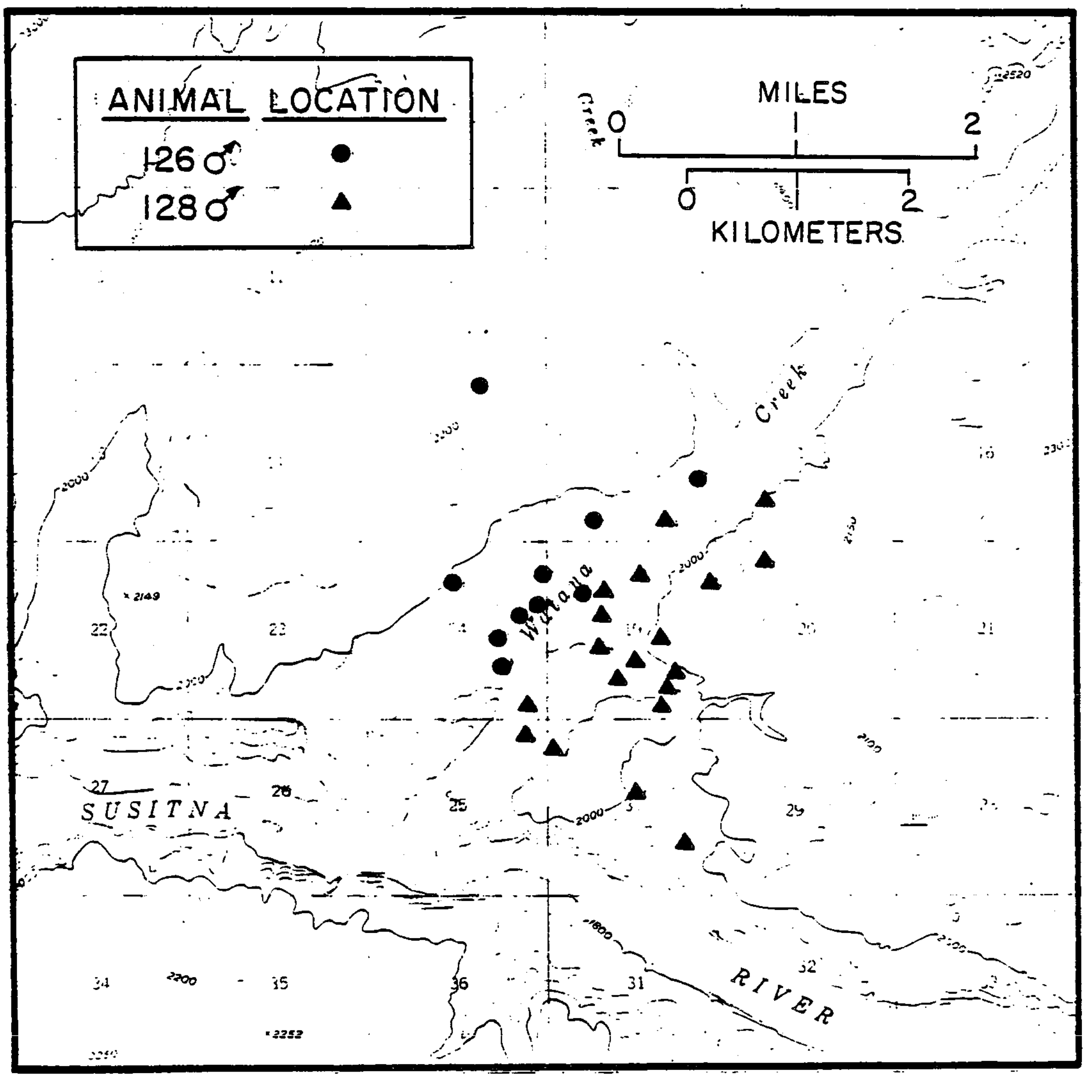

Figure 10. Plotted locations for radiocollared marten 126 and 128 during March and April 1981. Compare with those for May and June 1981 (Figure 11).

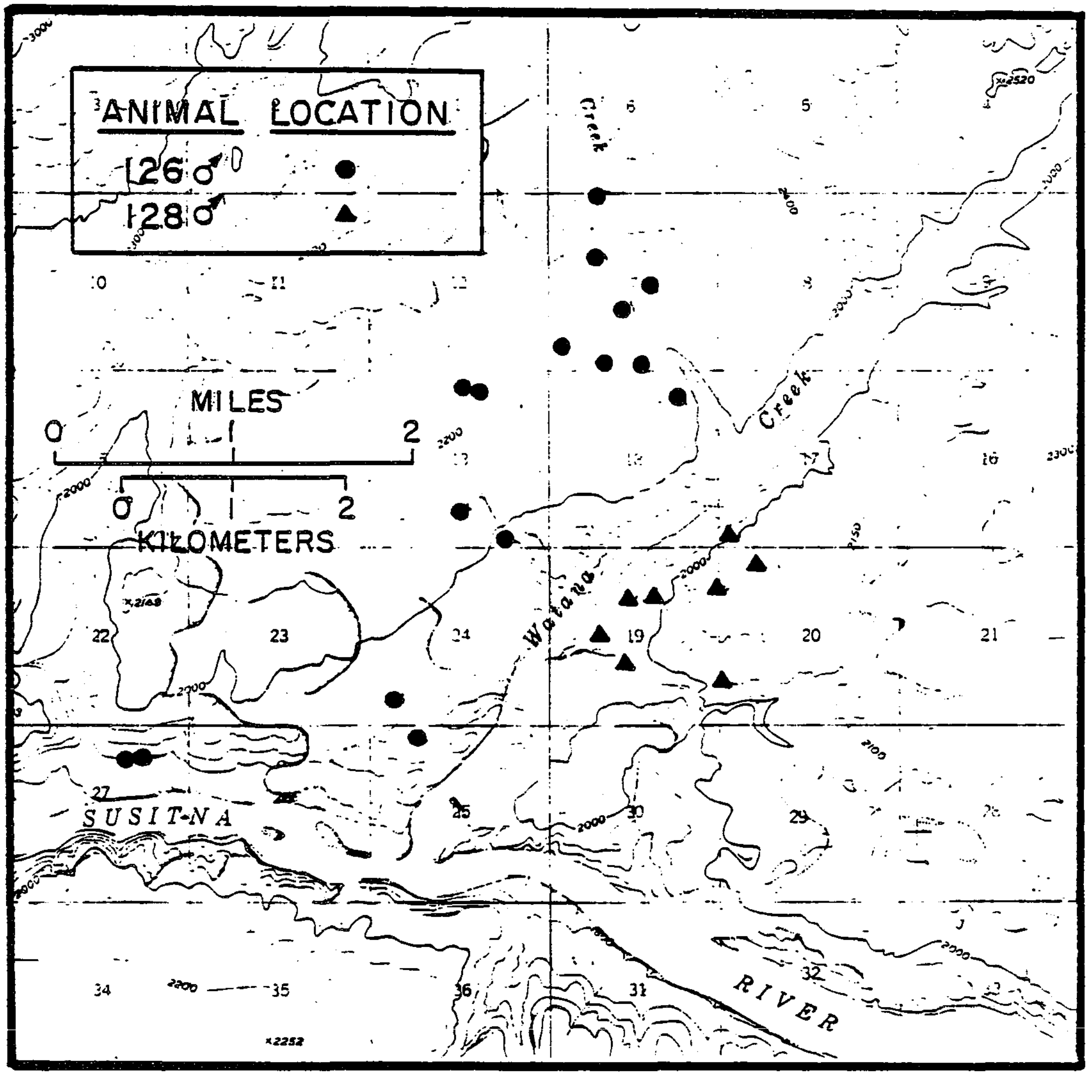

Figure 11. Plotted locations for radiocollared marten 126 and 128 during May and June 1981. Compare with plotted locations for March and April 1981 (Figure 10).

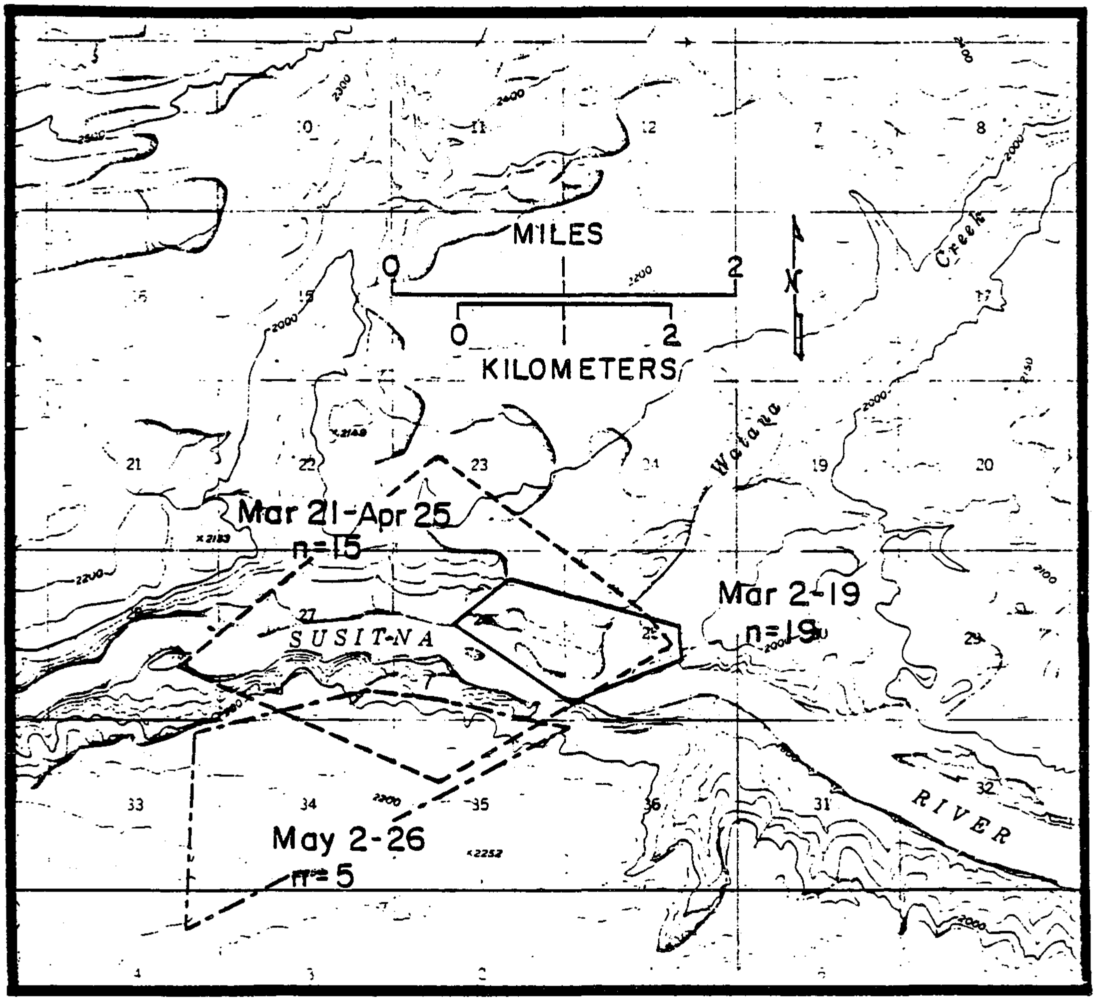

Figure 12. Home range shift by marten 512 in spring 1981.

for direct travel. As a result of these conditions, the home range concept used in my calculations (Mohr 1947) tends to drastically overestimate the area of home ranges of these two animals in spring 1981. I therefore excluded them in a second set of mean home range area calculations in Table 6.

A total of 1777 activity observations were made during two data collection periods. The first was 24 September - 20 October 1980, the second 24 February - 23 March 1981. Diel activity patterns during autumn 1980 are presented in Figure 13 and Appendix B. Marten were nocturnal during autumn 1980. Of 210 observations made between sunrise and sunset, 28% were classified as "active". Of 357 observations made between sunset and sunrise 91% were classified as "active". Activity patterns for late winter-early spring 1981 are more difficult to interpret (Figure 14). Variation among individual animals was pronounced. Number 515 displayed peaks of activity at 1500 and 2000 hours (Figure 30). Too few data were gathered for number 128 to observe a clear pattern, although a peak of activity may exist at 1900 hours (Figure 31). Data for 514 are more difficult yet to interpret (Figure 32). I could discern no distinct diel pattern for this animal.

In addition to differences in diel activity patterns, I found seasonal differences in the percent of daily time spent active. Marten spent more time active (66%) in autumn 1980 than they did in late winter-early spring 1981 (43%).

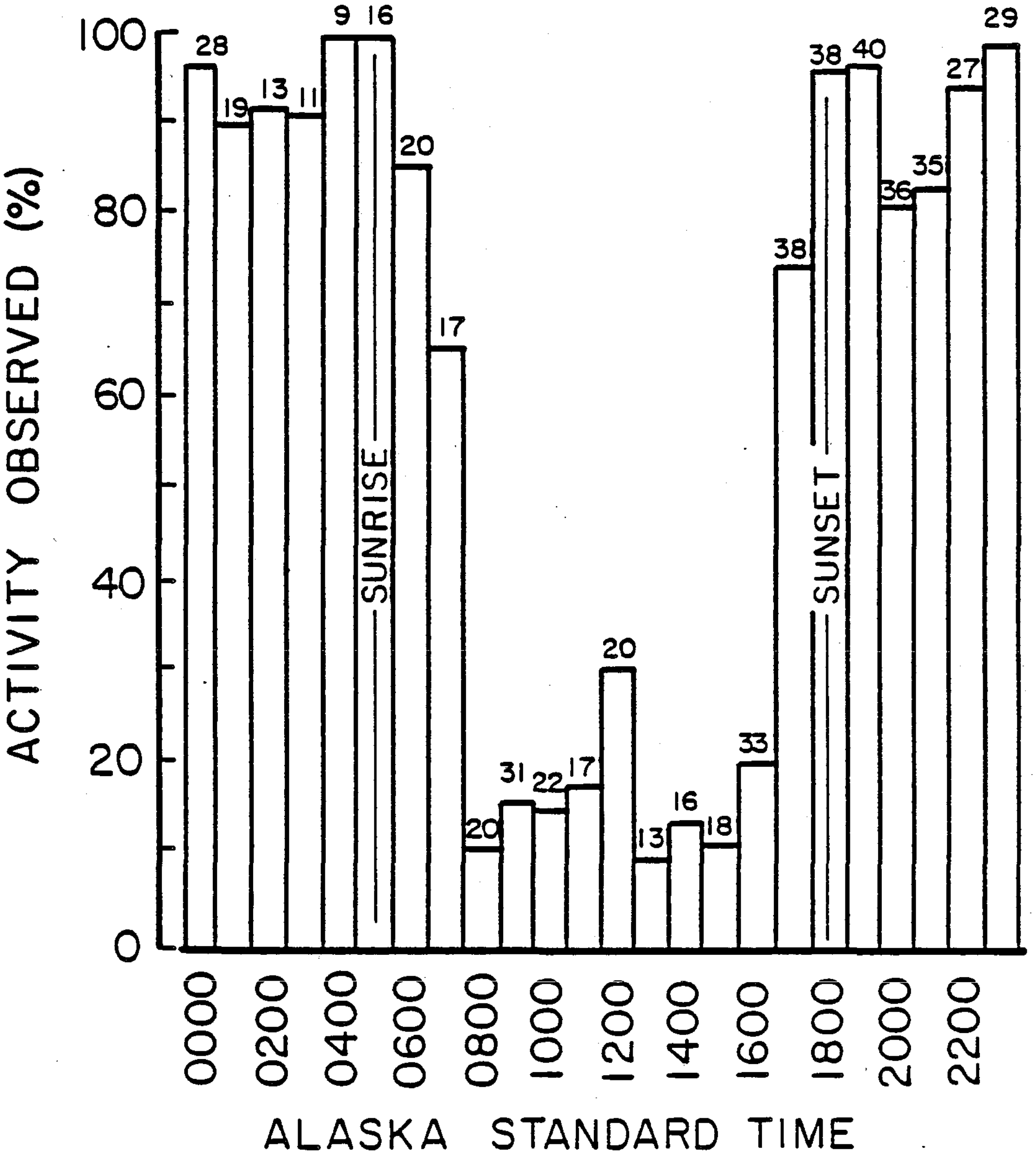

Figure 13. Diel activity pattern of 3 radiocollared male marten (518, 519 and 520) in autumn 1980. Patterns for individual animals are presented in Appendix B.

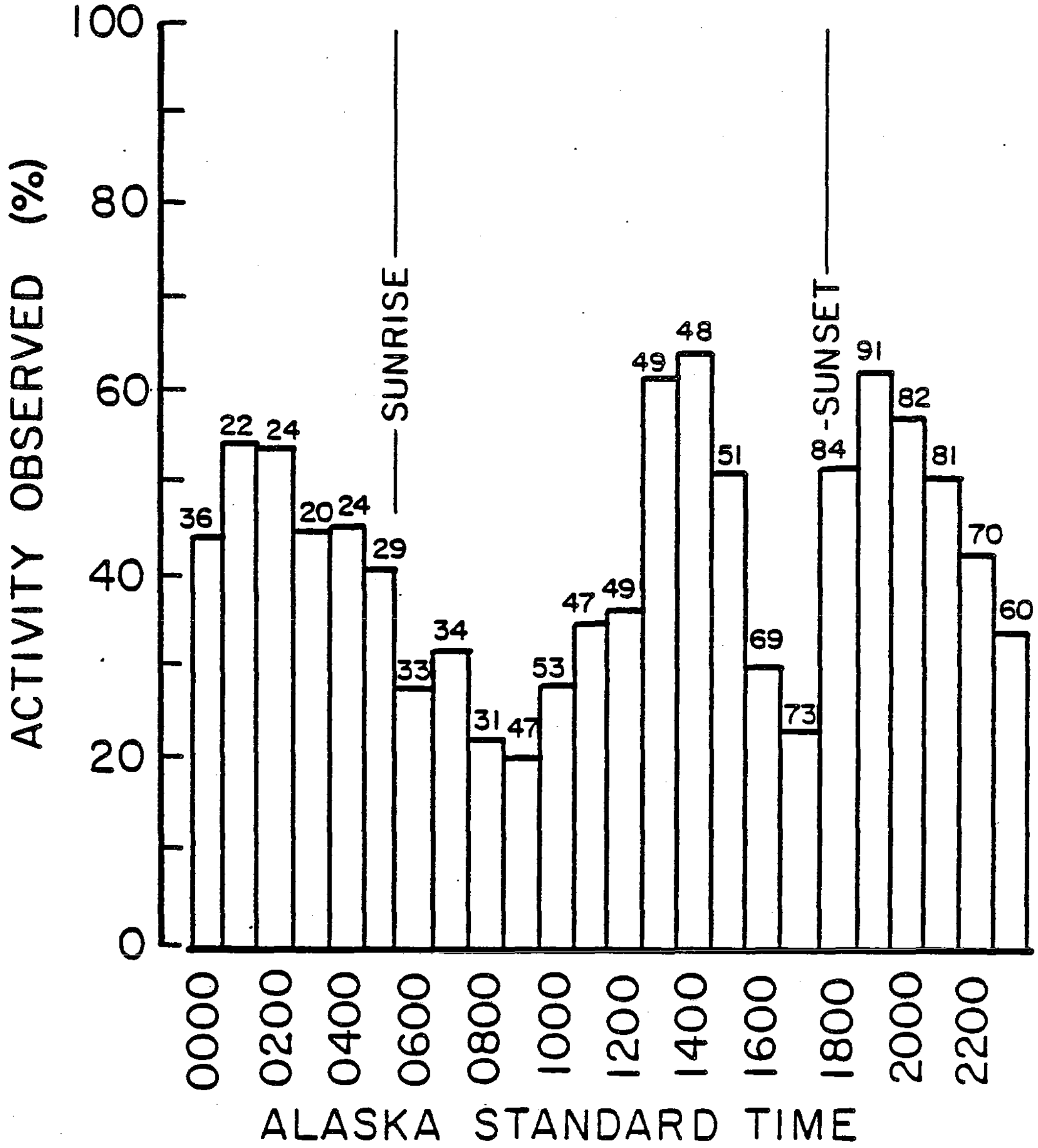

Figure 14. Diel activity pattern of 3 male and 1 female radiocollared marten (128, 512, 514 and 515) in late winter 1981. Patterns for individual animals are presented in Appendix B.

DISCUSSION

Marten home ranges in the upper Susitna Basin were found to share a number of characteristics with those described in other studies. Home ranges of adult males tended to be mutually exclusive, but frequently overlapped with those of females or juveniles. Home range sizes fell within the range of values presented in the literature for North American marten and were most similar to the findings of Archibald and Jessup (in press) for southern Yukon Territory, an area which is similar to the upper Susitna Basin in climate and vegetation (Table 8).

Telemetry-based home range sizes depend largely upon the techniques employed to calculate home ranges. A number of techniques have been applied to marten telemetry data and affect comparisons between studies from different geographic areas. Simon (1980), when calculating home range areas, excluded islands of unsuitable habitat larger than a set minimum size. Burnett (1981) used computer-generated 95% confidence elipses to examine the relative position of marten home ranges, although he acknowledged finding the technique inappropriate. Several workers (Spencer 1981, Mech and Rogers 1977, Major 1979) have applied the minimum area method (Mohr 1947) or variations thereof. This method is perhaps the best available for depicting the spatial relationships of adjacent home ranges, particularly where topography plays a major role in bounding home ranges, but gives no consideration to use intensity. The harmonic mean measure method of Dixon and Chapman (1980) does produce isopleths of use intensity and yields home range boundaries similar to minimum area methods, but Spencer and Barrett (1982) found that the

Table 8. Marten home range sizes (km^2) determined from radiotelemetry (n = number of animals upon which values are based).

Source	Simon 1980[1]	Spencer 1981[2]	Mech and Rogers 1977[2]	Major 1979[3]	Archibald and Jessup in press	Present Study[2]
Area	Sierra Nevada California	Sierra Nevada California	Northeastern Minnesota	Northern Maine	Southern Yukon Terr.	Southcentral Alaska
Mean home range area, males	2.85 (n=5)	4.89 (n=1)	15.7 (n=3)	7.6 (n=3)	6.2 (n=4)	6.82 (n=9)
Mean home range area, females	3.08 (n=3)	3.35 (n=3)	4.3 (n=1)	1.0 (n=1)	4.7 (n=4)	3.71 (n=3)

[1] Using modified minimum area (Harvey and Barbour 1965).

[2] Using minimum area method (Mohr 1947).

[3] Using minimum area method (Kohn and Mooty 1971).

technique produced unrealistic depictions of some home range shapes. These mathematical models do not take into account sampling biases inherent in many telemetry-based sampling schemes. An example of a temporal sampling bias with major habitat implications is described in the habitat use section. In my work the purpose of home range area estimation was to serve as a basis for the estimation of population density. Some of the study animals underwent movements which did not conform to a home range or activity area. Others can be so treated only with caution and qualification. In order to represent home ranges realistically, I found it necessary to delete some locations from the sample and to draw some home ranges with concave edges. The conditions under which I employed these methods are as follows:

1. In Figures 4-7 I deleted locations which did not conform to Burt's (1943) definition of home range. Locations which represented dispersal, migration or exploration beyond established home range limits were deleted from the sample. Deleted locations are shown in Appendix A, Figures 23-26.
2. I drew concave, rather than straight home range perimeters when drawing a straight boundary would have included a large area of unsuitable habitat (e.g. alpine tundra) or an area which was physically inaccessible (e.g. across a river or creek).

Sexual differences in home range size may be interpreted in terms of sexual differences in body size by using the appropriate allometric scaling factor. Harestad and Bunnell (1979) derived a home range area (ha)/body weight (g) regression equation of $H = 0.11\ W^{1.36}$ for carnivores.

Due to errors of computation, this equation does not describe the least-squares linear regression line for their data. My calculation of the equation yielded the following:

$$H = 0.019\ W^{1.36}.$$

This compares with a scaling factor of 1.22 which I derived (in Calder 1974) for terrestrial mammalian carnivores. Using mean weights of 0.867 kg and 1.307 kg for radiocollared female and male marten respectively, the male home range size predicted by Harestad and Bunnell is 74% larger than that of females. From my own equation, the predicted difference is 75%. The observed difference based upon my telemetry data is 84%. Thus, most of the difference in sex-specific home range sizes of Susitna marten is attributable to sexual size dimorphism and may be predicted approximately by employing the correct allometric scaler.

The home range size-body size relationship which I found for marten differs from published values and warrants comment. The value for American marten fell very close to the regression line calculated by Harestad and Bunnell (1979) for terrestrial carnivores. A similar relationship was reported by Gittleman and Harvey (1982) for this species. Using a mean body weight value of 1.09 kg for marten in the upper Susitna Basin, these animals had home range sizes ($\bar{x}$ = 5.3 km^2) approximately twice as large as predicted by the regression equation of Harestad and Bunnell (2.6 km^2). Gittleman and Harvey showed that some of the variation in size of home range (standardized for metabolic needs) may be explained by diet. Carnivores with a greater proportion of meat in their diet have larger home ranges than omnivores, frugivores or insectivores. The large difference between predicted and observed home range size of marten in the upper Susitna Basin suggests that these marten may be more carnivorous than those animals upon which the calculations of Harestad and Bunnell (1979) and Gittleman and Harvey (1982) were based. Data on the diet of my study animals (see Diet section) did not, however, provide support for this interpretation; marten in the upper Susitna Basin exhibited a degree of carnivory comparable to that shown at other North American sites. Other possible explanations for the large home ranges of my study animals are that my study area supported low densities of available food and that the telemetry techniques which I employed produced higher home range size estimates than those used in the regression calculations.

Reports from Alaskan trappers of marten movements beyond the limit of ordinary home ranges seem to be of two major types. The first is a seasonal elevational range shift. Trappers commonly report marten leaving their autumn ranges and moving up in elevation with the onset of severe low temperatures in late November or early December. The marten reportedly return to lower elevations with the onset of warmer weather in the spring. Such movements have been mentioned by Lensink et al. (1955) and Carey (1979). Leroy Shank (pers. comm.) of Fairbanks told me about elevational shifts by marten on his trapline on upper Beaver Creek, 65 km northeast of Fairbanks. Mr. Shanks said that marten are generally at lower elevations in early November and move upward in elevation by late November. He believed that marten moved back down in elevation after the end of the trapping season, after he had left the trapline.

It is difficult to evaluate these reports. They are probably based upon track observations or trapping success. A decrease in marten track densities in low elevation areas could be due to marten movements to higher elevations, or alternatively to decreased activities of animals in low elevation areas during cold periods. Abandonment of a home range at the time of year of greatest energetic stress seems to be a strategy with high risks. It also presupposes the existence of unoccupied suitable habitat above a marten's autumn home range. In a similar context, Archibald and Jessup (in press) remarked that, "it is highly unlikely that marten will move into unoccupied habitat during the winter".

Radiotelemetry data demonstrated that marten shift home ranges or change elevations within their home ranges during spring and possibly during autumn, however, the direction of the movements was opposite those often reported by interior Alaskan trappers. Home range shifts during mid-winter were not investigated since virtually no telemetry data came from this period. Therefore, I cannot refute the hypothesis that Susitna Basin marten undergo elevational shifts from early December to late February. Elevation shifts during spring can be explained in terms of food availability. Marten may move upward to find sunlit and snowfree areas in which to hunt for mice or forage for berries. Lower elevation areas in the upper Susitna Basin are generally in steep valleys or canyons and receive less direct insolation in spring than the flat benches above them.

My data suggest that during the coldest time of year marten use the lowest-elevation portions of their home ranges. The adaptive value of such a distribution is not apparent, for it is during mid-winter that thermal inversions are most common and severe. Such an interpretation also directly contradicts the prevailing view among interior Alaskan trappers that marten are at the highest elevations at the coldest time of year. I have no plausible interpretation of this finding, but I believe that it is a real characteristic of marten in the upper Susitna Basin rather than an artifact of data-gathering techniques.

The second type of extrahome range movement commonly reported by Alaskan trappers is mass movement or migration. Reports of such movements seem to be based upon observations of tracks or of the animals themselves. I have heard several accounts of these movements based upon the absence, sudden appearance and subsequent sudden disappearance of marten at traplines situated along the route of a migration. For example, J. Burns (pers. comm.) of Fairbanks observed shifts of abundance of marten on traplines in the Carey Lake area south of Lake Minchumina which he interpreted to be due to unidirectional movements of marten. These mass movements are often explained in terms of fire history and prey availability, some trappers claiming that marten prefer recent burns, others that they avoid recent burns. Other interpretations of marten migrations center on potential marten predators such as red foxes or lynx (Nelson 1973, p. 219). Reports of mass marten movements are difficult to evaluate because the movements are usually reported to have occurred in remote, inaccessible areas during winter and do not appear to be predictable spatially or temporally. I observed no evidence of such mass movements.

Diel activity patterns of marten in the upper Susitna Basin show pronounced seasonal variation. In autumn, marten were almost entirely nocturnal while in late winter and early spring activity was distributed much more evenly through the day. The findings of other studies on marten vary widely. Marten in California exhibited strongly diurnal activity patterns in winter (Zielinski 1981). Major (1979) found marten in Maine to be more active at night than during the day in summer although diurnal activity (55%) was much higher than I found. More (1978) reported that marten in southern Northwest Territories tended to be inactive during the day in summer and showed the highest amount of activity around dawn and dusk, and Burnett (1981) found a single activity peak just before dark in January and February. In an unsuccessful attempt to explain variation in activity, More (1981) found that time of day, weather and habitat type (combined) explained only 16-33% of the variance in activity, depending on season. Despite this range of conflicting and unexplained findings, some salient similarities in marten activity budgets are apparent. Marten spend more time active in summer and autumn than in winter. Zielinski (1981) found marten to spend twice as much time active in July and August as in March and April. Burnett (1981) found marten to be active only 37% of the time during January and February. My data indicate that marten spent 66% of their total time active in autumn, compared with 43% for late winter/ early spring. An obvious explanation for this reduced activity in winter is the energetic cost of exposure to cold air and the reduced efficiency of foraging when snow is deep. The energetic consequences of reduced activity and cold avoidance are discussed in the body condition section.

DIET OF MARTEN IN AUTUMN, WINTER AND SPRING

The food habits of free-ranging marten have been studied over a wide geographic area of North America. These studies, based largely upon contents of scats, utilize methods which are similar enough to allow some regional comparisons, although problems of inconsistent methodology recur. These problems include the definition of seasons, quantitative estimation of foods ingested from indigestible remains in feces and the ambiguity of the "frequency of occurrence" concept in relation to a taxonomic hierarchy of food classes. Most authors consider frequency of occurrence to be the proportion or percentage of the total number of scats in a sample which contain a species or other taxon, but some researchers (e.g. Lensink et al. 1955 and Francis and Stephenson 1972) have considered it to be the proportion or percentage of the total number of food item occurrences comprised by a species or other taxon. Another problem is the inability to distinguish between food item importance and preferability, described by More (1978). In spite of these difficulties, data on food habits do permit recognition of site-specific seasonal dietary shifts and can help explain observed habitat preferences. Food availability can affect foraging movements and therefore home range dimensions and shape. Thus, information on food habits is critical for interpretation of observations of distribution and habitat utilization.

Information on the diet of marten in Alaska is meager. The single published account is that of Lensink et al. (1955), who examined 576 scats of marten from the Castle Rocks - Lake Minchumina area. Studies of marten food habits elsewhere in North America have been available for over three decades. Some of these studies have been conducted in ecological settings similar to those in Alaska.

Marten have been characterized alternatively as microtine specialists or dietary opportunists (Strickland et al. 1982). Microtine rodents comprise the most important food class in most North American studies, although marten prey upon a wide range of small vertebrates and readily consume carrion when available. Red-backed voles (*Clethrionomys* sp.) have been found to be the most important prey species at many study sites. In contrast, the tendency of marten to prey selectively on some small mammal taxa over others has been observed repeatedly (Francis and Stephenson 1972, Soutiere 1979, More 1978, Weckwerth and Hawley 1962). The general order of small mammal "preferability" in North America appears to be as follows:

HIGH:	*Microtus* sp. *Synaptomys* sp. *Phenacomys* sp.
MODERATE:	*Clethrionomys* sp. *Zapus* sp. *Napeozapus* sp.
LOW:	*Peromyscus* sp. *Sorex* sp.

The objectives of this section of the study were as follows:

1. Determine the foods eaten by marten in the upper Susitna Basin;
2. Infer food preferences by comparing foods eaten with food items available; and
3. Interpret diet and food preferences in terms of habitat utilization and winter energetics.

MATERIALS AND METHODS

Collection and analysis of marten scats and gastrointestinal tract contents provided the basis of the food habits studies. The source of the material used for food habits studies is summarized in Table 9. Individual scats were collected from marten trails, resting sites and live traps where marten were captured. Contents of gastrointestinal tracts were taken from the carcasses of marten, purchased, or accepted as donations from local trappers. Gastrointestinal tract contents were divided into stomach and colon contents. Stomach contents were not considered in the analysis. Dried colon contents fell within the weight range of dried scats and were treated as equivalent sampling units in the analysis. All specimens were numbered, assigned codes for date and location and dried at room temperature.

Analysis was done using standard techniques for carnivore food habits studies (Korschgen 1980). Individual scats were weighed and broken apart dry. Food items were identified using reference collections of vertebrate skins and bones and berry seeds. Mammal hairs were identified by examining medullary hair structure (Moore et al. 1974). Food items were separated and collected in containers by season. The weights of these seasonal food item aggregates were measured with a top loading balance to the nearest 0.1 g. Volumes were measured by the water displacement method (Zielinski 1981). Food items which were suspected of having been ingested incidentally, such as leaves, inorganic matter and items ingested in traps, were disregarded in the analysis.

Table 9. Types of specimens used for determining marten food habits. Seasons are defined as follows: Spring, Mar-May; Summer, Jun-Aug; Autumn, Sept-Nov; Winter, Dec-Feb.

	Autumn 1980	Winter 1980-81	Spring 1981	Autumn 1981	Unknown Season	Totals
Scats from live traps	4	1	2	8	1	16
Scats found on ground	10	5	21	106	5	147
Scats found at resting sites	1	111	78	22	71	283
Colon contents	3	15	0	3	0	21
Totals	18	132	101	139	77	467

Frequency of occurrence for food item categories above the specific level (e.g., "microtines", "sciurids") was calculated assuming that the occurrence of remains of two species belonging to a higher level taxon in one scat represented only one occurrence of that taxon in scats. For example, a 20% frequency of occurrence value for microtines in marten scats indicates that 20% of the marten scats contained microtine remains, regardless of how much, or from how many species. In addition to percent frequency of occurrence, food item importance is expressed by volumetric percent, the volume of a food item expressed as percent of the total scat volume. Zielinski (1981) has shown that volumetric percent of scat remains most accurately approximates the ingested weight of prey of various sizes by a marten-sized mustelid and is the method of choice for indicating the relative importance of mammalian prey remains in marten scats. Seasons were defined as follows:

spring	March-May
summer	June-August
autumn	September-November
winter	December-February

Information on potential prey of marten came from studies of small mammal and bird distribution and abundance conducted by Stephen MacDonald and Brina Kessel of the University of Alaska, Fairbanks Museum (Kessel et al. 1982). MacDonald ran traplines for small mammals during three periods; August 1980, May 1981 and August 1981, using a modification of the North American Census of Small Mammals (Calhoun 1948). Each of 22 traplines consisted of a straight line of 20 stations spaced at 15.2 m intervals. Within 1 m of each station center were placed 2

Museum Special snap traps and one metal cone pitfall, 155 mm in diameter at the top. The snap traps were baited with a mixture of peanut butter, rolled oats and either walnuts or sunflower seeds. Traplines were run for 3 consecutive nights and checked once per day. Thus, each trapping session involved 1320 trap station-nights (2,640 trap-nights, 1,320 pitfall-nights) of effort. The total trapping effort was 7920 trap-nights and 3960 pitfall-nights. Habitats in which traplines were placed are described in Table 10.

RESULTS AND DISCUSSION

A total of 467 specimens representing scats or colon contents of marten were collected and analyzed. These specimens represented four three-month seasons, however, one of the seasons (summer 1981) was represented by too few scats to provide a basis for analysis (Table 9). An additional group of scats was of "unknown season". These scats varied greatly in age, some of them probably over 1 year. Scats came primarily (60.6%) from latrines at marten resting sites (Figure 15). Another 31.5% were found along marten trails in snow or at other sites. The results of food habits analyses based upon 3-month seasons are presented in Tables 11-12.

Microtines

Microtine rodents were the most important class of food during autumn, winter and spring, using either frequency of occurrence or volumetric percent as the index of importance (Tables 11-12). This high

Table 10. Habitat types of small mammal traplines in the upper Susitna Basin (S. O. MacDonald, unpublished data).

Habitat type	Number of traplines
Medium birch shrub thicket	2
Low-medium willow shrub thicket	2
Tall alder shrub thicket	2
Cottonwood forest	2
Paper birch forest	2
White spruce-paper birch forest	4
White spruce forest	2
White spruce scattered woodland	2
Black spruce dwarf forest	2
Cow parsnip-bluejoint meadow	2
Black spruce-white spruce forest	1
Wet sedge-low willow meadow	1
Total:	22

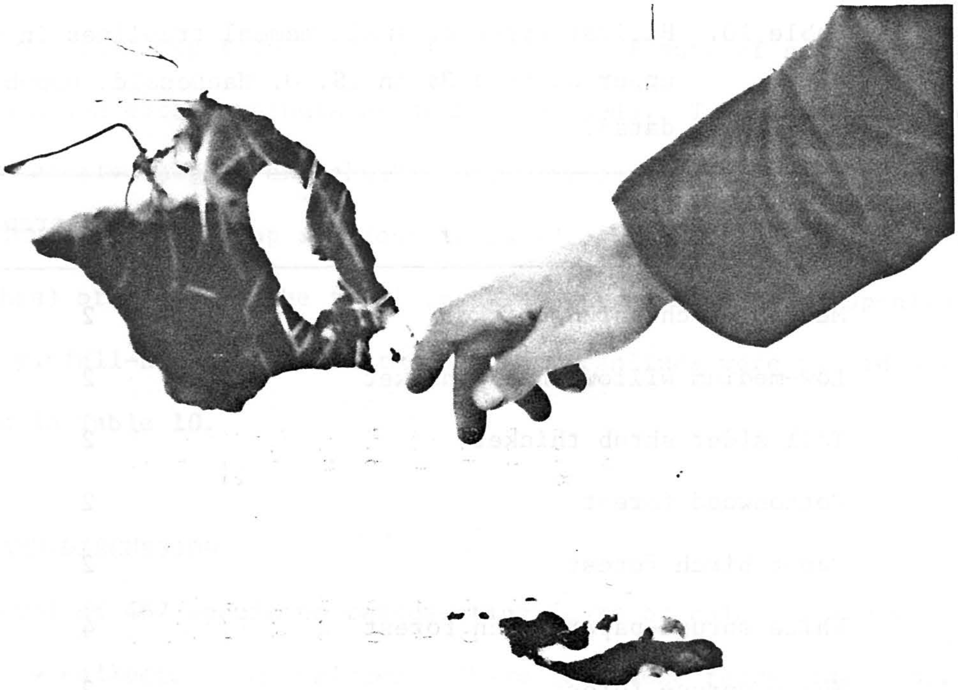

Figure 15. Entrance to an active red squirrel midden being used as a resting site by marten 512. Latrine area is in right foreground.

Table 11. Food items in marten scats by season, expressed as percent frequency of occurrence.

	Autumn 1980	Winter 1980-81	Spring 1981	Autumn 1981	Unknown Season	Total
Unknown mammal	0.0	0.8	4.0	0.7	0.0	1.3
Microtine	94.4	78.0	84.2	99.3	84.4	88.2
Soricid	11.1	1.5	3.0	0.0	1.3	1.7
Sciurid	5.6	10.6	15.8	0.0	3.9	7.2
Ungulate	22.2	0.0	2.0	1.4	6.5	2.7
Snowshoe hare	0.0	1.5	0.0	0.0	3.9	1.1
Muskrat	0.0	3.0	3.0	0.0	0.0	1.5
Bird	5.6	18.9	12.9	3.6	5.2	9.7
Fruit	38.9	29.6	28.7	1.4	22.1	20.5
Fish	0.0	0.7	1.0	0.0	0.0	0.4
Human foods	0.0	0.0	0.0	0.0	7.8	1.3
Total scats	18	132	101	139	77	467
Mean food items/ scat	1.7	1.7	1.6	1.1	1.4	1.5

Table 12. Food items in marten scats, by season, expressed as volumetric percent.

	Autumn 1980	Winter 1980-81	Spring 1981	Autumn 1981	Unknown Season	Total
Unknown mammal	0	0	2.8	1.0	0	1.1
Microtine	50.0	66.3	61.5	97.5	67.7	70.4
Soricid	0	0.7	1.1	0	0	0.6
Sciurid	6.7	7.4	17.0	0	6.5	9.0
Ungulate	30.0	0.3	1.1	0	5.4	2.3
Snowshoe hare	0	2.4	2.6	0	2.2	1.9
Muskrat	0	3.7	4.0	0	0	2.3
Bird	0	9.8	3.7	1.5	3.8	4.9
Fruit	13.3	8.8	6.0	0	5.4	5.7
Fish	0	0.7	0	0	0.5	0.4
Human foods	0	0	0	0	8.6	1.5
Total %	100	100	100	100	100	100
Total volume (ml)	30	297	353	202	186	1068

value and the value obtained by More (1978) in the Northwest Territories of Canada are the highest of any North American studies (Table 13). Microtine rodents have also been found to be the principal food of Old World pine marten (*Martes martes*) in Finnish Lapland (Pulliainen 1981). Northern red-backed voles (*Clethrionomys rutilus*) were the most common and important microtine species in marten scats from the upper Susitna Basin (Table 14). They represented 53.8% of the volume of microtine material which could be identified to species. Voles of the genus *Microtus* collectively comprised 38.7% of the total volume of microtine remains.

Strong year-to-year variation was observed in the specific composition of the microtine portion of the diet. In autumn 1980 red-backed voles comprised 100% of the volume of the microtine remains in scats, whereas in autumn 1981 the value was only 21.1% (Table 14). During both autumn trapping periods the proportion of red-backed vole captures to *Microtus* captures remained essentially the same, roughly 90% red-backed voles and 10% *Microtus* (Figure 16). This inverse relationship between densities of voles and their importance in the diet of marten in autumn 1981 suggests that marten do not take prey simply in proportion to their relative densities, but that marten adjust their foraging styles in response to prey densities. At low microtine densities marten appear to forage in a wide range of habitats and capture mostly red-backed voles, the most abundant microtine species. At high microtine densities marten seek out locally high concentrations of other species, particularly

Table 13. Major food items in the diet of marten from the present study and elsewhere. Values given are percent frequency of occurrence for all seasons sampled.

	Area				
	Northcentral Maine[1]	Southern Northwest Territories[2]	Sierra Nevada Mountains California[3]	Finnish Forest Lapland[4]	Glacier National Park, Montana[5]
Number of scats	412	499	300	2698	1758
Cricetids (except muskrat)	∿80	89	∿20	69.5	73.7
Shrews	7.0	∿6	2.2		7.6
Sciurids	∿7	6	22	2.8	12.0
Snowshoe hares	1.7	5	4.9	*	2.9
Ungulates	0.7	0	1.2	*	4.7
Birds	18.0	19	8.8	14.5	12.0
Fruits	*	∿23	∿5	13.5	29.2
Insects	8.3	∿14	8.0	*	19.0
Human foods	*	*	6.0	*	*

Table 13. Continued.

	Area				
	Banff and Jasper National Parks, Canada[6]	Interior Alaska[7]	Northcentral Idaho[8]	Southeastern Manitoba[9]	Southcentral Alaska[10]
Number of scats	200	466	129	107	467
Cricetids (except muskrat)	66.0	73	∿82	18.6	88.2
Shrews	1.6	0	1	1.9	1.7
Sciurids	10.2	<1	∿12	15.9	7.2
Snowshoe hares	1.6	<1	2	58.9	1.1
Ungulates	<1	<1	*	0	2.7
Birds	4.3	10	5	17.8	9.7
Fruits	5.2	17	12	0	20.5
Insects	5.2	0	9	0	<1
Human foods	*	*	*	*	1.3

[1] From Soutiere 1979, 67% of material from April-September.

[2] From More 1978, material from all seasons.

[3] From Zielinski 1981, material from all seasons.

[4] From Pulliainen 1981, scats from October-April over 4-year period.

[5] From Weckwerth and Hawley 1962, scats from all seasons over 5-year period.

[6] From Cowan and MacKay 1950, season unknown.

[7] From Lensink et al. 1955, 80% of material from June-August.

[8] From Koehler and Hornocker 1977, 63% of material from "winter".

[9] From Raine 1981, all winter scats.

[10] From present study, scats from autumn, winter and spring (see Table 11).

* Not mentioned or cannot be inferred from data given.

Table 14. Marten use of microtines, by season, based upon percent of total volume of microtine material in scats which was identified to species.

	Autumn 1980	Winter 1980-81	Spring 1981	Autumn 1981	Unknown Season	Total
C. rutilus	100.0	64.2	71.0	21.1	44.4	53.8
M. oeconomus	0	18.8	16.7	52.6	14.8	25.5
M. pennsylvanicus	0	10.4	8.6	19.6	21.0	13.2
S. borealis	0	4.6	3.7	6.8	16.1	6.4
L. sibiricus	0	2.0	0	0	3.7	1.1
Total	100.0	100.0	100.0	100.0	100.0	100.0

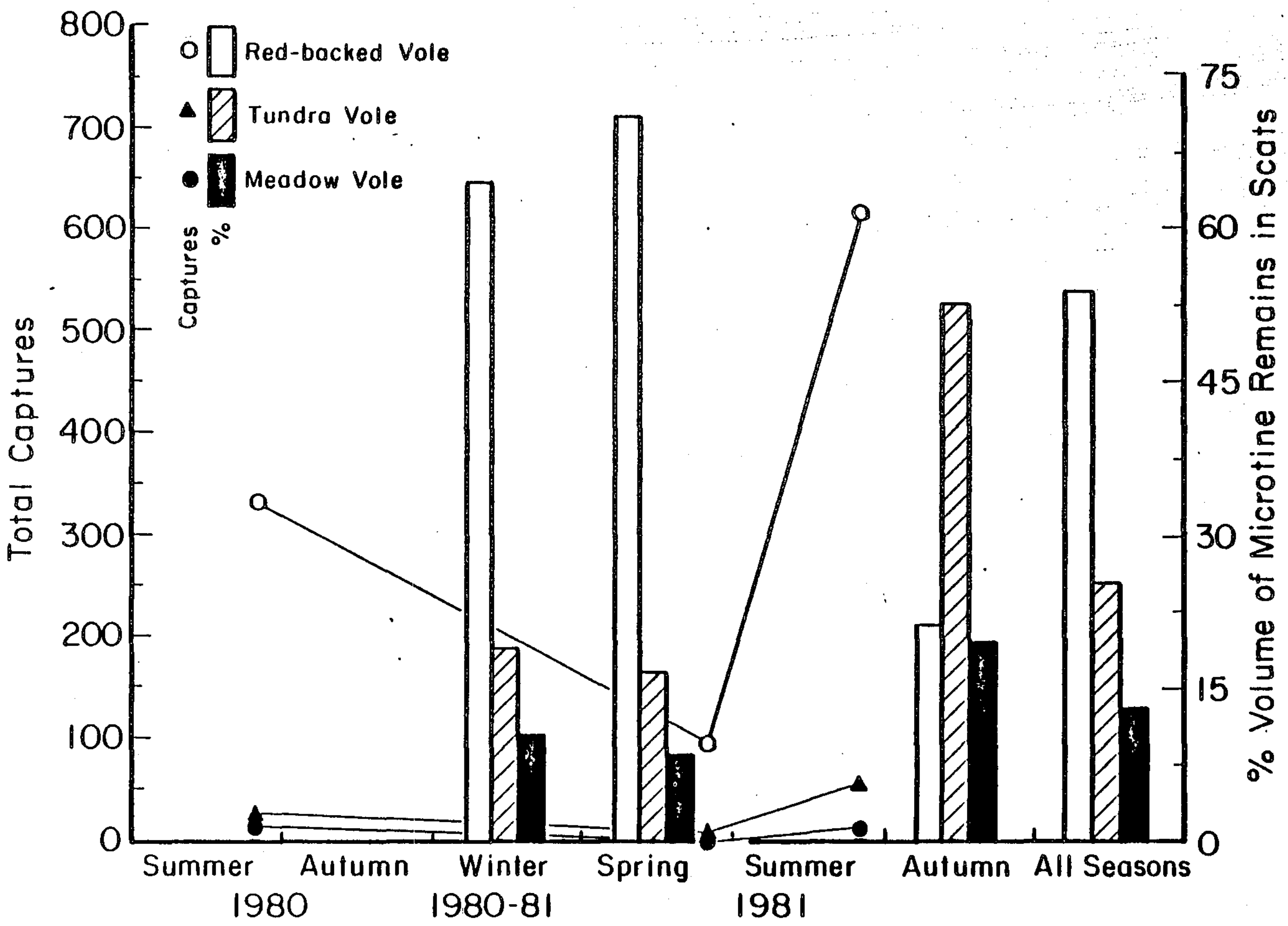

Figure 16. Microtine availability and utilization by marten in the upper Susitna Basin. Connected symbols represent total captures of a species during a trapping session (S. O. MacDonald, unpubl. data). Vertical bars represent volume of microtine remains in scats as a percent of the total volume of microtine material.

Microtus. Under the latter conditions marten prey primarily upon species which comprise a small minority of the microtine fauna.

Northern bog lemmings comprised 6.4% of the total microtine remains, a high value considering that MacDonald caught only 4 of this species in 1952 microtine captures. Conspicuous by its absence from the diet of marten was the singing vole (*Microtus miurus*). MacDonald found this species in moderate numbers in the upper Susitna Basin, but only in areas above the normal elevational range of marten.

Squirrels

Three species of sciurids are found in the study area and were recorded from marten scats - red squirrels, arctic ground squirrels (*Spermophilus parryii*) and northern flying squirrels (*Glaucomys sabrinus*). Hoary marmots (*Marmota caligata*) occur in alpine areas of the Talkeetna Mountains and Alaska Range, but live above the normal elevational limit of marten and were not recorded from scats. Squirrel remains were found in 7.2% of all marten scats. The volume of these remains was 9.0% of the total scat volume, making squirrels, as a group, the second most important food class in the diet of Susitna marten (Table 15). Red squirrels were the most important sciurid food item, followed by arctic ground squirrels and northern flying squirrels. The appearance of arctic ground squirrel remains in marten scats from winter and spring poses the question of how the ground squirrels were obtained. Arctic ground squirrels are in hibernacula at the time of year that their remains appeared in marten scats. Thus, marten must have entered the

Table 15. Sciurid food remains identified from marten scats, by season, expressed as volumetric percent.

	Autumn 1980	Winter 1980-81	Spring 1981	Autumn 1981	Unknown Season	Total
Sciurid, unknown species	0	0	2.3	0	0	0.8
Red squirrel	6.7	2.4	10.7	0	4.8	5.2
Arctic ground squirrel	0	4.4	3.4	0	1.6	2.6
Northern flying squirrel	0	0.7	0.6	0	0	0.4
Total sciurid	6.7	7.4	17.0	0	6.5	9.0

hibernacula and killed the squirrels or eaten cached squirrel carcasses which had been killed in autumn. I observed very few arctic ground squirrels in areas inhabited by marten in the upper Susitna Basin. Those ground squirrels were in gravel river bar habitats in various seral stages, adjoined by white spruce forest or woodland. Use of squirrels increased over the winter of 1980-81, from 6.7% (volumetric) in autumn 1980 to 17.0% in spring 1981. Squirrels appeared to be a non-preferred alternative food, used most heavily when microtine numbers were lowest.

Fruits

Berries of 4 species (*Vaccinium uliginosum, V. vitis-idaea, Empetrum nigrum* and *Rubus idaeus*) and the fruits of wild rose (*Rosa acicularis*) together comprised 5.7% of the volume of all scat material and occurred in 20.5% of the scats. This large difference between frequency of occurrence and volumetric percent results from the high digestibility of berries and/or indicates that marten eat a few berries or hips at a time. Scats containing mostly or entirely berry remains were seldom observed. Frequency of occurrence of fruits in scats showed strong seasonal and annual variation, ranging from 38.9% during autumn 1980 to 1.4% during autumn 1981. Utilization of fruit decreased over the winter of 1980-81, probably reflecting a decline in availability and preservation of fruit.

The importance of plant fruits in the diet of Susitna marten is difficult to evaluate. Under conditions of high abundance and availability of berries, marten were found to consume large amounts of some species. As winter progressed berry utilization declined, but some use of overwintered berries was noted as late as late April 1980. Strong preference for certain berry types was noted. Conspicuous by their absence from the scats of marten were fruits of *Rubus chamaemorus*, *R. arcticus*, *Viburnum edule*, *Shepherdia canadensis*, *Arctostaphylos* sp. and *Oxycoccus microcarpa*, all of which were widely distributed in the study area and are known to be eaten by other carnivore species (Martin et al. 1951, Jonkel 1978). I observed a berry crop failure in late summer and autumn, 1981. Few berries and hips were observed on plants in early August. A cold snap occurred in mid-month, the temperature at Watana Camp reaching -2.2 C on 16 August. Following this cold snap, virtually no blueberries remained on bushes and other berries and rose hips deteriorated quickly. This berry-hip crop failure is strongly reflected in marten food habits. Only 1.4% of autumn 1981 marten scats contained berry seeds or skins. The volume of these fruit remains was less than 0.5% of the total scat volume for the autumn.

Birds

Birds were the fourth most important food category (volumetric percent). I made no attempt to identify bird remains to species, but my impression is that most bird remains were those of galliform or passeriform species. These two orders comprise the majority of the avifauna found in forested habitats in the upper Susitna Basin. During winter the local avifauna is very limited. It is likely that most birds killed during winter months are spruce grouse (*Dendragapus canadensis*), willow ptarmigan (*Lagopus lagopus*) or gray jays (*Perisoreus canadensis*). It is difficult to compare the importance of birds with other classes of food item in the diet of marten. Bird feathers have high visibility in carnivore scats. Likewise, Zielinski (1981) found a captive ferret to produce more scats per unit weight of bird prey consumed than small mammal prey. Thus, both frequency of occurrence and volumetric percent probably overestimate ingested weight of birds.

Foods of Humans

The remains of foods of humans were found in 1.3% of all marten scats and comprised 1.5% of the total scat volume. These figures probably underrepresent the amounts of human foods consumed because of their high digestibility and resulting underrepresentation in scats. Marten obtained these foods by visiting the field camp used during this study. During March and April 1981, four marten (all radiocollared) frequently visited our field camp in search of food. Items they ate or carried away included a wide range of stored or discarded foods, including meat, cheese, produce and sweets.

General

Several salient similarities in the diet of North American marten can be observed in most or all of the sites where they have been studied.

These include the following:

1. Microtine rodents are the most important food of marten.
2. Marten prefer some microtine genera (e.g. *Microtus*) over others (e.g. *Peromyscus*).
3. Shrews, snowshoe hares, porcupines and flying squirrels have low importance in the diet of marten.
4. Squirrels, particularly of the genus *Tamiasciurus*, are most important during the spring months when microtine numbers and availability are lowest.
5. Utilization of fruits is highest in autumn and declines over winter.
6. Marten utilize carrion and a wide range of human foods opportunistically.

Microtine rodents were found to be the most important food of marten in the upper Susitna Basin. Squirrels were the second most important food type using volumetric percent as an indicator. Other major foods were plant fruits and birds (Table 12). Differences in the relative importance of food types can be attributed to differences in digestibility and patterns of ingestion. The relative importance of four food types as expressed by percent frequency of occurrence and volumetric percent are presented in Table 16.

Strong seasonal variation in diet was observed. Microtines appeared to be most heavily used in autumn and least important in spring. Squirrels, particularly red squirrels, were most important in spring and least important in autumn. Plant fruits, particularly ericaceous berries and rose hips, were most important in autumn and declined gradually in importance over the winter, probably reflecting increasing snow depths

Table 16. Food item importance based upon two measures of representation in marten scats.

Rank	% Frequency occurrence	Volumetric percent
1	Microtine	Microtine
2	Fruit	Sciurid
3	Bird	Fruit
4	Sciurid	Bird

and decreasing availability of fruits. Shrews were not utilized at all in autumn, but showed slightly increased use as winter progressed and preferred foods became less available. Consumption of carrion and human foods varied strongly, but not along seasonal lines, reflecting the strong contribution of chance to the availability of these foods. I suspect that human foods may be preferred over most natural foods. During winter and spring, when the availability of natural foods is lowest, human foods can prove a powerful attractant to marten. This characteristic of marten has important implications for solid waste disposal.

Data for microtine population densities and use by marten show that at low microtine population levels, marten select voles (primarily red-backed voles) on the basis of availability, while at times of microtine abundance marten capture tundra voles, meadow voles and northern bog lemmings in proportions much higher than the proportions in which these species are found in the microtine fauna. Weckwerth and Hawley (1962) observed a similar pattern in Montana, as did Francis and Stephenson (1972) in Ontario. It is of interest that MacDonald found no evidence of supraannual cycling in populations of tundra voles in the upper Susitna Basin such as Whitney (1976) found near Fairbanks. Although MacDonald observed strong year-to-year variation in absolute densities of *Clethrionomys* and *Microtus oeconomus*, the relative densities of the two species remained nearly the same. Thus, marten displayed major shifts in utilization of these two species in spite of the fact that their relative numbers remained essentially constant.

Heavy marten predation on species which comprise a small fraction of the microtine fauna may be interpreted in several ways. Species such as tundra voles and meadow voles are habitat specialists; they display much narrower range of habitat tolerance than red-backed voles. Habitat specialist microtines may be easier to hunt because of their predictable habitat associations and locally high population densities. They may be more palatable - an explanation frequently given for the low use by carnivores of shrews. And the habitats in which *Microtus* and *Synaptomys* tend to be found (i.e. graminoid meadows and marshes) may be easier habitats in which to forage.

Northern bog lemmings present an interesting problem with regard to their preference to marten, because of their apparent trap-shyness (M. L. Johnson in Maser and Storm 1979). Of the 4 bog lemming captures made by MacDonald in 1980-81, all were in cone pitfalls rather than snap traps. A small mammal sampling scheme based upon snap trapping may greatly underestimate the abundance of northern bog lemmings and therefore bias interpretation of marten preference for this species.

Caching by marten was not observed during the course of this study. In 36 km of snow tracking, caching of animal parts by marten was never observed. In a few cases marten were observed to have dug animal carcasses or parts from beneath the snow, but there was no evidence that the carcasses had been cached by marten. Pulliainen (1981) found caching by pine marten to be common in Finnish Lapland, but he did not describe centralized caching (hoarding) such as Sueur (1981) observed in short-tailed weasels and Haglund (1966) reported for wolverines.

Marten in the upper Susitna Basin exhibit food habits which are remarkably similar to those of marten elsewhere in North America. Important food items are in many cases the same species or ecological equivalents. My findings differe in this respect from those of Lensink et al. (1955, p. 364), who reported that, "food habits of marten in interior Alaska are most similar to those reported for Asiatic species". Other comparisons between our findings are difficult to make. The material examined by Lensink et al. came primarily from the summer months, whereas mine was entirely from other seasons. In addition, they used a frequency of occurrence concept different from mine. Patterns of seasonal dietary variation appear to have the same explanation in south-central Alaska as they do in areas farther south. During autumn marten utilize preferred prey, particularly habitat specialist microtines. As the cold season progresses and these voles become less abundant and available, marten rely more upon habitat generalist microtines, squirrels and shrews and are more strongly attracted to human food sources.

HABITAT USE BY MARTEN

The habitat requirements of marten in Alaska have not been critically examined. Marten habitat has traditionally been viewed rather simply as old growth conifer forest. It is true that marten are generally restricted to conifer-dominated forest or woodland habitats, however, there are many areas of conifer-dominated forest in Alaska in which marten are rare or absent. Habitat factors which favor the presence or abundance of marten, even on a large regional scale, are understood only in the most rudimentary terms. It has been difficult, with existing knowledge of marten habitat needs, to predict the value of a particular piece of land for marten habitat (U.S. Fish and Wildlife Service 1980) or to make informed statements concerning the effects upon marten of habitat alteration.

Considerable work has been done during the past decade elsewhere in North America on those aspects of marten habitat which relate to two major subjects: Wildfire and timber-cutting practices. Some of this work identifies habitat components which may be important to Alaskan marten. Koehler and Hornocker (1977), for example, reported that marten utilize open areas (such as recent burns) more in summer than winter. Spencer et al. (in press) report that marten in the Sierra Nevadas forage primarily in meadows and riparian areas, but rest mostly in mixed-conifer or red fir forests. Soutiere (1978) found that marten avoided 0-15-year-old clear-cuts in Maine, but utilized lightly-cut hardwood stands quite heavily. The latter two studies utilized non-parametric measures of association (such as chi-square) to test hypotheses that marten used forest types in proportion to their occurrence in the study areas. This technique has great value in evaluating habitat preference and I used a modification of it in the upper Susitna Basin.

MATERIALS AND METHODS

Data on habitat use by marten were gathered from 3 sources. First, 14 aerial transects were established and flown to record the vegetation types in which marten tracks were observed in a large area of the upper Susitna Basin. These aerial transects were positioned at 3.6 km intervals, perpendicular to the river, from Portage Creek to the Tyone River. Each transect was 3.6 km in length, centered on the river (Figure 17). The transects were sampled in autumn 1980 by flying along each of them in a Bell 206B helicopter. The helicopter flew at lowest possible elevation, generally 5-15 m above ground level, at an airspeed of 10-15 km/h. One observer counted the tracks of marten and other furbearers and one observer categorized the vegetation in which the tracks were observed. A third person recorded the observations. The vegetational distribution of tracks was compared with the mapped vegetation types crossed by the transects using vegetation maps produced at 1:24,000 scale by the University of Alaska Agricultural Experimental Station, Palmer, Alaska.

A second source of habitat preference data was snow tracking. From 30 September to 2 December 1981 marten trails in snow were followed on 32 occasions. Vegetation type was recorded every 72 m. Other variables recorded at each vegetation sampling point were snow

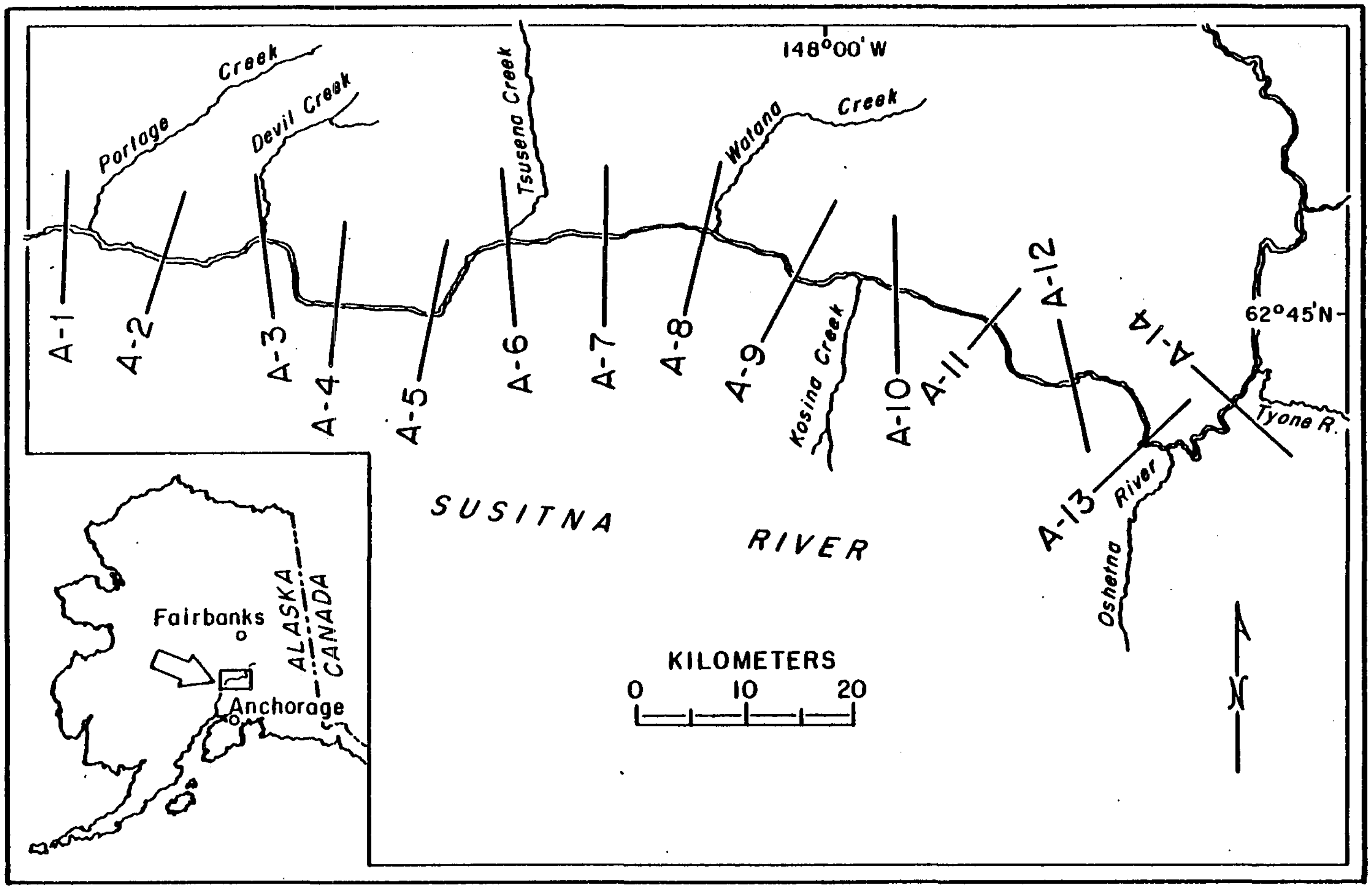

Figure 17. Aerial track transects on the Susitna study site.

depth, track depth and track density. Track density was defined as the number of marten strides within a circle 3.2 m in diameter, centered on the vegetation sampling point. Density of marten tracks was assumed to reflect active foraging for mice. The 72 m of marten trail between vegetation sampling points was the sampling unit for marten behavior types and was called a "segment". On each segment the following marten behavior types, observable in the snow, were counted and recorded: urination, defecation, nosing in snow, digging in snow, capture of microtine, capture of other prey and resting. An eighth behavioral category, "foraging index", was the sum of the four behavior types related to foraging — nosing, digging, microtine capture and capture of other prey. The distribution of these behavior types in five major habitat categories was compared with the expected distribution using the BMDP4F row by column independence test (Dixon et al. 1981). The 5 habitat designations were based upon the forest types at both ends of the 72 m marten trail segment. The resulting combinations were white spruce-white spruce, white spruce-mixed, white spruce-black spruce, black spruce-black spruce, black spruce-mixed and mixed-mixed. All of these were woodland types with canopy cover greater than 10% and less than 60% and were established using the criteria employed by the vegetation mapping group (University of Alaska 1982). No black spruce-white spruce segments were recorded; therefore, this category was deleted in the analysis. In order to examine associations between vegetational heterogeneity and frequency of behavior types, a variable transformation was conducted in which trail segments with the same vegetation type at both ends were recorded as "SAME" and segments with different vegetation types were coded as "DIFFERENT". A chi-square analysis was conducted on marten behavior frequencies in these two categories. The track density variable was compared between vegetation types (Kruskal-Wallis analysis of variance, BMDP3S) to determine whether significant differences existed.

The third type of habitat data dealt with the characteristics of marten resting sites. Resting sites were located by three methods:

1. Radio-tracking collared animals to resting sites.
2. Tracking marten to resting sites in very fresh snow.
3. Searching red squirrel middens for marten scat accumulations.

Variables recorded at resting sites included vegetation type, slope, aspect and elevation. Radiotelemetry was also used to identify resting site distribution within the home range. Autumn radiolocations of marten were plotted on 1:24,000 vegetation maps to determine the manner in which daytime locations were distributed within the home range. The use of this method was based upon the following 2 assumptions:

1. All locations were recorded during daylight hours.
2. Marten are always in resting sites with specific habitat characteristics during daylight hours in autumn.

My data (see Home Range and Movements section) showed that marten were found to be active for 28% of the observations made during daylight hours in autumn. Thus, a considerable error is involved in the second assumption.

RESULTS

Fourteen aerial transects were sampled by helicopter from 14 November to 20 November 1980. A total of 1353 marten trails were recorded in the sampling. The distribution of the tracks by vegetation type is presented in Table 17. Of the total number of marten tracks observed, 92.4% were recorded in forest or woodland vegetation types. Shrub types contained 5.4% of all marten tracks. The coverage of the transect lines by mapped vegetation types is also presented in Table 17. Marten tracks were found to occur more frequently in forest/woodland cover types than forest/woodland cover types occurred on vegetation maps of the transects. Marten tracks occurred less frequently in shrub cover types than shrub cover types occurred on vegetation maps of the transects. No statistical significance was found in these or other differences between observed and expected values in Table 17 because of the high variability observed in marten track densities on specific vegetation types within the study area.

Tracking of marten in snow yielded 499 vegetation sample points in autumn 1981. Urination was observed 89 times, defecation 42 times, nosing 91 times, digging 74 times, microtine capturing 6 times, capturing of other prey 2 times and resting 6 times in 36.0 km of marten trails. Observed and expected frequencies of occurrence of behavior types in vegetation types are depicted in Table 18. Both digging and foraging index presented departures from expected values which were signifcant ($P \leqslant 0.05$). Digging by marten in snow was observed more

Table 17. Habitat use by marten, November 1980, in relation to mapped vegetation types available.

Cover Type	Number of Marten Tracks	% of Total Marten Tracks (Observed)	% Coverage, Vegetation Mapping of Transect Lines (Expected)
Spruce forest	35	2.6	0
Birch forest	3	0.2	2.7
Mixed forest	54	4.0	5.4
Mat-cushion alpine	3	0.2	1.6
Sedge-grass alpine	7	0.5	3.0
White spruce woodland	525	38.8	8.7
Black spruce woodland	605	44.7	32.1
Mixed woodland	29	2.1	5.8
Low shrub	12	0.9	15.0
Medium shrub	35	2.6	17.9
Alder shrub	25	1.9	2.3
River ice	2	0.2	1.8
Lake ice	0	0	0.7
Creek ice	6	0.4	0.1
Marsh	3	0.2	1.6
River bar	9	0.7	1.0
Rock	0	0	0.2
Grassland	0	0	0.3
TOTALS	1353	100.0	100.2

Table 18. Results of chi-square analysis of marten snow tracking data from the Susitna study area. Departure of observed value from expected value is given in those cases where $P \leqslant 0.05$. B = black spruce woodland, M = mixed woodland, W = white spruce woodland.

	B-B	B-M	W-W	W-M	M-M	x^2	DF	P
Urination	-	-	-	-	-	6.40	4	0.17
Defecation	-	-	-	-	-	7.24	4	0.12
Nosing	-	-	-	-	-	7.81	4	0.10
Digging	+5.1	+2.0	-2.8	+1.9	-6.2	12.78	4	0.01
Kill mouse	-	-	-	-	-	4.38	4	0.36
Kill other	-	-	-	-	-	6.49	4	0.17
Rest	-	-	-	-	-	6.88	4	0.14
Index	+6.2	-1.3	+0.1	+3.3	-8.3	9.37	4	0.05
Relative frequency of habitat category	243	33	31	12	146			

frequently than expected in black spruce-black spruce, black spruce-mixed and white spruce-mixed stands. Digging was observed less frequently than expected in white spruce-white spruce and mixed-mixed stands. The foraging index, which includes digging, showed a similar pattern in most stand types. Chi-square analysis of behavior types in two vegetative heterogeneity categories revealed that digging and defecating both occurred with frequencies greater than expected on those trail segments where vegetation at opposite ends was placed in different categories (Table 19).

I assumed that track density was an index of active foraging by marten for mice. This assumption was based upon my observation that marten tended to walk or to bound with short strides in areas with high vole densities. Track density may also be correlated with other variables, however. For example, marten appear to leave deeper tracks and take shorter strides when snow is deep and soft. I conducted correlation analysis to determine whether track density was significantly correlated with snow depth. I found that the two were positively and significantly correlated ($P = 0.05$) over the range of snow depths observed, but that snow depth explained less than 1% of the variation in track density ($r = 0.09$).

The Kruskal-Wallis one-way analysis of variance of track density in three major vegetation types produced no significant differences in track density ($P = 0.89$). This suggests that track density is not an appropriate indicator of habitat use for foraging.

Table 19. Chi-square analysis of marten snow tracking data from the Susitna study area. Habitat categories are those in which vegetation type was the same or different at opposite ends of the 72 m trail segment. Departure of observed value from expected value is given in those cases where $P \leq 0.05$.

	Same	Different	x^2	DF	P
Urination	-	-	0.40	1	0.53
Defecation	-3.8	+3.8	4.16	1	0.04
Nosing	-	-	0.52	1	0.47
Digging	-3.7	+3.7	3.85	1	0.05
Kill mouse	-	-	0.27	1	0.60
Kill other	-	-	0.23	1	0.63
Rest	-	-	3.50	1	0.06
Index	-	-	0.72	1	0.40
Relative frequency of habitat category	419	48			

A total of 37 marten resting sites were located during the study. These sites were primarily cold season resting sites providing some degree of thermal protection. The characteristics of these resting sites are presented in Table 20. Red squirrel middens and red squirrel grass nests in trees together accounted for 84% of the resting sites observed to be used by marten. Twenty-six sites were active middens, characterized by fresh cone bracts, fresh squirrel tracks and/or a nearby squirrel. Marten entered these underground nests through the same entrances used by the resident red squirrel. They remained in them for hours at a time, usually all day. Telemetry signals from radiocollared marten using middens indicated that they remained motionless (probably sleeping) for hours at a time. It was unclear how resident red squirrels adjusted their activities to the presence of the marten. Frequently, when marten were radiotracked to squirrel middens during the day, a resident red squirrel was seen or heard scolding near the midden. The highest number of squirrel middens found to be used by a single marten was 6, (male number 512, spring 1981). Some marten use of red squirrel middens was observed in early autumn and late spring, however, heaviest use of middens was noted from early November to early April. The earliest observation of marten use of red squirrel middens in autumn 1980 was on 18 October. The earliest observation in autumn 1981 was on 28 September. The latest observation in spring 1981 was on 2 May.

Marten in the upper Susitna Basin were found to use red squirrel middens most heavily in winter. This is suggested by:

Table 20. Characteristics of 37 marten resting sites in the upper Susitna Basin.

Type of Site	Number	% of Total
Red squirrel midden, active	26	70
Red squirrel midden, inactive	2	5
Red squirrel grass nest, in tree	3	8
Burrow in ground	6	16
TOTAL	37	
VEGETATION TYPE		
Forest, white spruce	8	22
Forest, mixed (white spruce-paper birch)	17	46
Forest, mixed (white spruce-balsam poplar)	1	3
Woodland, mixed (white spruce-black spruce)	5	13
Woodland, white spruce	4	11
Woodland, black spruce	2	5
TOTAL	37	
ASPECT		
North	1	3
Northeast	1	3
East	2	5
Southeast	4	11
South	10	27
Southwest	6	16
West	6	3
Northwest	1	3
None	6	16
TOTAL	37	

ELEVATION

$\bar{x}$ = 564 m ± 61

Range: 451-722 m

SLOPE

$\bar{x}$ = 15.3° ± 11.9

Range: 0-45°

1. The dates of observed use of red squirrel middens by marten.
2. Accumulations of marten scats outside the entrances to red squirrel middens in spring. These marten latrines were found to consist of many scats distributed vertically through the winter's accumulation of snow.

No use of red squirrel middens by marten was observed during the summer months. During this period, marten appear to prefer above-ground resting sites where air temperatures are higher than those of subterranean tunnels.

My attempts to superimpose marten radiolocations on vegetation maps were largely unsuccessful because of the large error in location plotting compared with the size of the smallest vegetation mapping unit employed. I estimated the maximum radiolocation plotting error to be 200 m. The smallest mapping unit employed in the vegetation mapping was approximately 1.5 ha. An exception occurred in the Fog Lakes area, where vegetation was a homogeneous (and nearly pure) stand of black spruce woodland. When radiolocations of marten number 512 were plotted on the 1:24,000 vegetation maps, the distribution in Figure 18 resulted. The daytime locations of this marten during autumn 1981 are clearly not distributed randomly over the home range. The larger area of open black spruce (OBS) comprises most of area of the marten's home range, but is underrepresented in radiolocations during this season. A similar pattern was observed for number 655 during the same season. The plotted locations represent mostly resting sites, which are absent from the large open black spruce stand. Marten 512 and 655 rested primarily in small stands of old-growth white spruce (too small to be mapped),

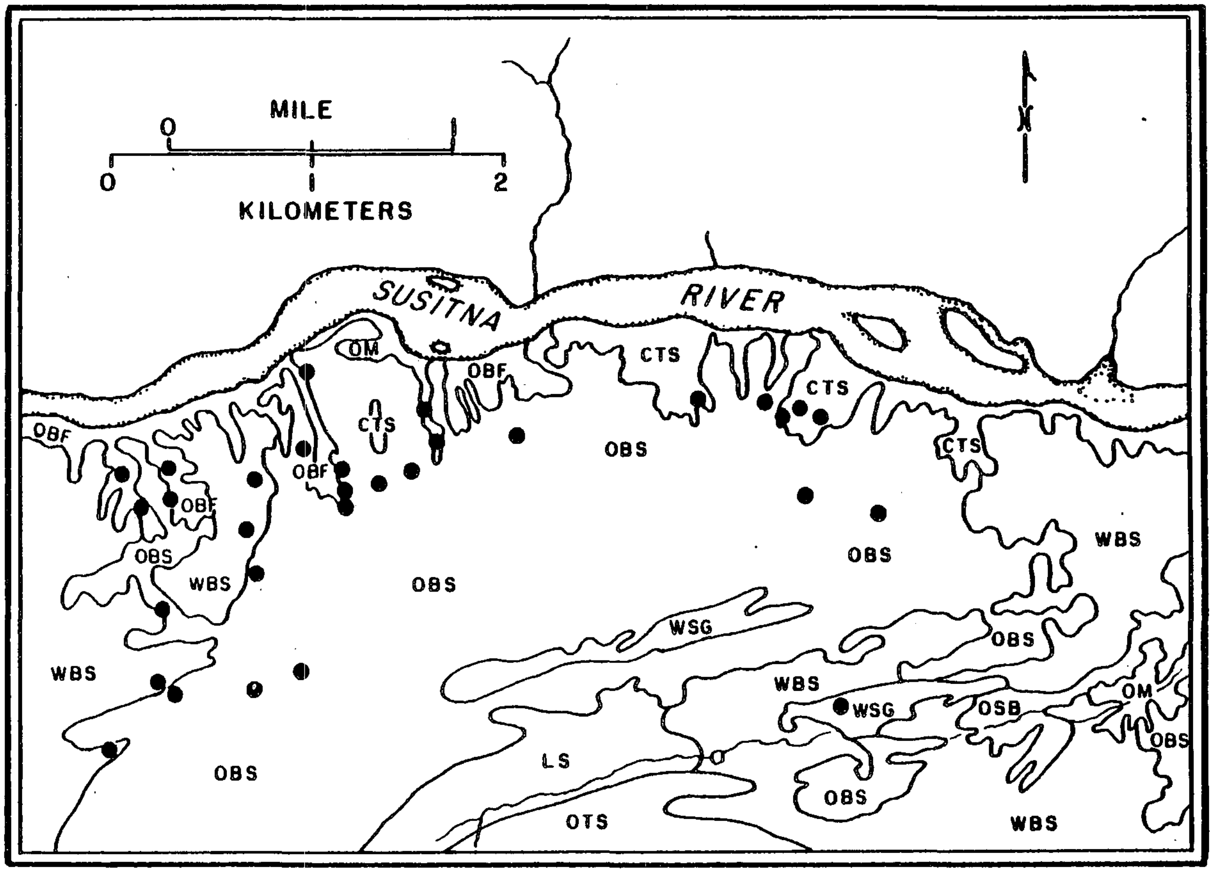

Figure 18. Radiolocations of marten number 512 in autumn 1981 plotted on vegetation map of upper Susitna Basin. Vegetation codes are as follows: CTS, closed tall shrub; LS, low shrub; OBF, open birch forest; OM, open mixed; OBS, open black spruce; OTS, open tall shrub; WBS, woodland black spruce; WSG, wet sedge-grass.

which occurred near the edge of the large stand of open black spruce or within the mapped stands of open birch forest (OBF) and closed tall shrub (CTS).

Other types of marten resting sites located include inactive red squirrel middens and red squirrel grass nests in trees. Marten were found resting in grass nests on four occasions in spring 1981. Three of the four instances were observed between 23 March and 25 March. In each case, an adult male was resting in a nest 3-8 m above the ground in a white spruce during midday, air temperatures were 0 ± 1 C, wind was from the northeast at 2-5 m/sec, relative humidity was 20 ± 2% and sunlight was direct and bright.

DISCUSSION

Care must be exercised in interpreting data on habitat utilization by marten when a variety of techniques have been employed to gather the data. Data from transects, for example, reflect the distribution of tracks, which is an estimator of habitat use based upon locomotion. Marten may make tracks in the course of a number of activities, including foraging for food, home range exploration/territorial maintenance, dispersal/migration and mate-seeking and reproductive behavior. Vegetation or habitat type is more important to some of these activities than others. For example, marten tracks probably show closer habitat associations when the marten are foraging for voles than they do when the marten are exploring or dispersing. I assume that at the time of year in question, foraging and home range exploration/territorial maintenance represent the major sources of marten tracks observed and that the closest track-vegetation type associations are due to the behavior of marten foraging for animal foods. Thus, there are probably some tracks which result from activities which are linked to specific habitat types, but other tracks which result from activities which have no or weak habitat links. Of course, the field worker cannot distinguish between the two, and tracks of the second type would tend to obscure relationships which might be apparent from the first. In addition, I suspect that track-habitat associations are further obscured by the use of methods of vegetation classification in transect runs (observed use) different from those used in vegetation mapping (expected use). Although both kinds of classifications were made using the same criteria, one effort (transect runs) was made from a low flying helicopter while the other (vegetation mapping) was based upon high altitude infrared photographs, supplemented by ground truthing. The resulting track-habitat relationships in the data should be used, I believe, only to identify the most salient and coarse habitat associations.

The second type of data, sign observed while snow tracking, considers those behavior-habitat associations which occur within the range of habitats in which marten tracks are found. Obviously, habitat types avoided by marten are underrepresented in this sampling scheme. I feel that these data are more reliable than those from transects and better enable one to distinguish between the various activity types which may contribute to track-habitat associations.

The third type of habitat data, resting site descriptions, is, I believe, relatively free of bias. A small bias was introduced by searching red squirrel middens for marten scat accumulations. Because only two marten resting sites were identified in this way, I believe that the sample approximated true winter resting site habitat preferences in the study area.

Data from snow tracking of marten suggest that during autumn of 1981 marten did most of their foraging in stands of black spruce and mixed conifer (black and white spruce). This conclusion is consistent with the finding that marten fed primarily upon tundra voles and meadow voles during that season (see Diet section) and the observation of S.O. MacDonald (pers. comm.) that these microtines were most abundant in wet sedge meadows surrounded by black spruce woodlands. It is interesting to note that urinating, defecating and resting showed no vegetation associations which were statistically significant. This lends credence to my earlier statement that foraging produces stronger track-habitat associations than other types of activities.

The characteristics of marten resting sites suggest a close spatial and habitat association between marten and red squirrels. Active red squirrel middens appeared to be particularly important to marten during the cold season and a major component of marten winter habitat. My general impression was that there were many more inactive red squirrel middens than active ones in the study area. The preference by marten for active red squirrel middens over inactive middens suggests that maintenance done on the underground nests by red squirrels makes them more suitable for use as marten resting sites. Such maintenance includes carrying in dry nest material such as grass, moss or fur. Johnson (1954) documented that red squirrel underground nests at middens provide a favorable microclimate in winter due to the insulating qualities of snow and the midden material itself. Raine (1981) located three subnivean marten dens in southeastern Manitoba, all of which were renovated (and presumably inactive) red squirrel middens on jackpine ridges. He also found the air temperature in an unoccupied subterranean fisher den to be -11 C when the air temperature at the snow surface was -26 C. Considering the heat generated by a marten, air temperatures inside squirrel middens occupied by marten may be over 25 C warmer than air at the snow surface during mid-winter cold spells. Use of squirrel middens by marten has been noted by other North American workers (Murie 1961, More 1981, Spencer 1981), however, my results indicate a closer ecological association between marten and red squirrels than any yet reported.

My frequent observations of red squirrels near middens being used by marten and the role of red squirrels in the diet of marten raise interesting questions concerning trophic and behavioral relationships between red squirrels and marten in the upper Susitna Basin. Although squirrels may temporarily abandon their nests to marten during warm winter days, during cold periods they remain underground (Pruitt and Lucier 1958, Pauls 1978). Thus, marten and red squirrels may use the same squirrel middens concurrently for resting sites. Whether marten attempt to kill red squirrels and how red squirrels evade capture by marten under these circumstances is not known. Marten do prey upon red squirrels, particularly in spring (see Diet section), but the limited role of red squirrels in the diet of marten in autumn and winter suggests that the two species coexist at resting sites most of the time.

Although red squirrels are apparently able to avoid marten at middens most of the time, marten predation on red squirrels at winter and summer nests doubtless occurs. On 26 April 1974 Mr. Charles Baille brought me a red squirrel nest which he had found in a cabin on Montana Creek, just east of the Nenana River in the Alaska Range. Mr. Baille entered the cabin to see a marten run from the nest and out of the cabin. The nest consisted of dry grass and fiberglass insulation. Within the nest I found two red squirrel tails and several marten scats. These scats were found to contain approximately 50% (volumetric) red squirrel hair, 30% northern red-backed vole hair and 20% snowshoe hare hair. The marten apparently killed the occupants of the nest before moving in.

Marten use of above-ground resting sites in summer is easy to interpret in terms of soil and air temperatures. Subterranean burrow air temperatures are near 5 C in summer when air temperatures at the soil surface are 15 C warmer (Pruitt 1957). I agree with Raine (1981) that many above-ground marten resting site descriptions, particularly those on tree branches, are meaningless since animals are responding to the presence of a human and not resting at all. I suspect that marten do occasionally use tree branches for resting sites in the upper Susitna Basin, however, it was never possible to confirm that their use of tree branches did not represent escape behavior.

High quality marten habitat in the upper Susitna Basin appears to be a mosaic of vegetation and topography types. Vegetation in optimal habitats consists primarily of black spruce woodland, old-growth white spruce forest and woodland and mixtures of white spruce and paper birch. Wet sedge and grassy meadows, highly variable in size and shape, occur within the black spruce woodland. Red-backed voles are common in a variety of vegetation types in the habitat, meadows are productive for lemmings and voles of the genus *Microtus* and stands of old-growth white spruce support red squirrels which occupy old and well-developed middens.

This habitat satisfies two basic needs of marten during autumn, winter and spring. First, it is productive of the foods, particularly microtines, which marten prefer. Second, it provides suitable resting sites which offer microclimatic protection. Traditional views of marten habitat use have not taken into account the latter requirement. The interspersion of these habitat types appeared to be important in the upper Susitna Basin. Active foraging for voles appeared to be more frequent in areas with vegetational heterogeneity. In addition, the occurrence of suitable resting sites close to suitable foraging areas provides energetic savings in terms of reduced daily travel. The belief that Alaskan marten thrive on unbroken, pure stands of conifer forest belies our ignorance of the life requisites of this species.

FAT RESERVES OF MARTEN IN WINTER

Winter energetic strategies have been considered for many northern vertebrates and consist of combinations of a broad range of morphological, behavioral and physiological traits which permit survival in the face of large body temperature - environmental temperature differences and varying degrees of food deprivation (Irving 1966). The energetic strategy employed by marten in winter is of considerable interest because of reported characteristics which suggest an energy imbalance. The marten is a small, rather elongate homeotherm with a high ratio of surface area to volume and poor body insulation in the form of subcutaneous fat (Strickland et al. 1982) or fur (Irving 1964). It has traditionally been believed to be active throughout the winter (Herman and Fuller 1974), is too large to make use of subnivean microtine tunnels for travel (Pruitt and Lucier 1958) and is exposed to ambient temperatures within 200 mm of the snow surface, the coldest mid-winter microclimate. Worthen and Kilgore (1981) recently reported an empirical lower critical temperature for marten of 29 C. Marten have very limited body fat reserves (pers. obser. and M. Strickland, pers. comm.), are not known to undergo metabolic rate depression as an energy conservation measure and have never been reported to hoard foods in the manner of some mustelids, such as short-tailed weasels (Sueur 1981) and wolverines (Haglund 1966).

Harlow (1981*a*) described an energetic strategy employed by badgers (*Taxidea taxus*) in winter. Wyoming badgers were found to have high body fat ratios in autumn which declined substantially by spring.

Mean fat content of 79 skinned carcasses was 30% in autumn and 19% in March. Badgers remained in subterranean burrows for extended periods (up to 70 consecutive days) in winter and underwent periods of metabolic rate depression accompanied by a reduction in heart rate and body temperature. This metabolic rate depression was found to result in a 27% reduction in the rate of energy expenditure.

It appears unlikely that marten could survive the winter with a combination of metabolic rate, microhabitat use and foraging style similar to that which they have been reported to display during warm months. The K-style characteristics of marten, such as high longevity and low fecundity (Strickland et al. 1982) suggest that they have evolved means of avoiding high mortality during cold months. The objectives of this phase of the work were to review those features of marten life history which bear upon winter energy budget and gather new data to test the hypothesis that marten use body energy reserves accumulated in summer and autumn to offset heat loss during cold periods in midwinter.

MATERIALS AND METHODS

Skinned carcasses of marten from the upper Susitna basin were purchased or accepted as donations from trappers from October 1981 to February 1982. The carcasses were necropsied and selected organs and omental fat excised and weighed immediately to the nearest mg. Organs weighed were heart, liver, kidneys and left and right gastrocnemius and soleus muscles. Contents of the gastrointestinal tract and urinary bladder were removed and not included in carcass weights. Organs and skinned carcasses were then dried at 80 C until a stable weight was attained. For small organs this required 2-4 days, for skinned carcasses, 7-12 days. Dried organs and carcasses were weighed. Skinned carcasses of 12 marten (7 males, 5 females) were analyzed for total body lipid after organ weighing. Carcasses were ground, an aliquot was freeze-dried and lipid extracted by refluxing for 8 hours in petroleum ether with a Soxhlet apparatus. Petroleum ether was chosen over chloroform-methanol because of its higher solubility of low-polarity depot lipids (Christie 1973). Total body lipid was expressed as a fraction of skinned carcass fresh weight. Skinned carcass fresh weights were standardized to 70% water content because of large differences in the water content of carcasses kept by trappers for varying lengths of time before being processed in the laboratory. Freshly skinned carcasses were found to contain approximately 70% water. Correlation analysis (BMDP6D, Dixon et al. 1981) was conducted on data from the 12 animals to determine the best predictor of total body lipid. The best predictor was then regressed over time for the winter of 1981-82 to determine if total body lipid changed significantly over time.

RESULTS

The skinned carcasses of 26 marten taken during the 1981-82 trapping season from the upper Susitna Basin were necropsied. Organ weights are presented in Table 21, and organ weights as a proportion of skinned carcass weights are presented in Table 22. Among the organs

Table 21. Fresh organ weights (g) of marten taken in the upper Susitna Basin in winter 1981-82.

	N	max	min	$\bar{x}$	SD
Skinned carcass	26	1014	431	745	177.3
Heart	15	12.18	6.78	9.62	1.64
Liver	26	54.01	14.33	29.75	9.82
Left kidney	16	5.82	2.79	3.97	0.98
Right kidney	16	5.63	2.58	3.86	0.92
Left gastrocnemius and soleus	13	8.81	4.06	6.71	1.57
Right gastrocnemius and soleus	14	8.66	4.25	6.61	1.52
Omentum	26	5.22	0.66	2.17	1.42

Table 22. Fresh organ weight/body weight ratios for marten taken in the upper Susitna Basin in winter 1981-82. Organ fresh weights are divided by skinned carcass fresh weights.

	N	max	min	$\bar{x}$	SD
Heart	14	0.0148	0.0105	0.0122	0.0012
Liver	26	0.0601	0.0263	0.0399	0.0090
Left kidney	16	0.0069	0.0038	0.0050	0.0007
Right kidney	16	0.0064	0.0040	0.0049	0.0006
Left gastrocnemius and soleus	13	0.0095	0.0071	0.0082	0.0007
Right gastrocnemius and soleus	14	0.0093	0.0073	0.0083	0.0007
Omentum	26	0.0062	0.0007	0.0028	0.0015

examined omenta and livers showed the greatest variability in weight. After adjustment for body size, omentum and liver weights were still the most variable. Since these organs are also depots for energy reserves, they were considered the most likely candidates for use as indices of total body lipid reserves. Other body fat depots (perirenal, subcutaneous) were not used as indices because of the difficulty in defining their limits.

Carcasses of marten caught during winter contained very limited body fat reserves. In most animals no subcutaneous or perirenal fat was observable, although in almost all animals examined, some omental fat was visible. Total body lipid of 12 marten trapped between 30 November 1981 and 26 January 1982 was 1.24-4.83% of skinned carcass fresh weight ($\bar{x}$ = 2.37%). The results of correlation analysis of two body fat indices with two measures of total body fat are presented in Table 23. Omentum fresh weight was found to be strongly correlated with total body fat (r = 0.84, $P < 0.001$, see Figure 19). Omentum fresh weight as a fraction of skinned carcass fresh weight was selected as the best predictor of total body fat because of the highly significant correlation and because of the ease of measurement of omentum fresh weights. Liver fresh and dry weight ratios were not selected as body fat indices because although they did show strong variability, they were not strongly correlated with total body fat.

Omentum fresh weight as a fraction of skinned carcass fresh weight was regressed on time for the period 30 October-26 January. The results of this regression are presented in Figure 20. For 26 marten of both

Table 23. Results of correlation analysis, marten body fat indices and total body fat.

Index Variable	Body Fat Variable	*r*	*P*
Omentum fresh weight/ Skinned carcass fresh weight	Total body lipid as percent of skinned carcass fresh weight	0.84	<0.001
Liver fresh weight/ skinned carcass fresh weight	Total body lipid as percent of skinned carcass fresh weight	0.85	0.78
Omentum fresh weight/ skinned carcass fresh weight	Total body lipid as percent of skinned carcass dry weight	0.85	<0.001
Liver fresh weight/ skinned carcass fresh weight	Total body lipid as percent of skinned carcass dry weight	0.15	0.64

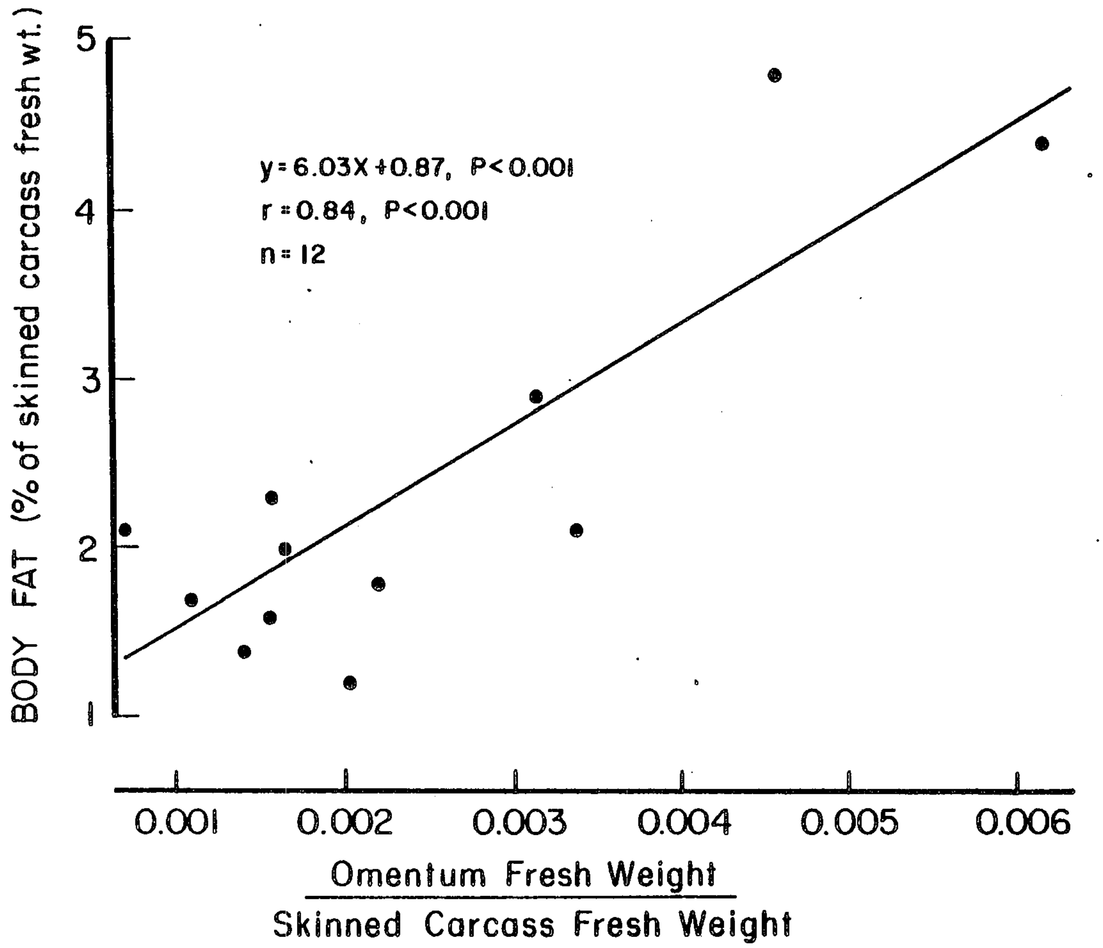

Figure 19. Scatterplot of body fat and omentum weight/carcass weight ratio for skinned marten carcasses in winter.

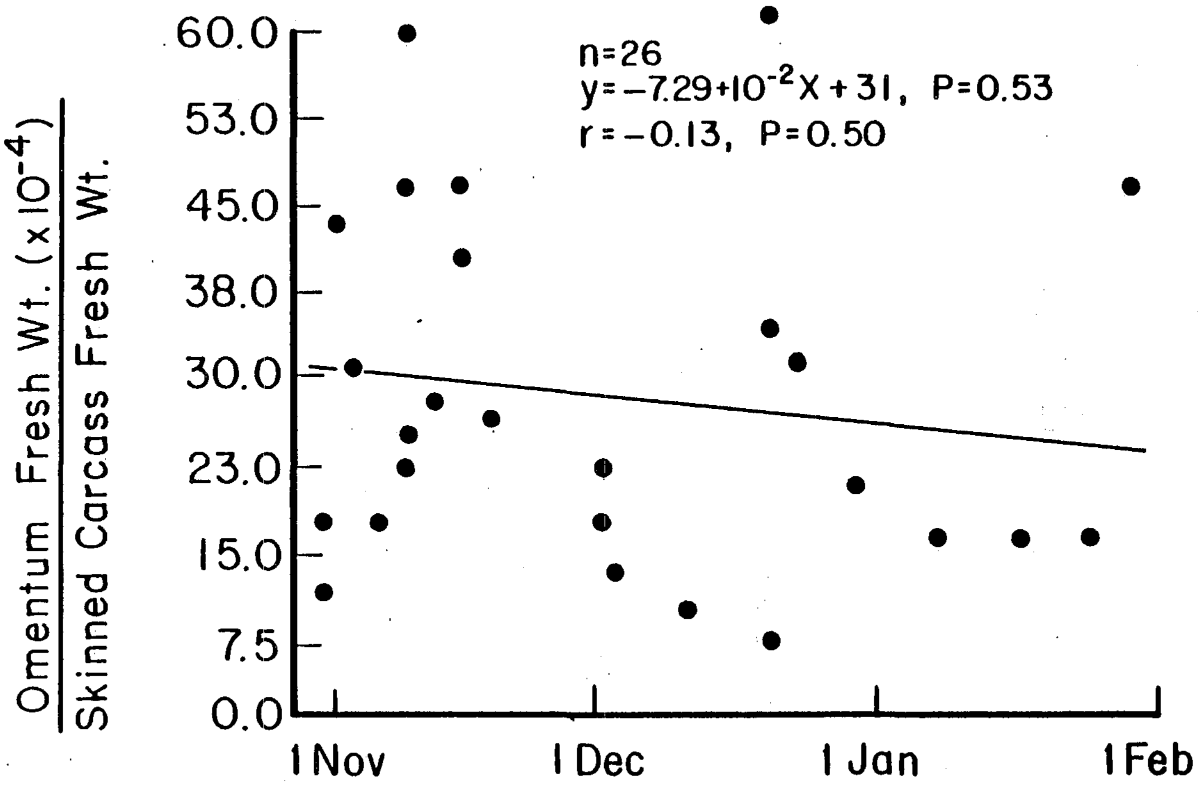

Figure 20. Regression of omentum fresh weight/skinned carcass fresh weight ratio on time for marten in the upper Susitna Basin, winter 1981-82.

sexes, the regression coefficient did not differ significantly from zero. I examined the plotted residuals and could discerne no departure from linearity. Thus, the null hypothesis that there is no change in total body lipid in marten over winter was not rejected. When values for males and females were regressed separately, neither regression coefficient differed significantly from zero (Figure 21). Again, no departure from linearity was apparent in the plotted residuals.

DISCUSSION

Data from telemetry studies (see Home Ranges and Movements section) suggest that marten in the upper Susitna Basin live at lower elevations in winter than in other months. Because of extreme thermal inversions in winter this implies that marten utilize the coldest portions of their ranges at the coldest time of the year.

Marten fat reserves were found to be extremely limited in winter. Twelve skinned carcasses were found to have a mean body lipid fraction of 2.37%. This is less than one-tenth the mean body lipid fraction found by Harlow (1981) in Wyoming badgers and falls well below the body fatness - body size regression line calculated by Pitts and Bullard (1969) for 49 species of mammals ranging in size from shrews to whales (Figure 22). Although data on changes in body fat reserves of marten over winter are inconclusive, they do suggest the possibility that marten undergo a decline in body fat from late October to late January. It is apparent that marten exhibit strong variation in total body fat

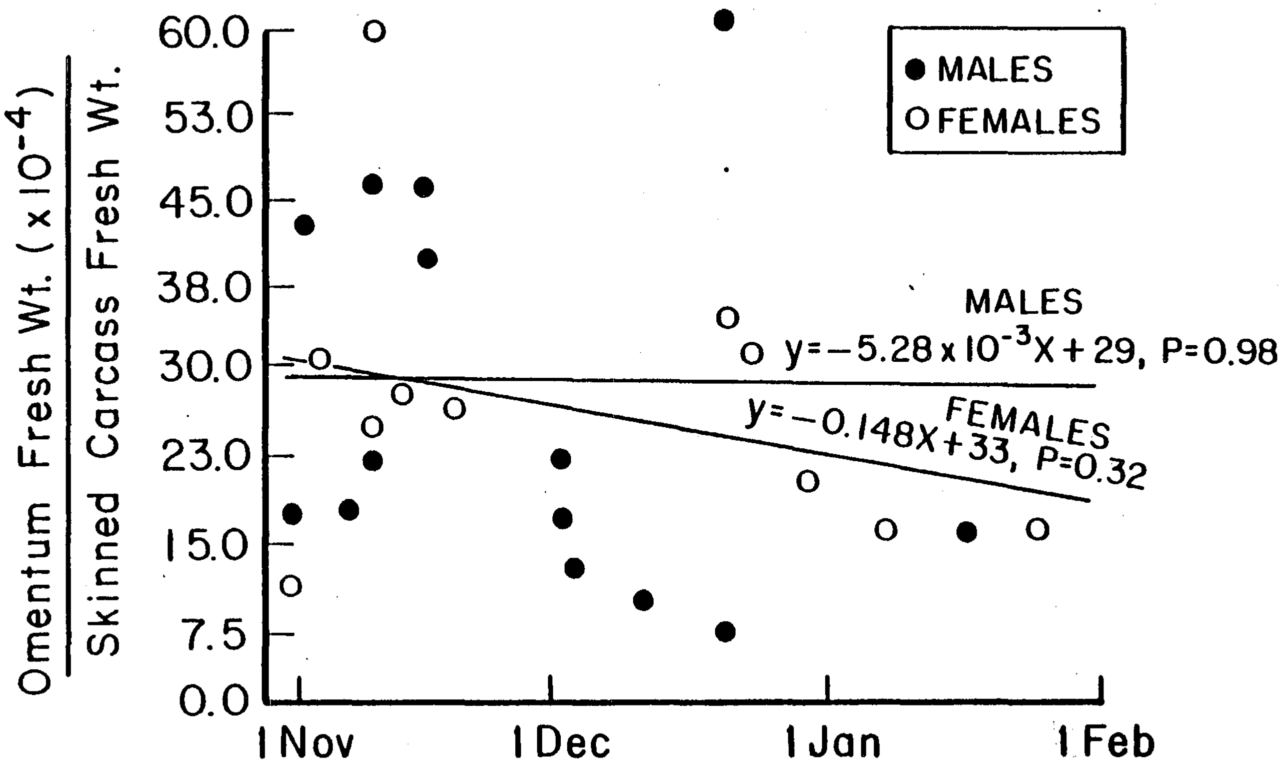

Figure 21. Regression of omentum fresh weight/skinned carcass fresh weight ratio on time for male and female marten in the upper Susitna Basin, winter 1981-82.

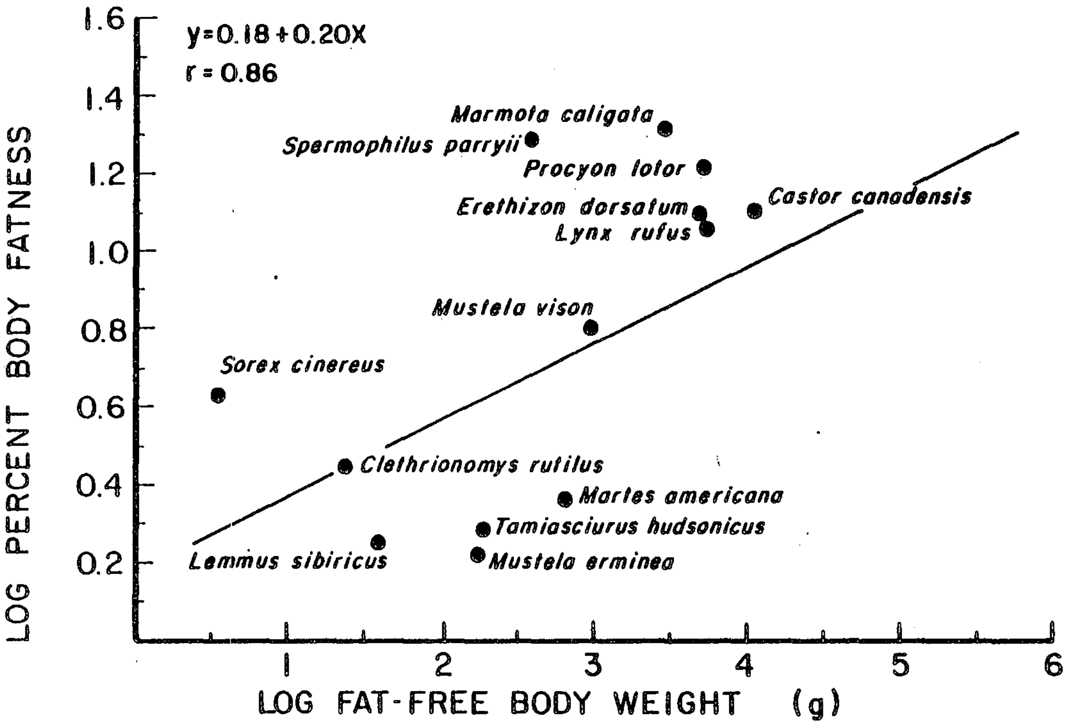

Figure 22. Body fatness — body weight regression line of Pitts and Bullard (1968). Value for *Martes americana* is from present study. Value for *Spermophilus parryii* is a midsummer (maintenance) value derived from Galster and Morrison (1976).

reserves and that a much larger sample size would be necessary to determine the significance of any seasonal change. Total body lipid values may be influenced by two factors which I should mention. First, all values given here and by Harlow (1981) are for skinned carcasses. There is, of course, some subcutaneous fat removed with the pelt in skinning. The amount of error thus introduced depends upon the amount of fat removed. Because marten have so little subcutaneous fat and because trappers attempt to remove as little fat as possible with the pelt, the error thus introduced is probably small. Indeed, a fresh marten pelt likely has a smaller lipid fraction than the skinned carcass, which would result in an unrealistically high estimate of total body fat if total body fat measurements were based upon skinned carcasses.

The second factor which must be considered as a source of bias is the body fat metabolized while an animal is in a trap. H. Behrisch (pers. comm.) has pointed out that body lipid reserves are depleted rather slowly under energetic stress because of the low solubility of fatty acids in mammalian blood. Thus, I have assumed (as did Harlow for badgers) that fat metabolism by marten caught in leghold traps in Alaska during winter is not an important source of bias in total body lipid values.

The extremely low winter values for total body lipid in marten emphasize the energetic difficulties encountered by these animals. The lack of a significant decline in body fat over the winter suggests that marten must balance caloric intake with energetic losses on a fairly short-term basis. Although I have shown that marten make heavy use of warm microclimates such as red squirrel middens for resting in winter (see Habitat Use section), without energy reserves, or large caches of food in or near their resting sites, they must be required to forage for food in extremely cold weather (< -40 C).

To calculate the energetic cost of foraging at -40 C for a marten, I examined the metabolic rate curve of Worthen and Kilgore (1981). They reported a lower critical temperature for marten of 29 C. By comparison, arctic foxes (*Alopex lagopus*), which weigh about twice as much as marten, have been reported to be thermoneutral down to -35 C (Underwood 1981). Worthen and Kilgore give no description of the pelage condition of their animals, but if representative of Alaskan marten in winter, the following resting metabolic rates would apply:

Ambient temperature (C)	Metabolic Rate (kJ g^{-1} $hour^{-1}$)
30	0.013
0	0.035
-40	0.067

Using a value of 39.7 metabolizable kJ/g fat, the length of time needed for a 1 kg marten resting at thermoneutrality to metabolize 1 g fat is 3.0 hours. The lengths of time required for a 1 kg marten to metabolize stored fat at various body fat levels are presented in Table 24. The time required for the marten with the highest proportion of body fat observed in this study to completely utilize all extractable body lipid, resting at thermoneutrality, is 143 hours. In the upper Susitna Basin, midwinter air temperatures can remain below -40 C continuously

Table 24. Lengths of time required for fasting marten to completely metabolize all body fat reserves at various body fat levels. The marten is assumed to weigh 1 kg and to be resting at thermoneutrality.

Total body lipid (%)	Total kJ in lipid	Time to metabolize (hour)
1.24	494	37
2.37	942	70
4.83	1921	143

for in excess of 2 weeks. Clearly, the amount of stored fat possessed by marten is not sufficient for resting metabolic energy needs for the duration of typical mid-winter periods of cold weather. The metabolic rate curve of Worthen and Kilgore also permits an approximation of the energetic cost of foraging on the snow surface in extreme cold. Their regression predicts that marten resting at -40 C must produce 0.067 kJ g^{-1} $hour^{-1}$. The assumption that marten will rest motionless at -40 C is specious, but the effect of movement would be to increase wind chill and heat loss. Using Powell's (1982) value of 126 metabolizable kJ for each 25 g small mammal, a marten would have to capture an average of one 25 g mouse every 2 hours to avoid a net energy deficit while foraging. A marten's thermoneutral resting energy needs of approximately 335 kJ/day would require 2-3 voles of 25 g each. The findings of Worthen and Kilgore (1981) are so inconsistent with those for other northern homeotherms that they must be questioned. It is possible that their techniques of metabolic rate measurement were in error, but a more likely interpretation is that their study animals were acclimated to temperatures much higher than those that free living marten encounter in winter.

While it is obvious that some of the assumptions in this exercise are not tested, the midwinter energetic problems for marten are apparent. On one hand, insufficient body fat reserves are present to allow marten to rest without feeding during periods of severe weather. On the other hand, foraging for small packets of energy (voles) at -40 C is a costly energetic proposition.

Marten may handle this energetic dilemma in one or more ways. They may avoid extremely low temperatures more successfully than I or other workers suppose. Marten may utilize red squirrel middens or other protected microhabitats for extended periods of time in severe cold, emerging infreqently to forage. In conjunction with the use of protected microhabitats, marten may undergo metabolic rate depression as an energy conservation measure. Such a strategy has been shown to be important to red squirrels (Pauls 1979) and other nonhibernators. Marten may also cache or hoard food more than I recognize. Small caches spread over a large home range would probably not confer great energetic security, but centrally stored foods, particularly near red squirrel middens, could do so. It may be that marten utilize caches made by other animals, including berries cached by microtines.

Marten in some areas of Alaska may undergo upward midwinter movements to take advantage of warmer temperatures at higher elevations. There was no evidence of such movements in the upper Susitna Basin, but they could conceivably have occurred between early December and mid-February, when our telemetry data were fewest. Winter movements to higher elevations appear most likely to occur in areas of Alaska where thermal inversions are common in winter and where topographic relief permits marten to make vertical movements.

SUMMARY

A study of the ecology of marten in southcentral Alaska was conducted from March 1980 to December 1981. Field work was carried out on Tsusena and Watana creeks in the upper Susitna Basin. Data were gathered on home range and movements, seasonal food habits, habitat utilization and energetic strategies in winter.

Movements were studied through the use of live-trapping and radiotelemetry. A total of 20 radiocollars were attached to 17 marten. These animals were located a total of 560 times. Adult male marten were found to possess mutually exclusive home ranges with a mean area of 6.62 km^2. Mean home range area for all females was 3.71 km^2. Extensive overlap was observed between the home ranges of adult males and other sex and age groups. Marten were never observed to have crossed open bodies of water; rivers and creeks presented barriers to travel during summer and in many cases formed home range boundaries throughout the year. The activity patterns of marten were studied through the interpretation of telemetry signals during two periods — autumn 1980 and late winter 1981. Marten were found to be nocturnal during autumn, but to have a more complex trimodal activity pattern in late winter. Marten spent more total time active in autumn than in late winter.

Food habits of marten were studied by collecting and analyzing scats and colon contents during four major seasons. A total of 467 specimens were examined. The most important foods of marten in autumn, winter and spring were found to be microtine rodents, which constituted

70.4% of the volume of all scat material. Sciurids were the second most important food category, consituting 9.0% of the volume. Red squirrels were the most important sciurid species. Other important food types were fruits and birds. Snowshoe hares, shrews and porcupines had low importance in the diet of marten. Among microtines, marten preferred habitat specialist types (e.g., *Microtus*) over northern red-backed voles, which are habitat generalists. This preference may be due to the fact that habitat specialist types are found in more predictable habitat associations and attain higher local population densities than habitat generalists. It may also be due to the fact that preferred species tend to have larger body sizes and may be easier to capture. Most food categories showed strong seasonal variation in the diet of marten. Microtines and fruits were most important in autumn, when availability was highest. Red squirrels were utilized most heavily in spring and appeared to be a non-preferred alternative food item. Human foods were highly preferred and taken when available. Marten appeared to seek human foods most aggressively in spring, when the availability of natural foods was lowest.

Habitat utlization was studied by the use of aerial transects, by snow tracking and by identification and description of resting sites. Fourteen aerial transects were established and sampled in autumn 1980. A total of 1353 marten trails were counted and placed in vegetation categories. The distribution of marten trails in vegetation types was compared with the coverage of the transects by mapped vegetation types. Marten tracks occurred in black and white spruce forest and woodland with frequencies greater than the frequencies with which these vegetation types occur along the transects. Snow tracking of marten in autumn 1981 yielded 499 vegetation sample points along 36 km of marten trails. Marten were found to dig into snow (a mouse foraging behavior) more frequently than expected in woodland stands dominated by black spruce. Digging in snow and defecating were both encountered with frequencies higher than expected in situations at the interface of different stand types. Black spruce woodland, particularly at interfaces with other forest types and along *Carex* meadows, was the most important vegetation type for microtine foraging.

Marten winter resting sites were located primarily by radiotelemetry. Of 37 resting sites located, 84% were red squirrel middens or red squirrel grass nests in trees. Most of the squirrel middens used by marten were active; the middens showed recent signs of red squirrel activity. Marten used middens for resting sites most frequently in winter. Observed use of grass nests in trees was confined to a brief period in spring. No marten use of red squirrel middens or nests was observed in summer. During this period marten used resting sites above ground where they were easily disturbed. Marten were frequently observed in tree branches during all seasons, but these observations largely reflected escape behavior rather than resting site preferences. Heavy marten use of squirrel middens and nests suggests a close spatial and habitat relationship between the two species which is not based upon predation.

The energetics of marten in winter was studied by examining body fat depots. I hypothesized that marten underwent no significant change in total body lipid proportion over the winter. Selected organs and fat depots were weighed and total body lipid was extracted using a petroleum ether-soxhlet technique. Omental fresh weight was found to be the best predictor of total body lipid and was regressed on time for the winter of 1980-81. The slope of the regression line did not differ significantly from zero; I failed to reject the null hypothesis. Skinned marten carcasses were found to have a mean total body lipid fraction of 2.37%, which falls below the value predicted by body size alone. The ecological implications of extremely limited body energy reserves in winter are discussed. It may be that marten handle this energetic dilemma by extended use of microhabitats, some form of metabolic rate depression, centralized caching of foods or combinations of these strategies.

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APPENDIX A. Plotted locations of radiocollared marten in the upper Susitna Basin.

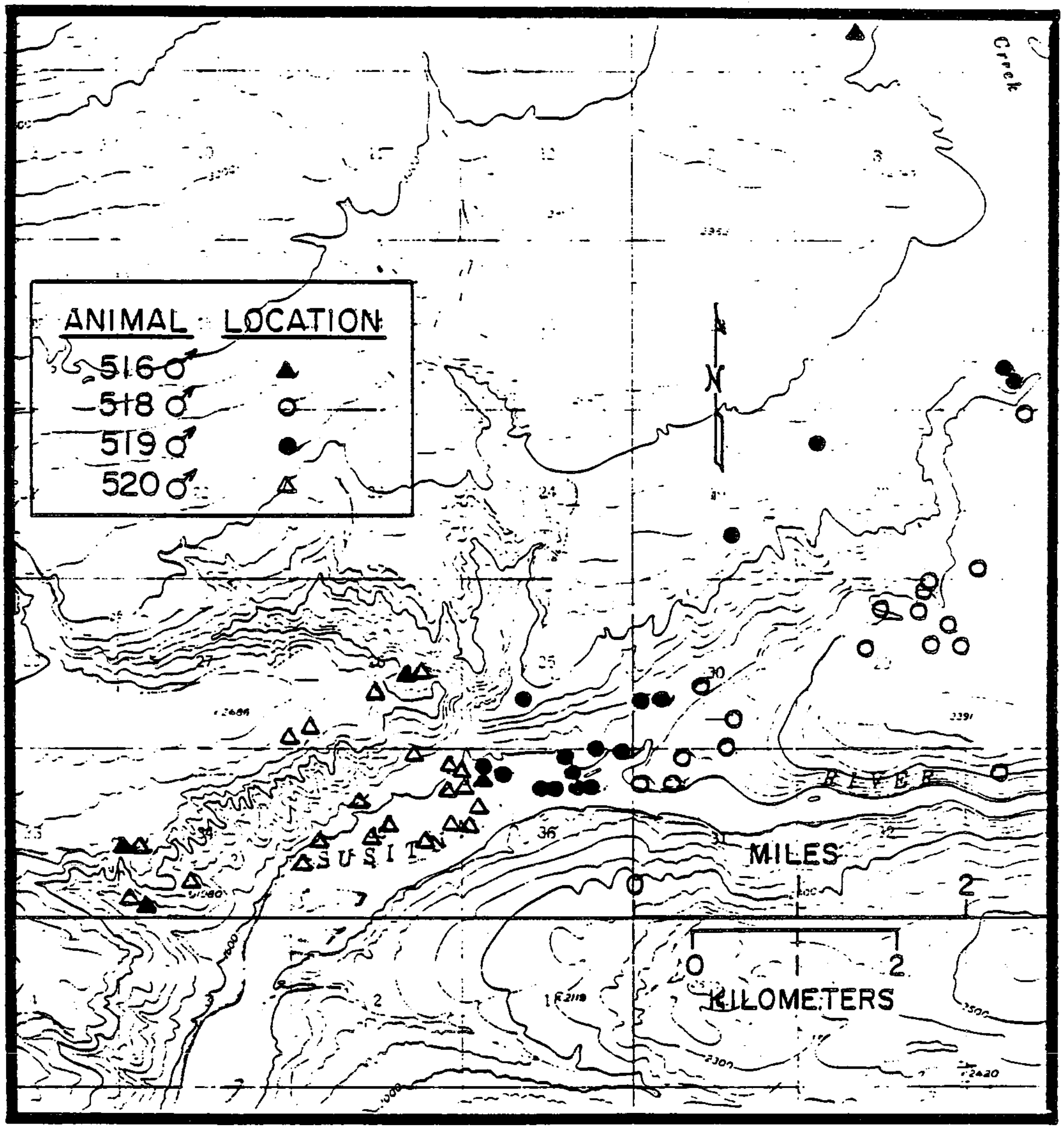

Figure 23. Locations for 4 radiocollared marten in the Susitna study area in autumn 1980.

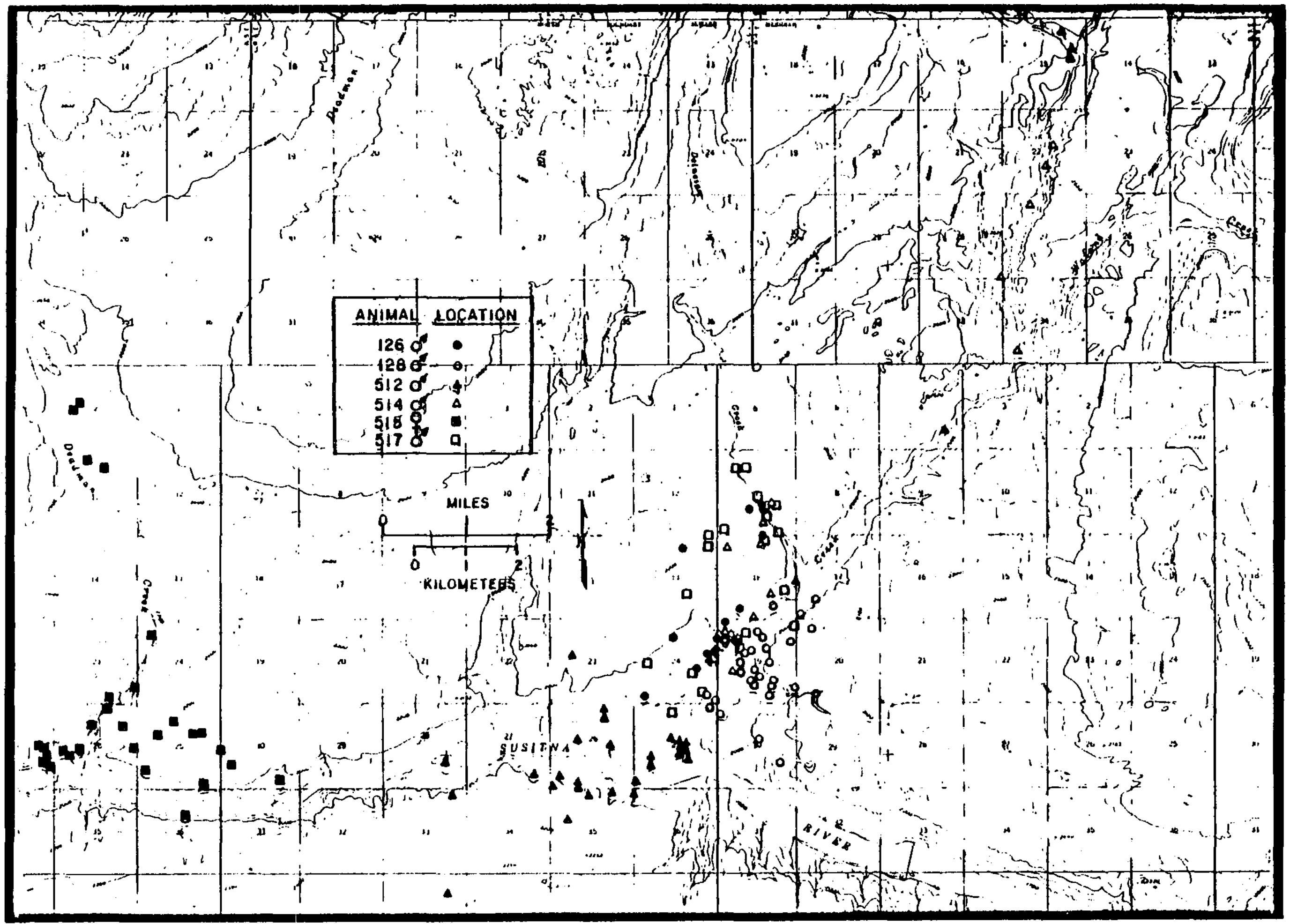

Figure 24. Locations for 6 radiocollared marten in the Susitna study area in spring 1981.

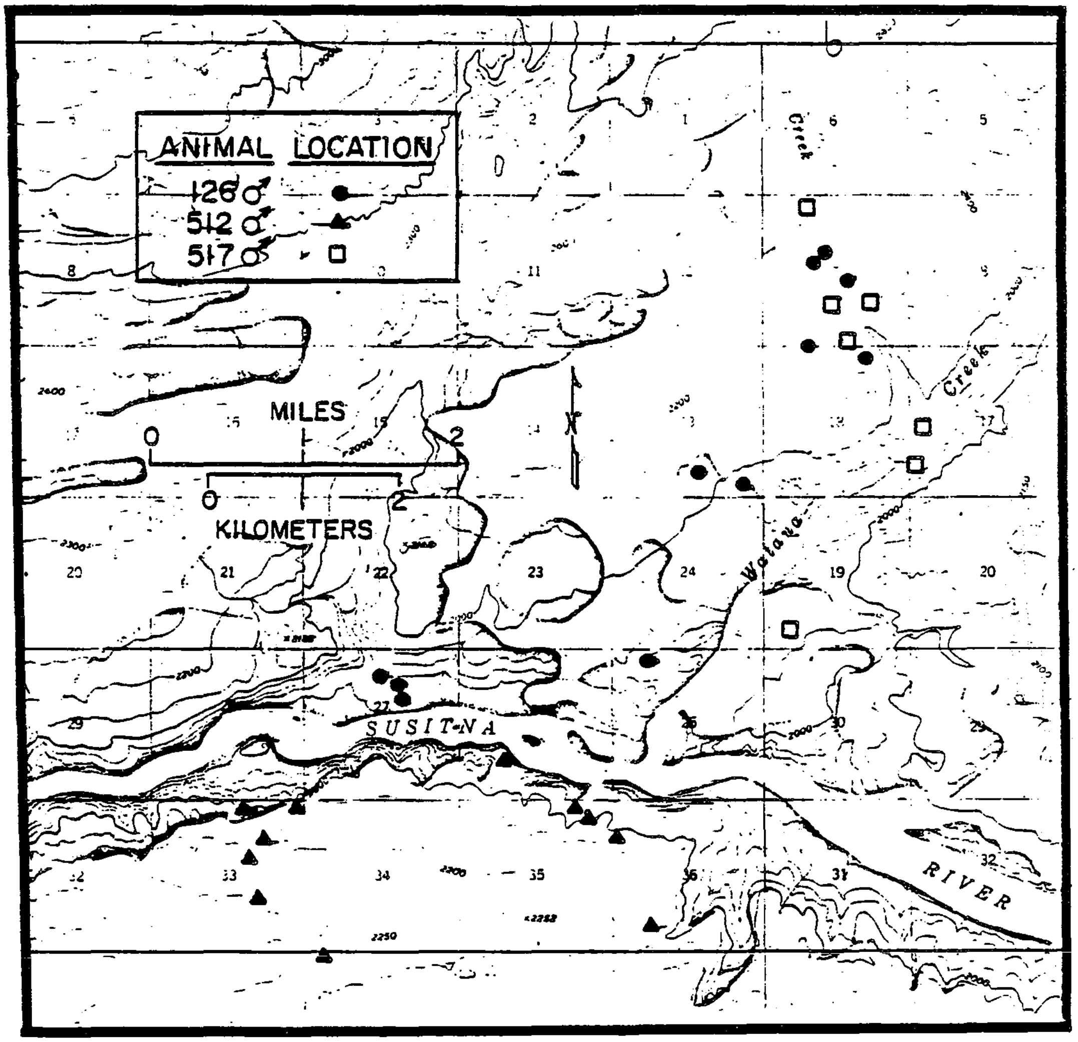

Figure 25. Locations for 3 radiocollared marten in the Susitna study area in summer 1981.

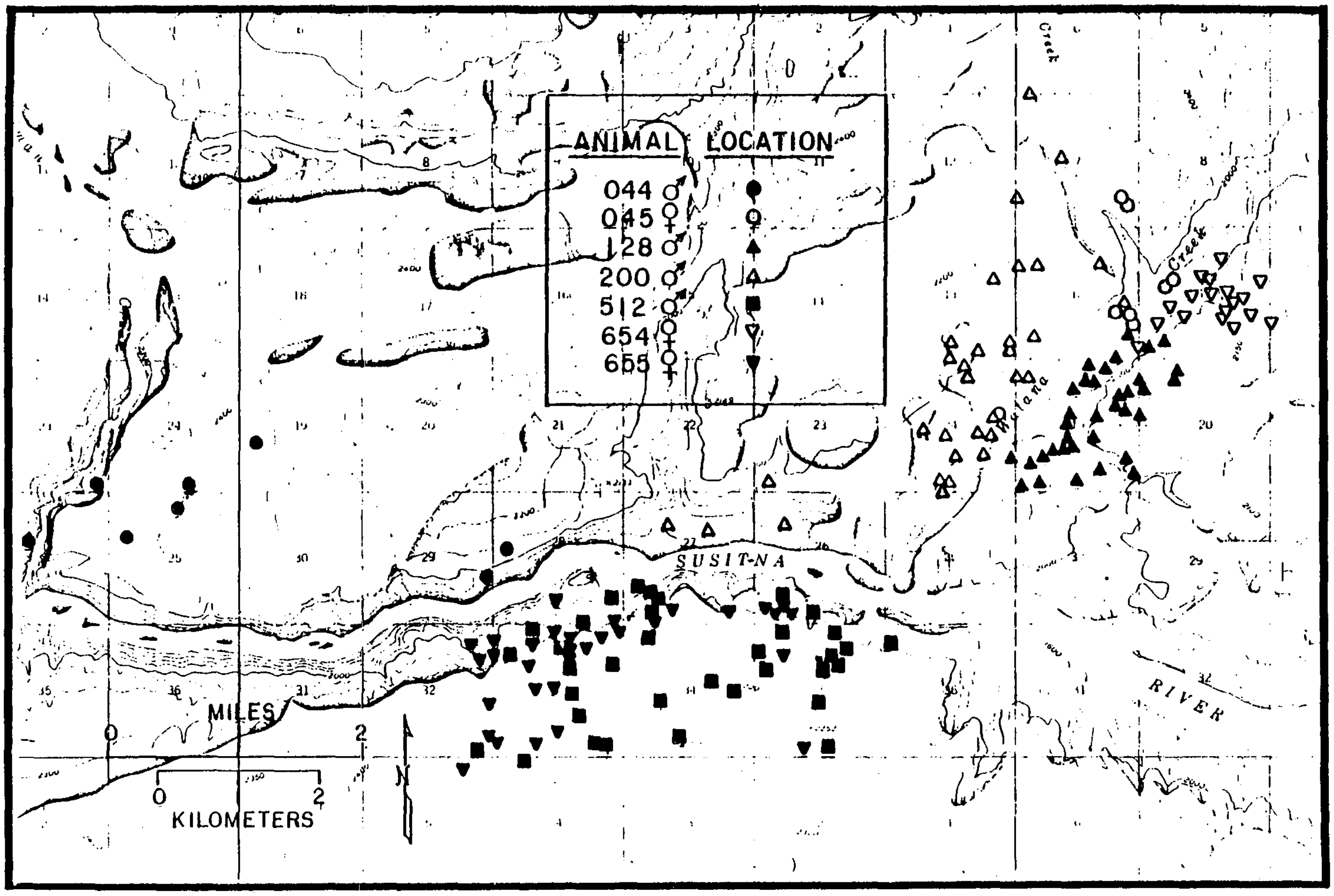

Figure 26. Locations for 7 radiocollared marten in the Susitna study area in autumn 1981.

APPENDIX B. Diel activity patterns of individual radiocollared marten in the Susitna study area.

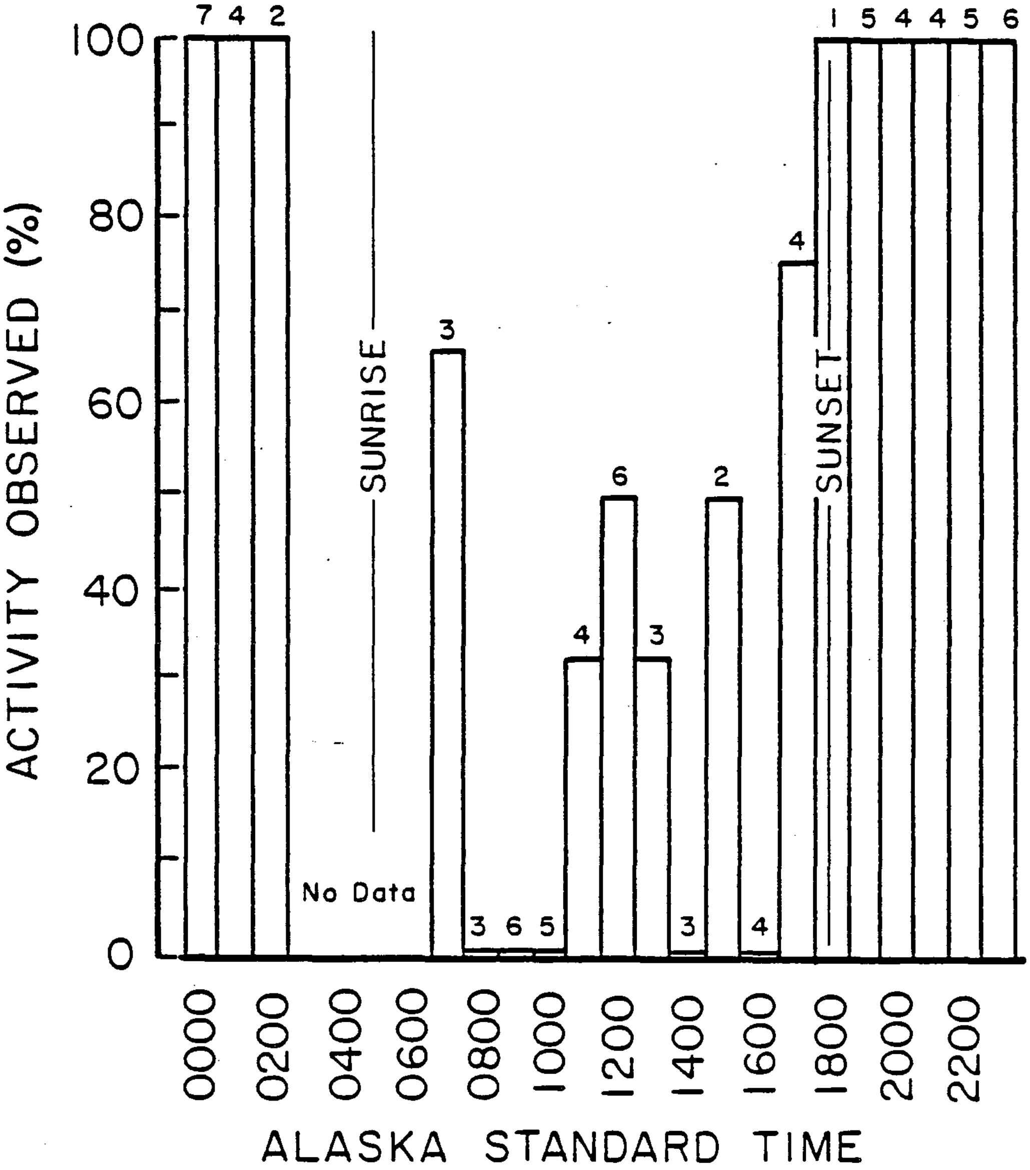

Figure 27. Diel activity pattern of marten number 518 in autumn 1980.

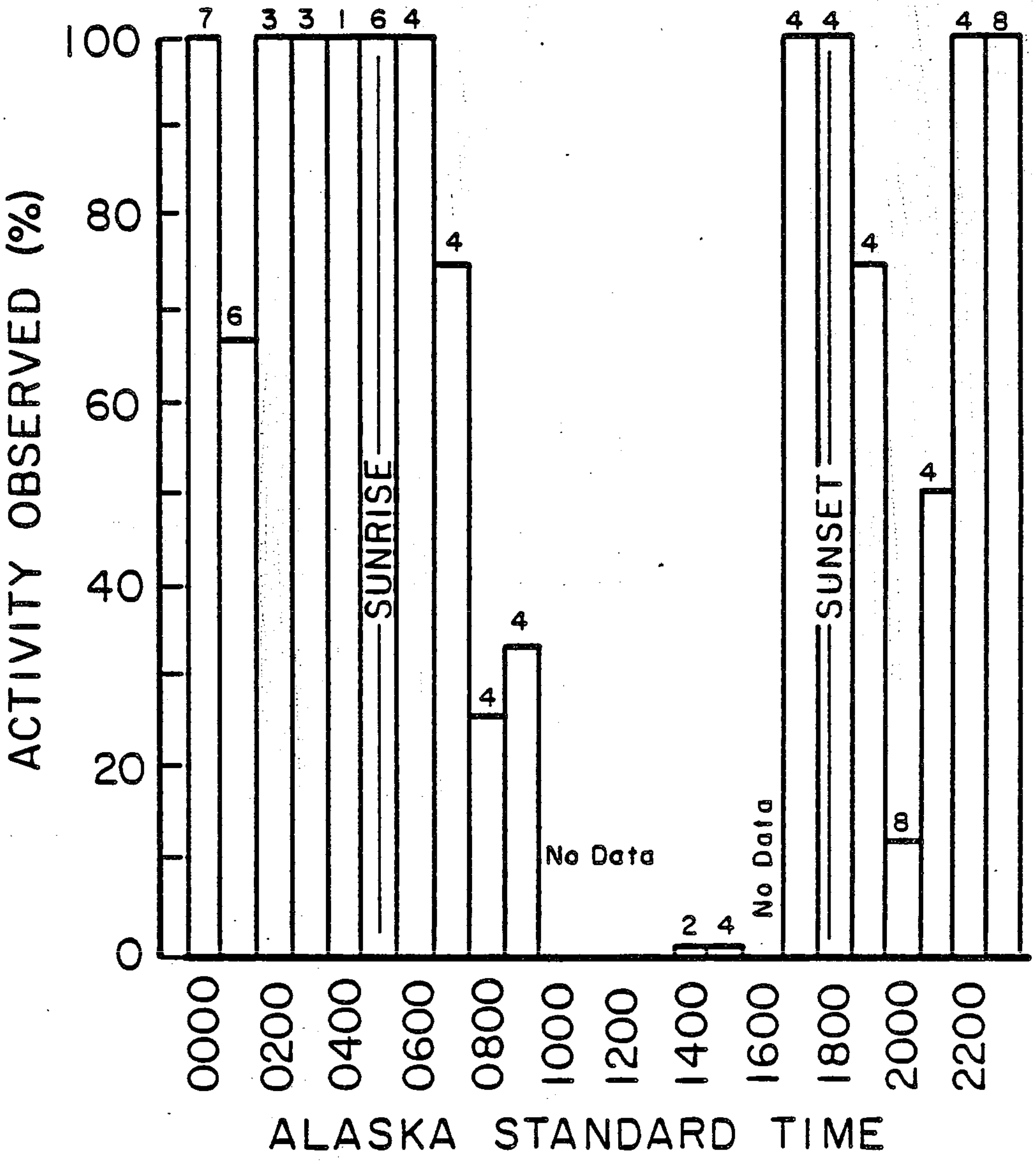

Figure 28. Diel activity pattern of marten number 519 in autumn 1980.

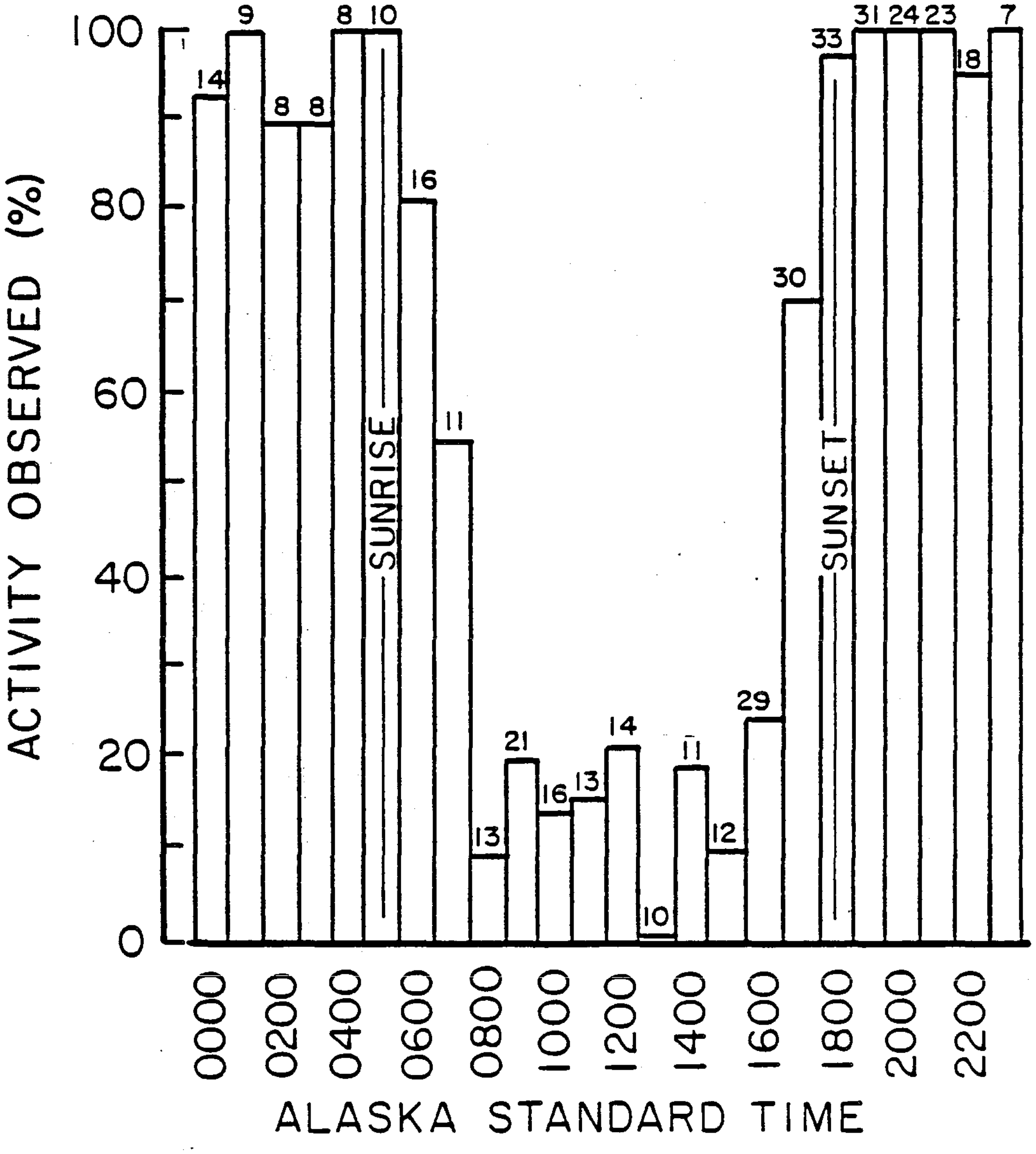

Figure 29. Diel activity pattern of marten number 520 in autumn 1980.

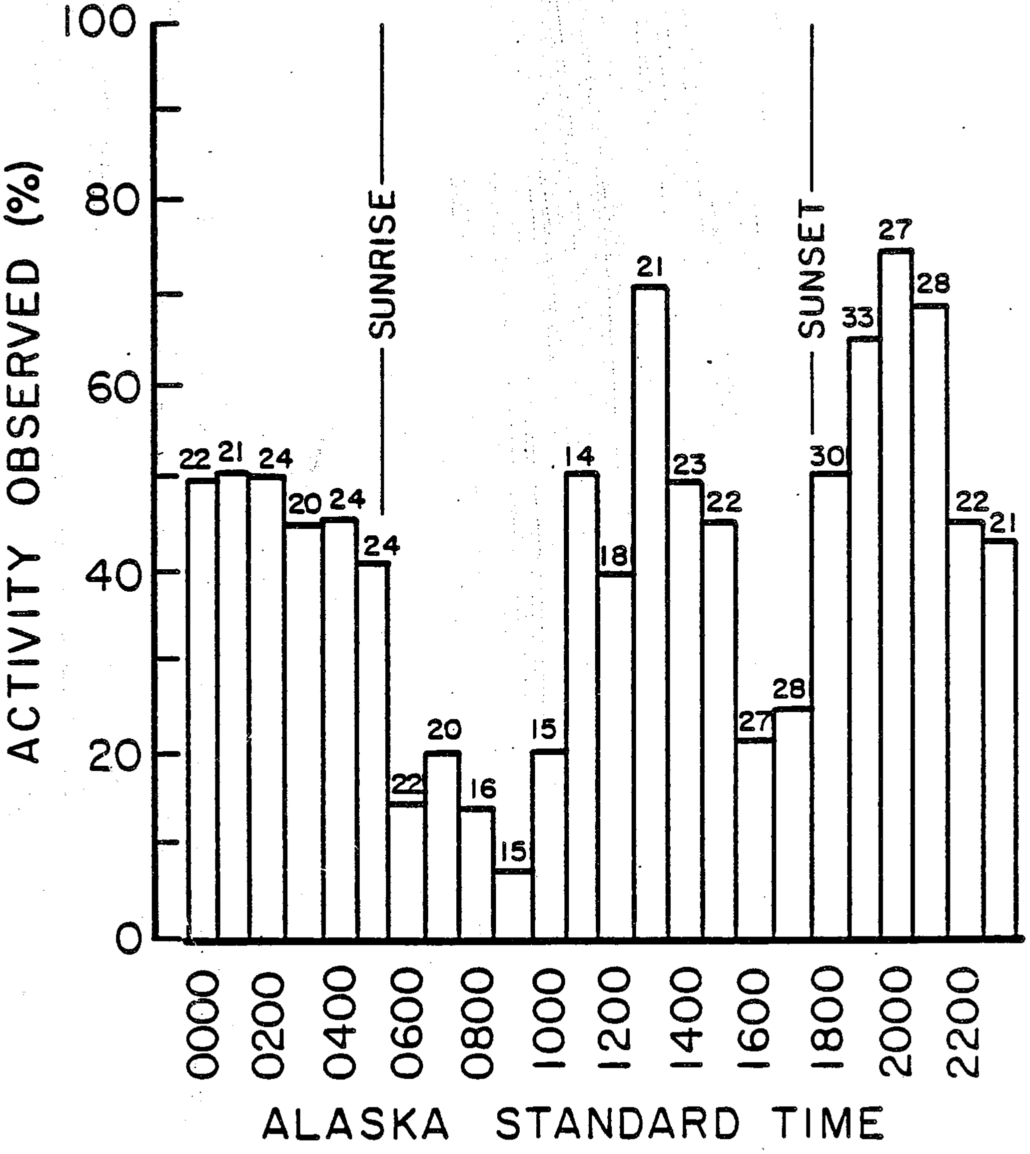

Figure 30. Diel activity pattern of marten number 515 in spring 1981.

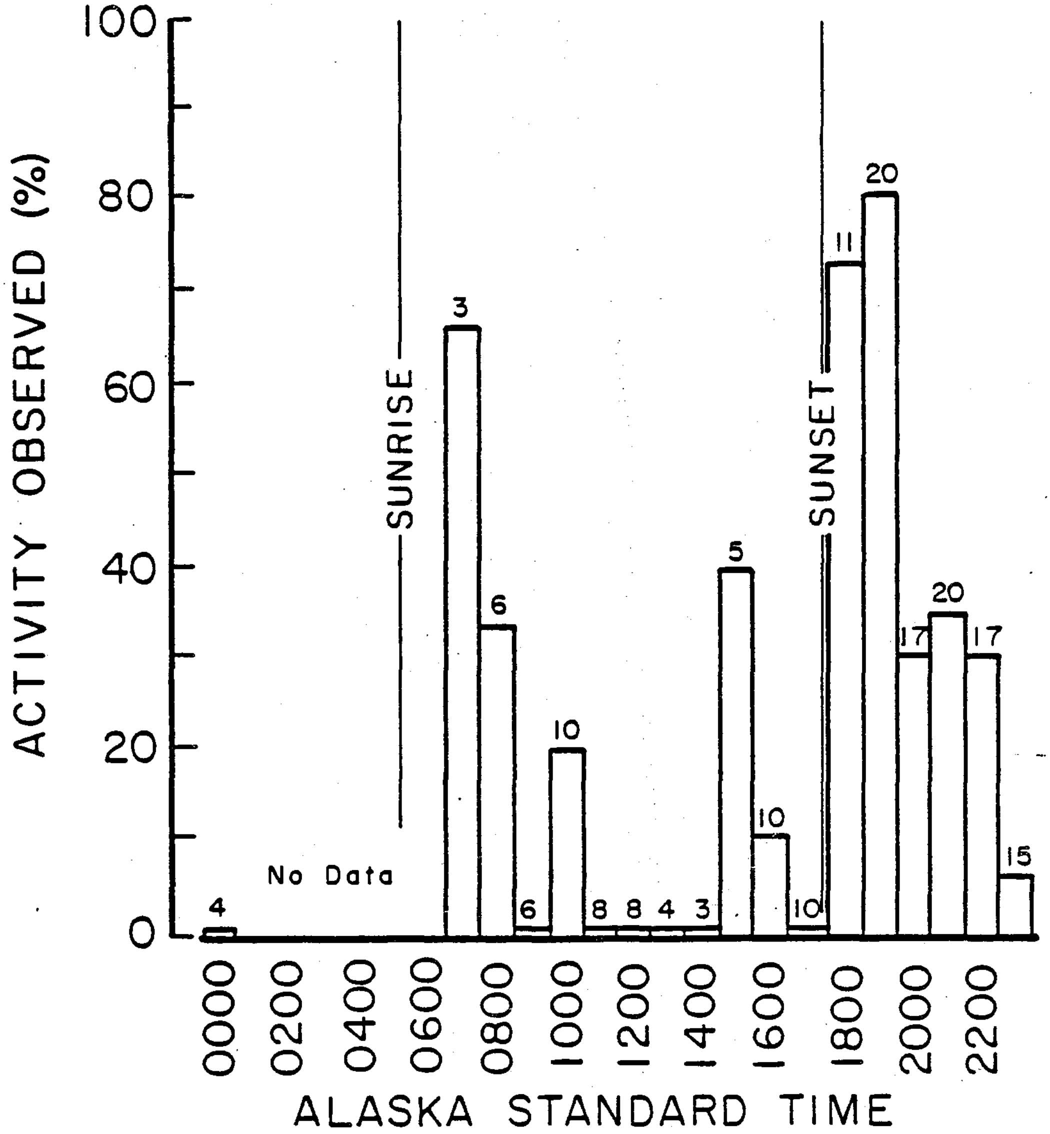

Figure 31. Diel activity pattern of marten number 128 in spring 1981.

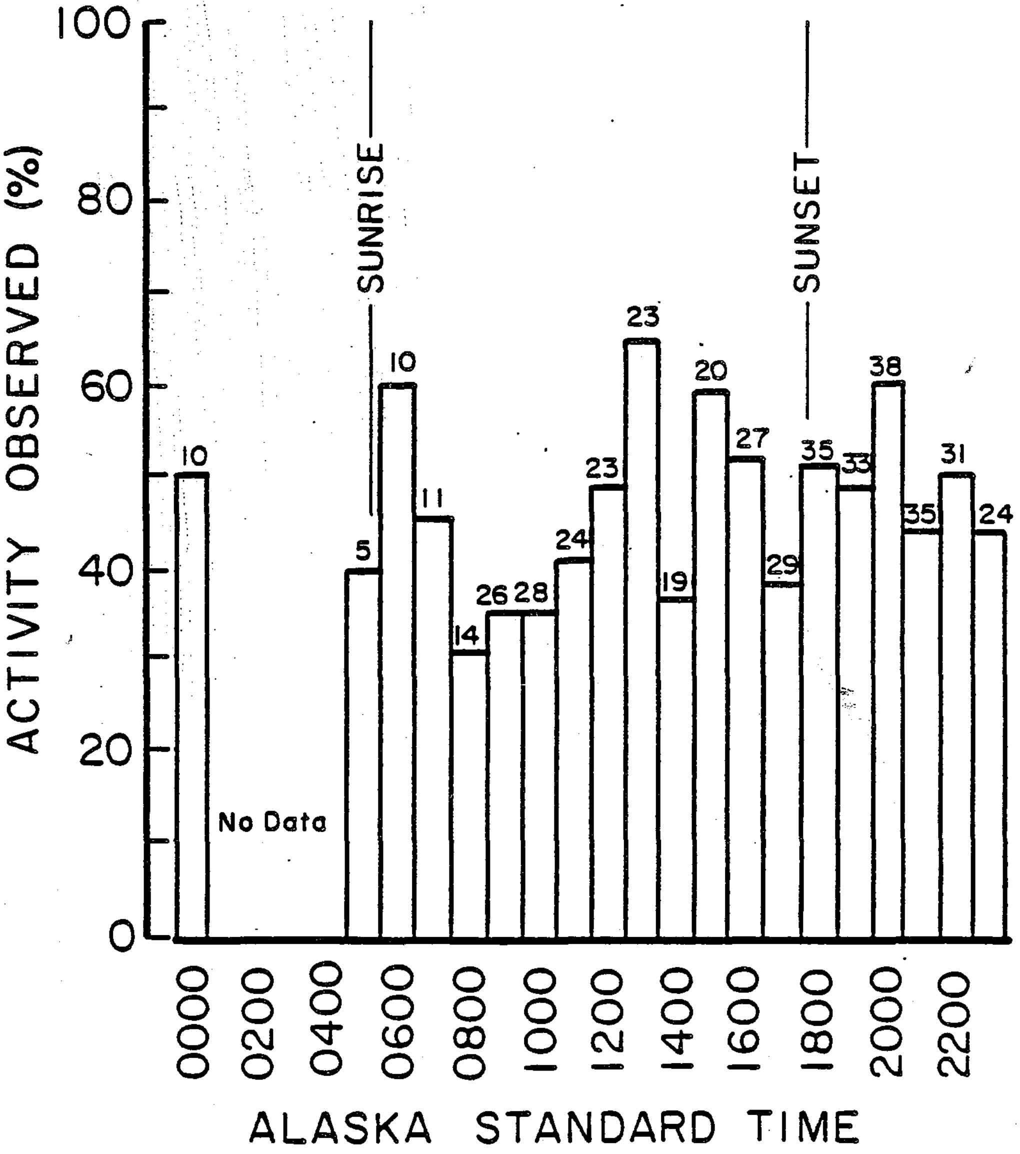

Figure 32. Diel activity pattern of marten number 514 in spring 1981.