

Summer and Winter Diets of Wolverines, *Gulo gulo*, in Arctic Alaska

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The diet of Wolverines (*Gulo gulo*) in arctic Alaska reflected annual and seasonal changes in food availability. The summer diet was more varied and contained more freshly killed prey items than the winter diet. Arctic Ground Squirrels (*Spermophilus parryi*) were the most frequent item in the summer diet. During winter, Wolverines relied heavily on scavenging to obtain food. The remains of cached Arctic Ground Squirrels were an important part of the winter diet, but remnants of Caribou (*Rangifer tarandus*) carcasses were probably critical to the survival of Wolverines overwintering in the study area. No fresh Caribou carcasses were available during winter 1979-80 and, although Wolverines were able to subsist on Caribou bone and hide during midwinter, nutrition apparently was not adequate for successful reproduction the following spring.

Key Words: Wolverine, *Gulo gulo*, Arctic Ground Squirrel, *Spermophilus parryi*, Caribou, *Rangifer tarandus*, food habits, arctic, Alaska.

The objective of the study was to determine summer and winter food habits of Wolverines (*Gulo gulo*) in an area with no wintering populations of large herbivores. Wolverines are generally believed to eat a variety of foods in summer including carrion, birds' eggs, insects, and berries, but few studies of summer foods of free-ranging Wolverines have been conducted (Krott 1959; Gardner 1985). In all studies reporting on winter food habits, wintering populations of large herbivores have been the most important food item (Pulliainen 1963; Makridin 1964; Haglund 1966; Myrberget et al. 1969; Rausch and Pearson 1972; Myhre and Myrberget 1975; Hornocker and Hash 1981; Gardner 1985). Wolverines have been known to kill prey as large as Moose (*Alces alces*) (Haglund 1974), but most investigators agree that larger mammals in the Wolverine's diet are usually obtained as carrion. All the studies of Wolverine food habits cited above were conducted in forested areas which had some alpine habitat.

Study Area

The study area was located in northwestern Alaska along the upper portions of the Utukok and Kokolik rivers (between 68°30' and 69°N and 160°30' and 162°30'W). The area is treeless, the vegetation characterized by tussock tundra, dry upland meadows, cutbank and floodplain vegetation, and talus and outcrop vegetation (Spetzman 1959). Caribou (*Rangifer tarandus*) are seasonally abundant in the study area from late May until the end of September. Essentially no Caribou have wintered in the area in recent years. Moose occur only

occasionally, rarely in winter. Besides Wolverines, mammalian carnivores include the Grizzly Bear (*Ursus arctos*), Wolf (*Canis lupus*), Red Fox (*Vulpes vulpes*), Arctic Fox (*Alopex lagopus*), Short-tailed Weasel (*Mustela erminea*), and Least Weasel (*Mustela nivalis*). Smaller mammals that occur in the study area include the Hoary Marmot (*Marmota caligata*), Arctic Ground Squirrel (*Spermophilus parryi*), lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*), voles (*Microtus oeconomus*, *Microtus miurus*, *Clethrionomys rutilus*), and shrews (*Sorex* spp.). Depending on habitat type, from 20 to 50 species of birds have been reported to breed in areas adjacent to the study area (Irving and Paneak 1954; Kessel and Cade 1958; Maher 1959).

Methods

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

Scat analysis was the main method of determining winter (September-April) food habits. Scats were collected along Wolverine trails from September

through March and from natal den sites used in March and April. Scats were dried, broken apart, separated into categories, and each category weighed. The categories were Caribou, Red Fox, Arctic Ground Squirrel, other small mammals (as a group), birds (including feathers and eggshells), and soil. Soil was a major component of some scats; these were broken into sieves and washed to separate food remains from soil.

Scats collected along winter trails were analyzed by three time periods: early winter (September–November), midwinter (December–February), and late winter (March–April). Food categories were expressed as a frequency of occurrence and as a proportion of the total weight of all food remains (percentage dry weight).

Scats collected at dens or rendezvous sites were analyzed as a group because they were deposited in large piles and the date of deposition was unknown. Therefore, only percentage dry weight over the entire winter was calculated for these scats. The percentage dry weight data were compared among collection sites and among years.

Frequency of occurrence of soil in scats was determined by dividing the number of scats containing soil by the total number of scats collected along winter trails for each winter period. The percentage dry weight was determined by dividing the total weight of the soil by the total weight of all scat material collected during each winter period and at the rendezvous sites.

Results and Discussion

Analysis of Food Habits

Wolverines were observed capturing, carrying, caching, or eating 48 food items during 362 five-minute observation periods in summer (Table 1). The first five minutes of flight time over the Wolverines was considered a sampling unit. There was only one food item per sampling unit, except for one case when

a Wolverine captured two Arctic Ground Squirrels within the same five-minute period. Food items were not identified on 15 occasions and were visually identified or determined by the method of capture on 33 occasions. Of the identified food items, 58% were Arctic Ground Squirrels, 18% were other small mammals, and 18% were Caribou.

These results and other observations suggest that diet was more varied in May and June than in August. Evidence found at a rendezvous site used by an adult female Wolverine (F7) and her two kits on 2 June 1979 indicated that the Wolverines had been eating Arctic Ground Squirrels, Willow Ptarmigan (*Lagopus lagopus*) eggs, and small mammals. During 149 minutes of hunting behavior on 4 June 1979, F7 made 34 searches for food items in tussock tundra. She pounced on seven occasions, probably for small mammals but possibly for ptarmigan chicks, and was successful at least twice. In addition, she captured and cached an adult ptarmigan, found or caught a squirrel, and on two occasions appeared to find and eat eggs.

In late summer, the radio-collared Wolverines increased their time spent in hunting squirrels. The number of five-minute sampling units in which squirrel hunting was observed (Table 1) was significantly higher in August than in the other summer months (May–July) combined ($\chi^2 = 5.11$, $0.025 > P > 0.01$, $df = 1$), and Wolverine hunting and feeding activity involved squirrels much more frequently than all other food items combined ($\chi^2 = 12.27$, $P < 0.001$, $df = 1$).

For winter food habits analysis, 82 scats were collected along Wolverine trails, most during November, February, and March 1979–80. Caribou and Arctic Ground Squirrels remains occurred in 37% and 40% of the scats, respectively, and made up 35% and 32% of the total scat weight, respectively. The remains of lemmings, voles, and shrews as a group occurred in 30% of the scats but made up only 6% of

TABLE 1. Number of times feeding behavior (capturing, carrying, caching, or eating food) by Wolverines was observed from the air during 362 five-minute observation periods during summer in northwestern Alaska, 1978–1981.

Food Item	May	June	July	August	Total
Caribou	1	4	1		6
Marmot		1			1
Arctic Ground Squirrels	3	1	4	11	19
Other Small Mammals	3	3			6
Willow Ptarmigan		1			1
Total Identified	7	10	5	11	33
Total Not Identified	3	2	1	9	15
Grand Total	10	12	6	20	48
5-min Observation Periods	95	122	50	95	362

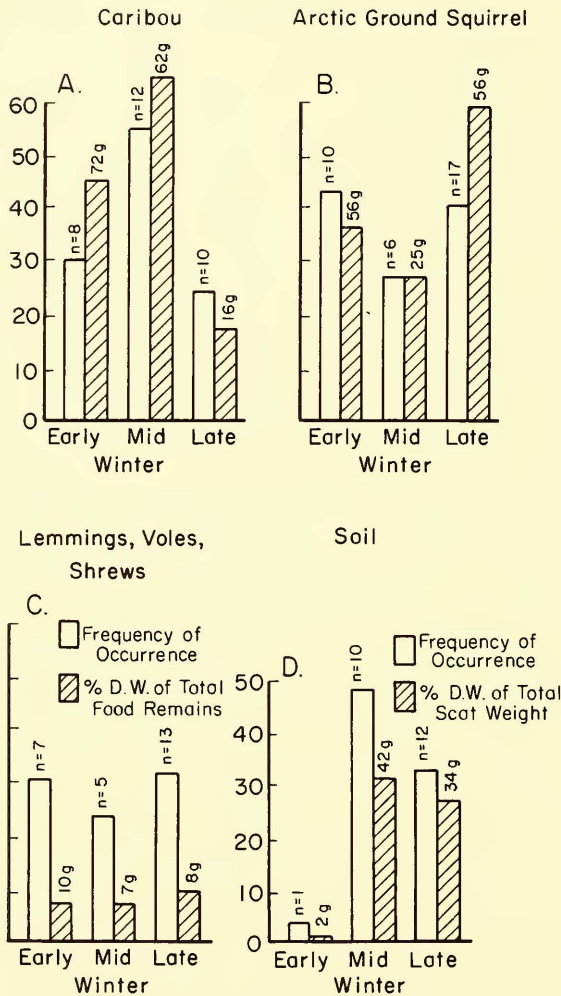


FIGURE 1. Frequency of occurrence and percentage dry weight (D.W.) of the three most common food categories and of soil ingested by Wolverines in arctic Alaska during three periods in winter.

the total scat weight. No attempt was made to sort lemming, vole, and shrew remains into separate categories or to identify them by species because of their low prevalence in the scats. The remains of birds and/or eggs occurred in only 11% of the scats and made up only 3% of the total scat weight. There were 13 g (3%) of unidentified food remains and 78 g (18%) of soil. Caribou remains were more frequent in scats from midwinter than from early or later winter ($\chi^2 = 6.26$, $0.02 < P < 0.05$, $df = 2$), but the frequency of occurrence of squirrel and other small mammal

remains showed no significant change during winter (Figure 1).

The percentage dry weight of Caribou and squirrel remains showed seasonal changes that corresponded to the changes in frequency of occurrence (Figure 1). This correspondence resulted from the fact that when the remains of Caribou or squirrels occurred in a scat, each made up 80–100% of the total weight of all food remains in the scat in 80% and 85% of the scats, respectively. When other small mammal remains occurred in the scats, they made up 80–100% of the total food remains in the scat only 52% of the time. Note that percentage dry weight for Caribou is higher than frequency of occurrence in early winter and in midwinter but not in late winter; percentage dry weight for Arctic Ground Squirrels is higher than frequency of occurrence only in late winter (Figure 1). In early winter and in midwinter, 62% of the heaviest scats (i.e., weighing more than the average for that period) contained Caribou and most contained 80–100% Caribou. In late winter, 70% of the heaviest scats contained squirrels. None of the heaviest scats in any period contained the remains of other small mammals as the primary food category. These results suggest that the importance of Caribou in the Wolverine diet declined in late winter, whereas the importance of squirrel increased.

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

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

If it can be assumed that soil is passed through the intestinal tract at the same rate as Caribou and squirrel remains, then it appears that soil is primarily ingested while Wolverines are eating squirrels and that soil is more often associated with squirrels eaten in midwinter than in early or late winter. This is further supported by the proportionally lower percentage dry weight in relation to frequency of occurrence for soil in midwinter (Figure 1). Because squirrels occur less frequently in scats in midwinter, soil by weight should be proportionally less.

I believe the relationship of soil and squirrel remains is due to the use of cached squirrels, particularly in midwinter. Although fewer squirrels may be ingested in midwinter, those that are eaten are almost certainly cached squirrels. While we were radio-tracking Wolverines in the winter, it was common to find a Wolverine partially or wholly hidden in a freshly excavated hole in the snow with soil and vegetation spread around on the surface of the snow. In one instance, an adult male Wolverine was half submerged in the snow, his tail and haunches protruding above the surface. At my approach, the Wolverine ran from the hole where he had been feeding on a squirrel frozen into the soil. Half of the squirrel's body was still in the hole. The carcass was shredded and thawed where the Wolverine had been gnawing. It appeared as though the sides of the hole had also been gnawed, suggesting that this is how much of the soil in the scats is ingested.

Some of the squirrels in the winter diet may be dug out of hibernation while alive or after dying due to starvation or exposure. On 24 March 1980 I found a hole which a Wolverine had excavated through 15 cm of snow and 25 cm of soil in upland tundra with a slope of less than 10°. At the bottom of the hole was an enlarged cavity with squirrel hairs in it. The symmetrically round hole leading to the cavity was 17 cm in diameter.

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

Scats collected at natal den sites represent food consumed primarily in March and April (late winter). Of 5864 g of scats collected at natal den sites (representing at least 300 individual scats based on the average weight of scats collected along Wolverine trails), Caribou and squirrels accounted for 92% of the dry weight of food items in the scats. The percentage of Caribou and squirrels differed among years and among individuals (Figure 2). Scats collected at what was believed to be the location of F7's 1978 den

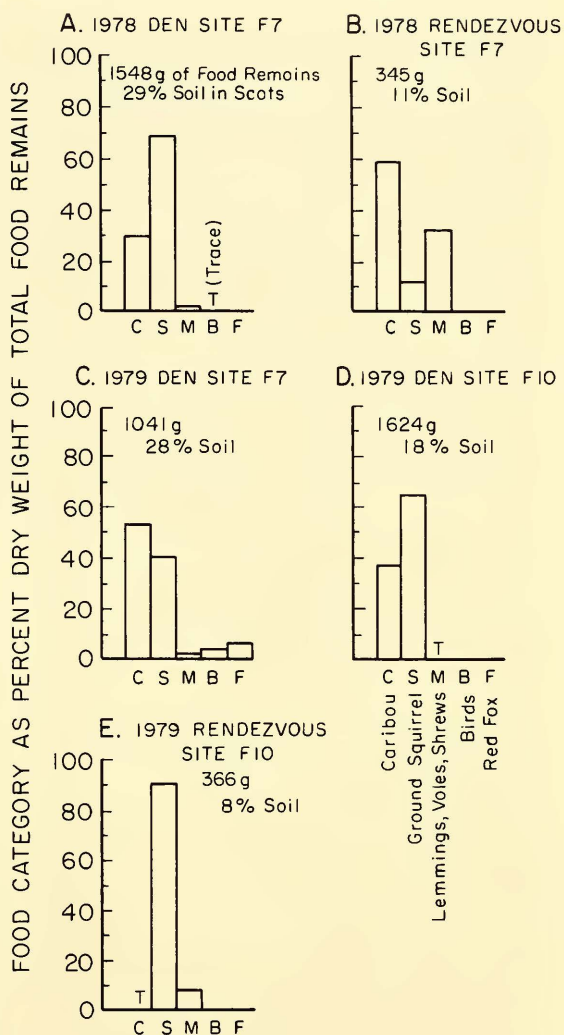


FIGURE 2. Percentage dry weight of food remains collected at Wolverine natal den sites and rendezvous sites in arctic Alaska and the percentage of the total scat weight made up of soil.

contained 69% squirrel and 29% Caribou remains by percentage dry weight (Figure 2). From scats collected at F7's 1979 den, the percentage of squirrel remains was only 40% and Caribou was 52%. Scats were not collected from F7's 1978 den until summer 1979 when the den site was discovered by a field assistant on 11 June 1979. The den site was recognizable by the piles of scats and broken, matted vegetation where the tunnels and beds had been located. F7 and her 4-month-old kit had been captured in June 1978 in a

nearby drainage at a rendezvous site. The high percentage of squirrel remains in the scats collected at the 1978 den could have been due to the fact that the den site itself had been used periodically as a rendezvous site during May and June 1978. F7's 1979 den was used only until 29 April, so the scats from this den represent food eaten in March and April 1979, which is the denning period.

Scats collected at F10's 1979 den contained 63% squirrel remains and only 37% Caribou remains (Figure 2). A relatively high percentage of squirrel remains by weight was found at the den, although F10 was known to have abandoned the den in late April 1979. The soil associated with food remains from this den was 10% less than soil in scats collected at F7's 1978 and 1979 dens. This difference in soil content suggests that more of the squirrel remains at F10's den were from fresh kills and that fresh Arctic Ground Squirrels may have been more available to F10 than to F7 in late winter. F10's home range contained more suitable squirrel habitat, with higher terrain and numerous south-facing slopes.

Scats collected at rendezvous sites were deposited primarily during May and June. At a rendezvous site used from 12 to 20 May 1979 by female Wolverine F10 and her two kits, a much higher percentage of squirrel remains (89% of the dry weight of all food remains) was found than at any other scat collection site (Figure 2). Soil in the scats accounted for only 8% of the total scat weight.

Scats from a rendezvous site used by F7 and one kit were collected on 29 June 1978, at which time the two Wolverines were still using the site. The date of the initial establishment of the site is unknown. Most of the scats probably represent food items eaten in May and June. The skeleton of a Caribou was found about 600 m from the site. It was probably the remains of a Caribou which had died during the spring migration in May or June. As might be expected, Caribou ranked high (58%) among food remains in the scats from this site (Figure 2). Lemming, vole, and shrew remains were high (23% by weight) relative to the other scat collections analyzed.

Seasonal Changes in Food Availability

Wolverines were opportunistic in their food habits, responding to temporarily abundant or easily procurable food. Their diet reflected annual and seasonal changes in food availability. Late winter marked the beginning of a plentiful and varied food supply for Wolverines in the study area. Arctic Ground Squirrels emerged from hibernation from late March to mid-May. The earliest date of emergence observed during the study was 9 March 1980, although emerging squirrels were usually not a common sight until late March or early April. Immediately following emergence from hibernation,

squirrels established breeding territories and were aggressive towards each other. Green (1977) reported that agonistic interactions peak 2 to 3 weeks after the first squirrels emerge and that squirrels are particularly vulnerable to predation at this time. It is therefore not surprising that a relatively high proportion of squirrel remains occurred in scats collected at the natal den sites and along tracking routes in March and April. Wolverines were still eating cached squirrels in March; however, the decrease in the proportion of soil in scats from January and February to March indicates that the Wolverines began to consume freshly killed squirrels in March.

Other food items began to increase in the diet in May. Lemming, vole, and shrew remains in scats and observations of Wolverines capturing or eating these small mammals were highest in May and June, a time when small rodents become vulnerable to predation as their nest sites and runways are exposed by melting snow. Birds and eggs were more available in June, the peak of the nesting season. The spring migration of Caribou through the study area usually began in late May, and calving peaked between 2 and 10 June. Adult Caribou dying during migration or calves dying at birth and shortly afterward provided carrion for Wolverines at this time of year.

As the summer progressed, squirrels made up an increasing proportion of the diet as other food items became less available and squirrels again became vulnerable to predation due to dispersal. Dispersal peaked in August. At this time, squirrels were the most important food item in the Wolverine's diet.

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

By early October, the availability of food for Wolverines began to decline. Sightings and fresh sign of Caribou and squirrels were absent by the end of November. The number of squirrels in the diet was reduced by midwinter and most of those that were eaten were probably obtained from caches made in summer and fall.

Caribou remains were important to Wolverines in the study area during midwinter 1979-80. Caribou remains eaten by Wolverines that winter were mostly the remnants of carcasses buried by scavengers or bone and hide lying on the tundra. Several winter scats (10%) were found that consisted entirely of Caribou bone fragments bound by a white powdery matrix. Sometimes the only excrements found along winter trails of Wolverines were small amounts of chalky liquid. Kruuk (1972) analyzed the fine white powder in Spotted Hyena (*Crocuta crocuta*) droppings and found that it consisted of

$\text{Ca}_3(\text{PO}_4)_2 \cdot 1.5\text{Ca}(\text{OH})_2$, which is the formula for inorganic matter in bone. He concluded that bone is digested by the hyena and only the inorganic matter is excreted. Bone may contain up to 40% organic matter, mostly collagen. Kruuk postulated that hyenas are able to use all the organic matter present in bones, not just the marrow. Van Zyll de Jong (1975) suggested that Wolverines are also morphologically and behaviorally adapted to a scavenging lifestyle.

Caribou composed a major portion of the Wolverine's winter diet despite the fact that Caribou generally do not occur in the study area during most of the winter. In this area, where Caribou occur in large numbers only during the summer, Wolverines were able to subsist during winter 1979–80 on Caribou remains comprising mainly bone and hide, occasionally supplementing their diet with squirrels gnawed from the frozen tundra. The Wolverine's ability to survive the most severe time of the year on such a meager diet attests to its efficiency as a scavenger.

There is evidence that such a restricted diet in winter 1979–80, however, may have had some effect on Wolverine reproduction in the study area. One adult female Wolverine (F19) was considered to be malnourished that winter, perhaps even on the verge of starvation, based on her poor physical condition and the unusual number of visits she made to baited live traps (Magoun 1985). In addition, spring 1980 was the only spring in four years (1978–81) in which one adult female Wolverine (F7) failed to raise young. Three other radio-collared adult females also failed to raise young that summer. Although the Wolverines were able to survive the winter, their reproductive potential may have been limited by food shortages (Magoun 1985). Furthermore, the movements of an adult female (F24) in winter 1981–82 indicated that Wolverines will leave an established home range when food is scarce (Magoun 1985).

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