

Diet of wolverines (*Gulo gulo*) in the western Brooks Range, Alaska

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Abstract

Migratory caribou herds are an important component of the North American tundra. We investigated the wolverine (*Gulo gulo*) diet in the migratory range of the Western Arctic Caribou Herd in north-western Alaska. Within this area, caribou are absent or occur at low densities for large parts of the year, and thus show a strong seasonality in abundance. Analyses of stomach and colon contents suggested that wolverines primarily consumed caribou during the winter, and that the dietary dependence was related more to caribou mortality than to caribou abundance in the area. We also found indications that wolverines may switch between moose and caribou during periods of low caribou abundance, but that such a switch did not affect wolverine body condition. Our results thus support previous observations that wolverines primarily consume ungulates. However, a better knowledge of how alternative food sources are utilized will be necessary to predict the dietary and demographic responses of wolverines to variations in caribou abundance. We also suggest that further efforts should be made to investigate the effects of other ungulate-dependent predators on wolverine feeding ecology, because such predators may function both as competitors and as suppliers of carrion for scavenging.

The wolverine (*Gulo gulo*) is a terrestrial mustelid that primarily inhabits tundra and taiga in Palearctic and Nearctic regions (Wilson 1982). Small and fragmented populations in both North America and Scandinavia have recently attracted attention to the management and research of the species (Landa et al. 2000; Rowland et al. 2003; Flagstad et al. 2004; Ruggiero et al. 2007; Dalerum et al. 2008). Although relatively small, weighing from 10 to 20 kg (Pasitschniak-Arts & Larivière 1995), the wolverine has been characterized as an ungulate-dependent carnivore. Several studies have emphasized the importance of large ungulates for wolverines during winter, primarily as carrion (Haglund 1965; Rausch & Pearson 1972; Gardner 1985; Magoun 1987; Persson 2003; Lofroth et al. 2007), but our knowledge of the utilization of alternative prey, particularly during summer, is not as well understood (Banci 1987; Magoun 1987; Landa et al. 1997).

Throughout Arctic North America, large herds of caribou (*Rangifer tarandus*) are a prominent component of

the tundra ecosystem. Many of these herds undertake large-scale seasonal migrations, resulting in drastic seasonal changes in their abundance in any one location in their range (Bergerud 1988). The Western Arctic Caribou Herd (WACH) inhabits the western Brooks Range, Alaska, and during recent years has numbered approximately 400 000 animals (Dau 2003). The WACH winters on the northern Seward Peninsula, and migrates to the northern foothills of the Brooks Range for calving during early June. During autumn and spring, the herd migrates through the western Brooks Range from the Chukchi Sea coast to as far east as the Upper Kobuk River. Such temporal fluctuations in caribou distribution may impose strong effects on the population dynamics of carnivores that depend on them as a primary food source (Taylor 1984), but our knowledge of how these herds affect resident carnivores is limited (Berger et al. 1999).

In this study, we examined the wolverine diet in relation to caribou abundance within the migratory range of the WACH, by analyses of wolverine stomach and colon

contents. We hypothesized that wolverines would behave as generalist predators in this system, and tested three predictions regarding wolverine diets: (1) caribou will be the most utilized prey by wolverines; (2) annual variations in caribou availability will be reflected in wolverine diets; and (3) annual variations in caribou availability will be reflected in wolverine body condition.

Methods and study area

Study area

The study was conducted within the Noatak and Kobuk River drainages in the western Brooks Range, Alaska ($68^{\circ}35'–65^{\circ}15'N$; $162^{\circ}55'–159^{\circ}15'W$; Fig. 1), covering an area of approximately 100 000 km². Most of the WACH pass through the study area during the spring and autumn migrations each year (Dau 2003), although the percentage of the herd that passes through varies between years. Spring migration usually occurs during April/May; autumn migration usually occurs during September/October. Caribou groups may remain in the study area even between migration periods. Other ungulates occurring in the area are Dall's sheep (*Ovis dalli*), moose (*Alces alces*) and occasionally single or small groups (less than five individuals) of muskoxen (*Ovibos moschatus*). Other potential mammalian prey species include beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), snowshoe hare (*Lepus americanus*), Arctic ground squirrels (*Spermophilus parryi*) and microtine rodents such as the red-backed vole (*Clethrionomys rutilus*) and the tundra vole (*Microtus oeconomus*). Potential avian prey species include ptarmigan (*Lagopus* sp.) and several species of migratory geese, waterfowl and small passe-

rines. Brown bears (*Ursus arctos*), wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), river otters (*Lutra canadensis*), mink (*Mustela vison*) and American martens (*Martes americana*) are common predators in the area. Sheefish (*Stenodus leucichthys nelma*), dolly varden (*Salvelinus malma malma*) and chum salmon (*Oncorhynchus keta*) spawn within the two river systems.

The topography varies from broad, flat river valleys to rugged mountainous terrain in the Baird and Schwatka mountains. Elevations range from sea level to 1200 m a.s.l. The vegetation is diverse and includes permafrost tundra, coniferous forest and vast stands of willow (*Salix* sp.), alder (*Alnus crispa*) and balsam poplar (*Populus balsamifera*) along riparian zones. Temperatures range from $-45^{\circ}C$ in winter to temperatures of $30^{\circ}C$ in summer. The annual precipitation ranges from 500 to 1500 mm, with most of it falling during July and August.

Estimates of caribou availability

We used three crude indices to estimate temporal patterns in caribou availability during the study. First, estimates of total herd size were taken from the results of aerial photographic censuses that were conducted twice during the study period (i.e., 1996 and 1999; Table 1). Second, we created a crude index of caribou presence within the study area using locations from platform transmitter terminal (PTT) satellite radio collars fitted to 66 caribou from 1995 to 2002. We delineated our study area, and counted the raw number of locations each year within these boundaries. We standardized these raw counts of locations each year by dividing them by the number of collared caribou in each year. These standardized location counts were used to estimate the annual and seasonal

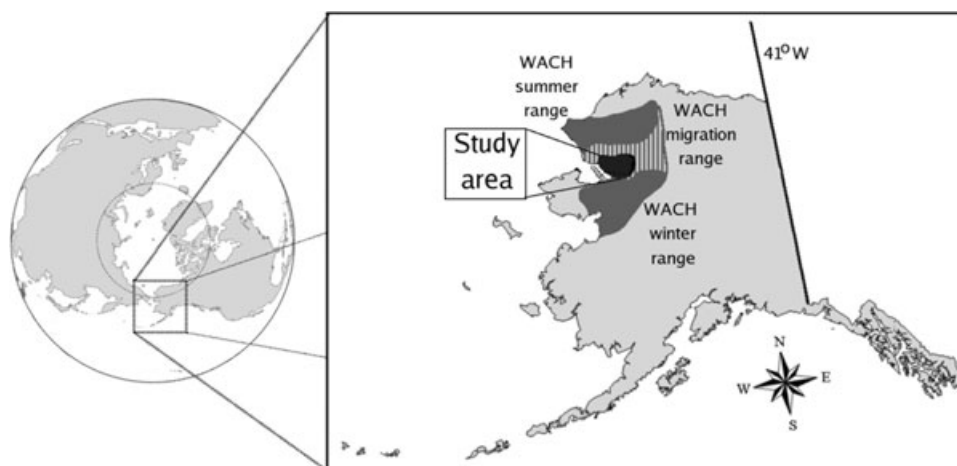


Fig. 1 Wolverine collection area and the seasonal ranges of the Western Arctic Caribou Herd (WACH; data upon which map is based is from Dau 2003) in north-western Alaska. The summer range is typically used from July to August, whereas the winter range is usually used from October to April.

Table 1 Estimates of caribou availability for the Western Arctic Caribou Herd from 1995 to 2002.

Year	Estimated herd size ^a	Mortality (%) ^b	Caribou presence ^c
1995–96	463 000	19	16.8
1996–97		15	12.25
1997–98		7	3.83
1998–99	430 000 ^d	17	13.00
1999–2000		23	6.91
2000–01		16	15.50
2001–02		15	12.06

^aHerd sizes were estimated from aerial photographic censuses conducted by the Alaska Department of Fish and Game, and are quoted from Dau (2003).

^bMortality rates were estimated from conventional VHF or platform transmitter terminal (PTT) collars (Dau 2003), and were calculated as annual mortality over “collar years” ranging from 1 October to 30 September. Values are quoted from Dau (2003).

^cCaribou presence is indexed as the number of caribou locations per animal per year within the Noatak drainage. The index values were calculated from 66 caribou fitted with PTT satellite collars by the Alaska Department of Fish and Game. We calculated the standardized number of locations per year by dividing the index values by the number of collared animals for the given year.

^dRecent data (Dau 2005) suggest that this value was an underestimation, and the most recent herd size (2003) was estimated to be 490 000 animals.

Table 2 Number of collected wolverine carcasses, number of stomachs analysed, number of colons analysed and number of animals with an estimated body condition index.

Winter	Carcasses	Stomachs	Colon	Renal fat
1995–96	2	2	2	2
1996–97	58	41	42	31
1997–98	7	6	1	4
1998–99	14	11	2	8
1999–2000	29	22	15	25
2000–01	24	20	16	11
2001–02	13			
Total	147	102	78	81

patterns of caribou presence in the study area. Finally, we used average annual caribou mortality rates estimated from conventional VHF and PTT satellite radio collars (the numbers of collars per year ranged from 93 to 108) (Dau 2003). Annual mortality was estimated for “collar years”, defined from 1 October to 30 September. All data on caribou abundance were collected by the Alaska Department of Fish and Game (Western Arctic Caribou Herd Working Group 2003).

Wolverine specimen collection

We purchased 148 wolverine carcasses from local hunters within the migratory range of the WACH between 1996 and 2002 (Table 2; see also Dalerum et al. 2007). We collected stomach contents from 102, and colon contents from 78, of these animals. In the remaining animals the stomach and/or colon was empty. We also collected both

kidneys, including the surrounding fat, from 81 animals. We recorded the approximate date and location of harvest and harvest method for each carcass, if this information was available. Forty of the animals were trapped and 21 were shot. We did not have reliable information of the hunting method for the remaining animals. Most animals were from the lower Kobuk and Noatak rivers. Hunters harvested wolverines from November through to April, but most wolverines were harvested during February and March.

Estimates of wolverine body condition

We used renal fat deposition as an index of animal body condition (Riney 1955). We extracted all adipose tissue surrounding both kidneys. Tissue was weighed and then dried at 100°C for up to 3 days. We derived the dry weight, and calculated the percentage of fat in the adipose tissue by dividing the dry weight by the wet weight.

Stomach and colon content analysis

We washed the stomach and colon samples over a sieve with a mesh size of 1 mm, and dried the remaining material for 24–48 h at 80°C. We weighed the dried material to the nearest gram. We separated and individually weighed prey remains when possible. When separation of prey remains was not possible, we visually estimated the percentage volume for each prey category, and multiplied that by the total weight of the sample. We identified prey remains using reference materials and published guides (Day 1966; Brom 1986; Teerink 1991). We pooled remains identified as red fox, wolverine, Dall’s sheep and Arctic ground squirrel into an “other mammal” category. Unidentified mammal remains were categorized as “unknown mammal”. We labelled items not fitting into any other category as “miscellaneous” (e.g., primarily soil).

Statistical analysis

We analysed the diet composition from stomach and colon contents using a generalized linear model with a log link and a Poisson-distributed error structure (Crawley 2002). In the model, we used raw frequencies of occurrence as the response variable, and stomach/colon, year of harvest, sex of harvested wolverine and prey type as independent factors. We tested if the harvest method (i.e., shot or trapped) affected the likelihood of a stomach containing caribou or moose using logistic regressions, with the presence or absence of caribou and moose, respectively, treated as response variables, and with the harvest method treated as a factor.

We used weighted linear regressions to explore the wolverine dietary response to fluctuating caribou availability, as well as the effect of diet and caribou abundance and mortality on wolverine body condition. We used yearly averages of the percentage weight of dry stomach content of caribou and moose as response variables, and yearly indices of caribou presence and caribou mortality as predictors, to explore the dietary effects of caribou abundance and mortality. We used annual averages in wolverine renal fat as response variables, and abundance and mortality estimates of caribou as predictors, to test for effects of caribou abundance and mortality on wolverine body condition. We similarly used annual averages in wolverine renal fat as response variables, and the percentage dry weight of caribou and moose in stomachs, to test for the effect of diet on wolverine body condition. In the analyses, we did not include data from the years 1995–96 and 2001–02, because only two stomachs were analysed in 1995–96 and no stomachs were analysed in 2001–02. We further fitted the regressions using weighted least squares using the number of stomachs analysed each year as the weighting factor to account for unequal sample sizes between years.

Average values are given with standard errors. Statistical significance was set at $P = 0.05$, and all tests were two-tailed. Analyses were conducted with the statistical software R (release 2.3.0, for Linux; see <http://www.r-project.org>).

Results

Caribou abundance

The WACH ranged from 430 000 to 460 000 animals between the photographic census counts of 1996 and 1999. There was both annual and seasonal variation in caribou presence within the study area. The years 1997–98 and 1999–2000 had a lower caribou presence than the other years (Table 1). There was strong seasonal variation in caribou presence, with caribou generally being more abundant in spring than during autumn (Fig. 2). The estimated annual adult mortality within the WACH ranged from 7 to 23% over the study period (Table 1). However, we have no spatial resolution of where this mortality occurred within the herd's range.

Wolverine diet

Caribou were the most utilized food by wolverines during winter. On average, caribou constituted 58% of the dry weight of wolverine stomach contents, and 75% of the dry weight of colon contents (Fig. 3a, b). Caribou constituted 33% of the observed prey occurrences in stomachs,

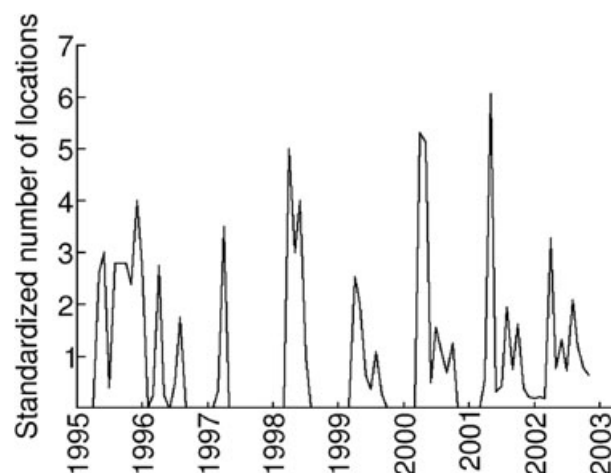


Fig. 2 Presence of caribou from the Western Arctic Caribou Herd (WACH) within the Western Arctic National Parklands, expressed as the average number of relocations per month standardized by the number of animals carrying a collar within a given year. The data are based on relocations from 66 platform transmitter terminal (PTT) satellite collars fitted to caribou within the WACH from 1995 to 2002. The satellite data were provided by the Alaska Department of Fish and Game. The tick marks for each year represents 1 January.

and 42% in colons (Fig. 3c, d). Moose were the second most important prey item, constituting 24% of the dry weight of stomach contents, but only 1.5% of the dry weight of colon contents. Other prey identified in small quantities included microtine rodents, Arctic ground squirrels, porcupines, wolverines, red fox, sheep and ptarmigan. Based on the frequency of occurrence, the diet composition was significantly different between stomach and colon contents ($\chi^2 = 11.66$, $df = 5$, $P = 0.04$; Fig. 3c, d). Wolverine diet composition also varied between years ($\chi^2 = 48.94$, $df = 25$, $P = 0.003$; Fig. 3). However, the proportion of the diet that consisted of caribou and moose remained relatively constant, from 85 to 100% of the dry weight, in all years except 2000–01, suggesting that wolverines switched between these two main prey items. During 2000–01, the stomach contents contained a large portion of muskoxen and Dall's sheep. There was no difference in diet composition between males and females ($\chi^2 = 2.21$, $df = 5$, $P = 0.81$), nor did the harvest method affect the likelihood of a stomach containing caribou ($\chi^2 = 0.13$, $df = 1$, $P = 0.72$) or moose ($\chi^2 = 2.59$, $df = 1$, $P = 0.11$).

There were no significant relationships between caribou presence and either dietary importance of caribou (% dry weight caribou = $69.7 - 1.01 \times$ caribou presence, $F_{1,3} = 0.31$, $r^2 = 0.09$, $P = 0.617$) or moose (% dry weight moose = $45.89 - 1.95 \times$ caribou presence, $F_{1,3} = 1.24$, $r^2 = 0.29$, $P = 0.347$; Fig. 4a, c). Caribou mortality was, however, significantly related to the

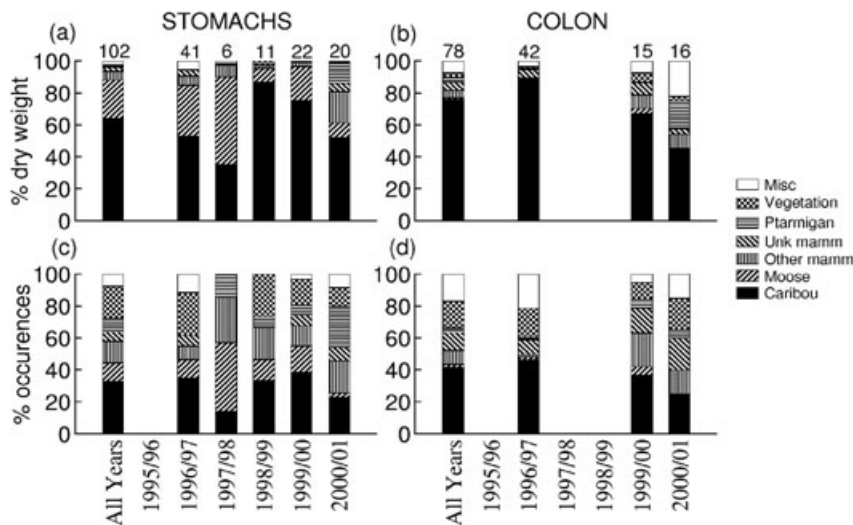


Fig. 3 Wolverine winter diet during the study: (a, b) presented as the percentage of the dry weight of stomach ($N = 102$) and colon ($N = 78$) contents; (c, d) presented as the percentage of occurrence. The number of stomach and colons analysed are indicated at the top of each bar.

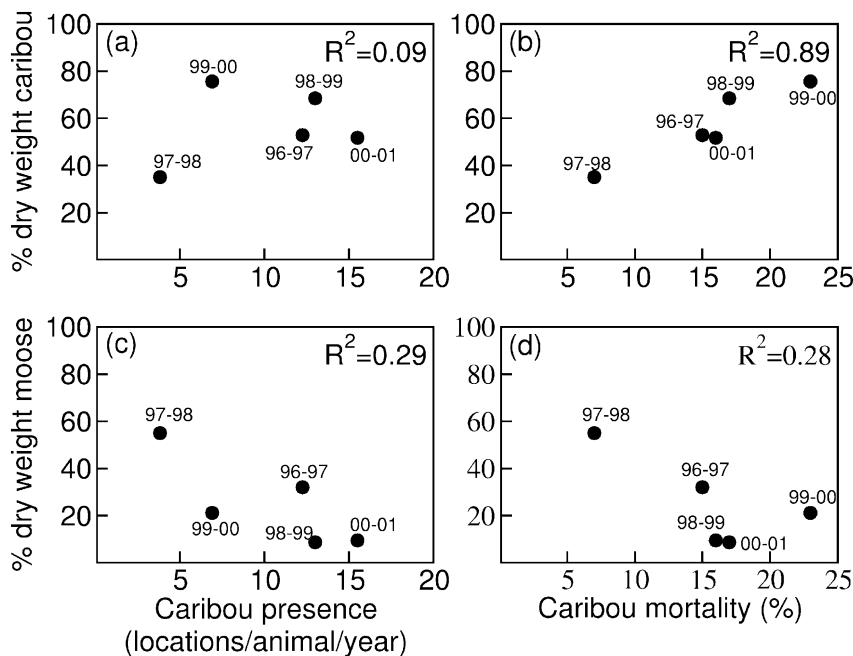


Fig. 4 Relationships between the dietary importance of (a, b) caribou and (c, d) moose expressed as the percentage of dry stomach content, and annual presence and mortality of caribou from 1996 to 2000. The relationship between caribou mortality and the dietary importance of caribou are significant ($P = 0.017$), but not between caribou mortality and the dietary importance of moose ($P = 0.356$), nor between caribou presence and the dietary importance of caribou ($P = 0.617$) and moose ($P = 0.347$).

dietary importance of caribou (% dry weight caribou = $12.96 + 2.71 \times$ caribou mortality, $F_{1,3} = 23.4$, $r^2 = 0.89$, $P = 0.017$), but not to the dietary importance of moose (% dry weight moose = $51.67 - 1.67 \times$ caribou mortality, $F_{1,3} = 1.99$, $r^2 = 0.28$, $P = 0.356$; Fig. 4b, d).

Renal fat indices were not related to caribou abundance (% renal fat = $0.56 - 0.01 \times$ caribou presence, $r^2 = 0.17$, $F_{1,3} = 0.621$, $P = 0.488$), caribou mortality (% renal fat = $0.82 - 0.03 \times$ caribou mortality, $r^2 = 0.45$, $F_{1,3} = 0.491$, $P = 0.213$), dietary importance of caribou (% renal fat = $0.82 - 0.03 \times$ % weight caribou, $r^2 = 0.18$, $F_{1,3} =$

0.670 , $P = 0.473$), or the dietary importance of moose (% renal fat = $0.82 - 0.03 \times$ % weight moose, $r^2 > 0.01$, $F_{1,3} > 0.001$, $P = 0.972$).

Discussion

Dietary importance of caribou

Our results support our first prediction, that caribou would be the most utilized food in our study area. Within the summer range of the WACH, where caribou

are absent during winter, Magoun (1987) showed that wolverines still relied heavily on caribou for their winter diet. Such similarity in dietary dependence of caribou for both the migratory and the summer ranges of the WACH emphasizes the strong importance of caribou for wolverine populations throughout the herd's range. Similarly, Ballard et al. (1997) showed that wolves within the migratory range of the WACH fed extensively on caribou. However, wolves persisted at lower densities than predicted by the average annual ungulate abundance, which indicates that seasons with low caribou abundance may function as bottlenecks for large carnivores in these regions. We therefore stress that caribou should be regarded as a foundation species (*sensu* Soule et al. 2003) for carnivores in the North American Arctic.

Although wolverines have been observed to kill large ungulates (Haglund 1965; Pulliainen 1968; Magoun 1985), they probably rely substantially on scavenging (Banci 1994). Scavenging by wolverines was supported by our results, where we found a stronger relationship between diet and caribou mortality than between diet and caribou presence in the study area. This scavenging behaviour suggests that factors influencing caribou mortality, such as predation by wolves and grizzly bears, may have important implications for wolverine ecology. We therefore suggest that further efforts should be made to explore the effect of sympatric ungulate predators on wolverines, particularly because these may function both as competitors and as suppliers of carrion.

We found differences in the diet compositions estimated from stomach and colon contents, most notably a larger proportion of caribou in the colon than in the stomach samples. The difference between colon and stomach content could have been attributed to an increased influence of baits used by hunters or trappers in stomach samples, by different digestibility of diet components or possibly by differences in the time since the intake of food. Because there was no detectable effect of harvest method on stomachs and colons containing either moose or caribou, it is unlikely that baiting caused the observed patterns. However, because the different digestibility, even among ungulate prey, may bias their diet contribution estimated from wolverine faeces (van Dijk et al. 2007), the different digestibility of diet components may have caused at least part of the observed discrepancy between stomach and colon content. Also, we can not rule out that the different time lag since feeding between stomach and colon may have affected the results. However, because the difference did not change the relative ranks of caribou and moose in the diet, we do not believe that this discrepancy affected our overall conclusions.

Wolverines and temporal fluctuations in caribou abundance

Although wolverine diet varied between years, there was no strong relationship between caribou presence and the proportion of caribou in wolverine diets. Hence, our analyses contradicted our second prediction, that annual fluctuations in caribou would be reflected in the wolverine diet. However, we found indications that the observed annual diet variation may have been caused by a switch between caribou and moose, where wolverines may have compensated for the low dietary intake of caribou by increasing their intake of moose. Such compensation would suggest that wolverines act as large ungulate specialists that switch between ungulate food sources depending on availability, according to a generalist feeding strategy.

As neither caribou presence, nor caribou mortality or dietary dependence of either caribou or moose were related to wolverine body condition, such a potential diet switch does not seem to have negatively affected the nutritional status of wolverines. The lack of a nutritional effect of wolverine diet also contradicted our third prediction, that variation in caribou availability would be reflected in wolverine body condition. The results indicate that the two large ungulates in our study area are equally profitable for wolverines from an energetic standpoint, and that moose may buffer the effects of temporal availability of caribou. As moose are primarily non-migratory, a prey switch from caribou to moose would allow wolverines to maintain an ecological niche as a scavenger on ungulate carcasses, even during periods of low caribou abundance. Previous studies in both North America and Europe have similarly emphasized the dietary importance of large ungulates (Rausch & Pearson 1972; Magoun 1987; Landa et al. 1997; Lofroth et al. 2007), and wolverines seem to adopt this suggested role as a large ungulate specialist throughout their geographic range. However, in this area moose occur at lower densities than caribou do during migration periods (Ballard et al. 1997), and we suggest that the resident moose population may be too small to buffer the effects of a drastic decline in caribou abundance.

Conclusions

Although we confirmed that wolverines in north-west Alaska primarily consume caribou, we suggest that alternative prey (primarily moose) may be able to buffer the effects of declines in caribou abundance to some extent for wolverine population dynamics. We further suggest that factors affecting large ungulate mortality might have a strong influence on wolverine ecology. We emphasize

that efforts should be made to explore how these factors might affect wolverine populations, and that efforts should be made to identify alternative food resources, and to identify how their temporal and spatial variation may affect wolverines. Such information would be crucial for estimating the demographic responses of wolverines to variations in abundance and availability of large ungulates.

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