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Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada

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We examined the seasonal food habits of wolverine *Gulo gulo* in subboreal and interior wet-belt montane environments in British Columbia by analyzing scats collected during the course of two concurrent wolverine studies. Understanding foraging ecology for a wide-ranging carnivore such as the wolverine is important, particularly because reproduction has been demonstrated to be closely linked to food abundance. Wolverine diet was shown to vary regionally and seasonally. Regional variation was related to differences in prey availability between study areas. Moose *Alces alces*, caribou *Rangifer tarandus*, and hoary marmots *Marmota caligata* were abundant and common prey items within both study areas. Mountain goats *Oreamnos americanus* and porcupine *Erithizon dorsatum* were more abundant and more frequent prey items in the Columbia Mountains, while snowshoe hare *Lepus americanus* and beaver *Castor canadensis* were more abundant and more frequent prey items in the Omineca Mountains. Within the winter season, diet choices by reproductive females were different than other sex and age classes. Caribou, hoary marmots and porcupines were found in significantly higher frequencies in the diet of reproductive females. Foraging observations concurred with the findings of scat analyses. Dependence of reproductive females on a species of current conservation concern (caribou) and one which could be affected by issues related to climate change (hoary marmot) may present conservation issues for wolverines in the future.

Key words: British Columbia, food habits, foraging, Gulo gulo, wolverine

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Wolverines *Gulo gulo* are active year round. They are opportunistic feeders, thought to be primarily scavengers, but may spend considerable time hunting small and medium-sized prey (Hash 1987, Hatler 1989, Banci 1994). Large mammals (particularly ungulates) comprise the majority of their diet (Rausch & Pearson 1972, Myhre & Myrberget 1975, Hornocker & Hash 1981, Gardner 1985, Banci 1987, Magoun 1987, Landa et al. 1997). Medium and small-sized mammals (ground squirrels,

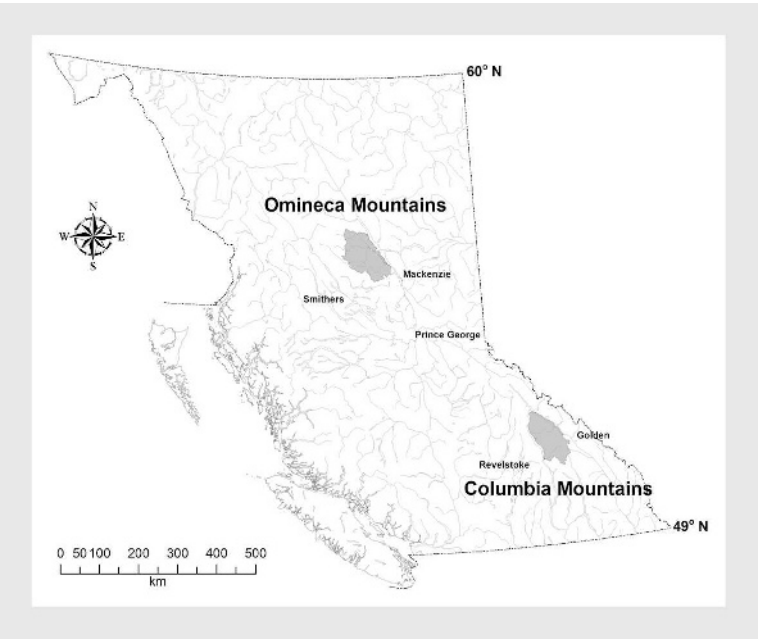

Figure 1. Location of Omineca Mountains and Columbia Mountains wolverine study areas in British Columbia, Canada.

marmots, snowshoe hare *Lepus americanus*, porcupine *Erithizon dorsatum*, squirrels and small rodents) become primary prey when larger food items are not available and may be important when females are provisioning young (Banci 1987, Magoun 1987, Landa et al. 1997). Ground-nesting birds (ptarmigan *Lagopus* spp., grouse and waterfowl) seasonally comprise a part of their diet where available. Vegetation has been reported in the diet of wolverines, but it may be consumed incidentally with prey rather than as a primary food source (Banci 1987). Energetic demands may be pronounced during winter when snow may impede movement. However, food resources may also be most concentrated and available at this time. Nutritional demands are likely greatest in females while kits are nursing from late winter through spring (Iversen 1972). Provision of supplemental food during early winter has been shown to increase reproductive rates for wolverine (Persson 2005) suggesting that females are food limited and that reproductive costs can be compensated for by high food abundance. Landa et al. (1997) suggested that abundance of small mammals may be a factor in wolverine kit survival. Food habits of reproductive females may differ from those of males and non-breeding females due to the requirement to regularly provision kits, typically reared in a snow-covered den of rock and woody debris (Magoun & Copeland 1998). Characterising these differences is of conservation interest because survival of adult female wolverine is the key determinant of population growth, and variation in food availability affects reproductive success (Krebs et al. 2004, Persson 2005).

In western Canada, wolverines are listed as 'Special Concern' (COSEWIC 2003). Because wolverine reproduction is strongly influenced by food availability (Persson 2005), understanding seasonal food habits is a critical element in evaluating status and developing conservation measures for populations at risk. In this paper we present data which describe and compare seasonal food habits of wolverine from two distinct study areas in montane ecosystems in British Columbia.

Study area

The data for our analyses were collected as part of two related studies of wolverine ecology in British Columbia. The Omineca Mountains study was conducted during 1995-2001. The study area was approximately 8,900 km^2 in size and was located in the Williston Reservoir Basin in north-central British Columbia (Fig. 1). It included Sub-boreal Spruce, Boreal White and Black Spruce, Spruce Willow Birch, Engelmann Spruce-Subalpine Fir and Alpine Tundra biogeoclimatic zones (Meidinger & Pojar 1991). Lower elevation forests were

dominated by white *Picea glauca* and black spruce *Picea mariana*, subalpine fir *Abies lasiocarpa* and lodgepole pine *Pinus contorta*. Upper elevation forests were primarily Engelmann spruce *Picea engelmannii* and subalpine fir. Alpine habitats were dominated by herbaceous meadows, tundra and non-vegetated communities. Elevations ranged within 675-2,200 m a.s.l. Extensive forest harvesting, with associated major forestry roads, had occurred in the eastern and northern portions. The western and southern portions of the study area had relatively little forest harvesting. The study area was bordered on the east by a hydroelectric reservoir.

The Columbia Mountains study was conducted during 1994-2002. This study area encompassed 7,000 km^2 of rugged mountainous terrain in the interior wet-belt of southern British Columbia (see Fig. 1). Elevation varied from 460 to 3,385 m a.s.l. The study area included Interior Cedar Hemlock, Engelmann Spruce Subalpine Fir and Alpine Tundra biogeoclimatic zones (Meidinger & Pojar 1991). Valley bottoms were dominated by dense stands of hemlock *Tsuga heterophylla* and western redcedar *Thuja plicata*. Mid to upper elevations were covered in Engelmann spruce and subalpine fir. Alpine environments were covered by herbaceous meadow, low shrub, tundra or non-vegetated habitats. Due to the steep topography avalanche chutes were common. Extensive forest harvesting had occurred within a large portion of the study area. The study area contained a major transportation corridor and a hydroelectric reservoir. Fifteen percent of the study area was within protected areas contained in two national parks.

Moose *Alces alces*, caribou *Rangifer tarandus* and small numbers of mountain goat *Oreamnos americanus* represented the available large prey in the Omineca Mountains study area. Medium and small prey included hoary marmot *Marmota caligata*, beaver *Castor canadensis*, red squirrel *Tamiasciurus hudsonicus*, flying squirrel *Glaucomys sabrinus*, porcupine, a number of species of mice, shrews and voles and six species of grouse and ptarmigan. Large prey occurring in the Columbia Mountains study area included caribou, moose, mountain goat, mule deer *Odocoileus hemionus* and elk *Cervus elaphus*. Medium and small prey included hoary marmot, Columbia ground squirrel *Spermophilus columbianus*, red squirrel, flying squirrel, beaver, porcupine, a number of species of mice, shrews and voles, and four species of grouse and ptarmigan. Wolves *Canis lupus*, black bears *Ursus americanus* and grizzly bears *U. arctos* were the large predators which occurred within both study areas. Canada lynx *Lynx canadensis* occurred within the Omineca Mountains, whereas cougar *Felis concolor* occurred within the Columbia Mountains study area.

Material and methods

We defined two seasons of activity (summer and winter) for wolverines during which behaviour and habitat use was consistent and influenced by biological imperatives (e.g. rearing young) and weather phenomena. Summer commenced in mid to late May with the emergence of marmots from hibernation and the conclusion of natal den use by adult females. This season included the period when female wolverines were provisioning weaned young and the subsequent mating season. Summer concluded when marmots were observed to begin hibernation (October). Winter was the period when there was consistent snow cover at the treeline. During this time ungulates were mostly concentrated on winter ranges. Start and end dates for seasons varied slightly among years. The winter season was slightly longer in the Omineca Mountains study area due to a cooler, more boreal climate.

We examined wolverine food habits by analysing the contents of scats collected in the course of our studies, and the stomachs of carcasses obtained from trappers. Scats were collected during snow trailing, at site investigations of recent radio-telemetry locations, and from reproductive dens following their abandonment by adult females and their kits. Samples were kept frozen until such time as contents could be processed. Wolverine stomachs were cut open and contents rinsed through a series of standard Canadian soil sieves with decreasing mesh sizes of 6.35, 5.6, 2.0 and 1.0 mm. Scats were soaked in water, rinsed and sieved in the same manner. Stomach and scat contents were dried in a fume hood for 24 hours at 25°C. Samples were separated into animal guard hair, bone fragments, feathers and other components. Animal guard hairs were spread out onto a 100 grid cell sampling sheet and randomly sampled from 10 cells. Guard hairs were sandwiched between two microscope slides with green acetate and heated to soften the acetate and create a negative impression of the scale structure. Guard hairs and scale impressions were examined under a compound phase contrast microscope. Medullae, scale structures and colour banding were

Table 1. Percent occurrence of prey items in scat samples from the Omineca Mountains and Columbia Mountains study areas (includes samples with confidence rankings A-D). Numbers in brackets represent the total number of samples each prey family occurred in.

	Season	
Prey Family	Winter (N = 558)	Summer (N = 15)
Bovidae	8.6 (48)	0 (0)
Castoridae	4.3 (24)	20 (3)
Cervidae	52.9 (295)	33.3 (5)
Erethizontidae	19 (106)	6.7 (1)
Leporidae	5.2 (29)	0 (0)
Muridae	1.8 (10)	6.7 (1)
Mustelidae	3.4 (19)	13.3 (2)
Sciuridae	23.8 (133)	40 (15)
Soricidae	1.4 (8)	0 (0)
Zapodidae	0.2 (1)	0 (0)
Unknown	42.1 (235)	53.3 (8)

used to identify guard hairs by comparing them with illustrations of reference hairs, photographs (Moore et al. 1974) and reference slides of known specimens. Each slide was given an identification confidence rating of A, B, C or D based on how many of the identification criteria (medulla structure, scale structure, colour banding, slide quality and other corroborating data) were positive. Ratings were assigned as follows: A: ≥ 3 of four criteria met; B: two of four criteria met; C: one of four criteria met; D: no criteria met. Samples with rankings of A and B were identified to species. Samples with a rating of C were identified only to family. In order to attain a rating of C, at least one of the matches must have been from the first three criteria. Samples with a rank of D were classified as unknown. Bone and feathers found in scats were identified when possible using reference collections.

Scat and stomach sample data were summarized by tallying the number of samples that an individual species was present in (frequency of occurrence). Data were analyzed using contingency tables and log-likelihood ratio χ^2-analyses.

Foraging events were recorded from aerial observations, site investigations and snow trailing observations.

Results

We analyzed 24 stomachs and 223 scats from the Omineca Mountains, and 350 scats from the Columbia Mountains. Most samples were from the winter season. Summer had fewest samples as this season was relatively snow free, making tracking wolverine and finding scats more difficult. There was also no commercial trapping during this season. No identifiable remains (empty stomachs or no hair in scats) were found in nine samples from the Omineca Mountains samples and in 42 of the samples from the Columbia Mountains.

We eliminated trapper samples from our analyses because there was a significant difference in the frequencies of food items in trapper submitted samples vs other samples from the Omineca Mountains study area ($\chi^2 = 49.1$, df = 7, $P < 0.001$), primarily due to the prevalence of beaver in the trapper submitted samples. This may reflect the use of beaver as bait or trapping effort biased to low elevation habitats.

Seasonal results are summarized for both study areas by family (confidence rankings A-D) in Table 1. Bovidae and Erethizontidae were only present in samples from the Columbia Mountains while Castoridae, Muridae, Soricidae and Zapodidae were only present in samples from the Omineca Mountains. Wolverine hairs (Mustelidae) were found in samples from both study areas. The presence of wolverine hair in samples may be from grooming. Although we have evidence of intraspecific conflicts resulting in mortalities, there are few instances of cannibalism in our studies or published literature (Flook & Rimmer 1965).

Prey species composition of summer and winter samples was significantly different between the two study areas ($\chi^2 = 1.72$, df = 9, $P < 0.001$; Table 2). Mountain goats and porcupine were found in 14.8 and 36.5% of all scats in these seasons in the Columbia Mountains, but not at all in the Omineca Mountains. Beaver was present in 10.6% of all samples from the Omineca Mountains but not at all in the Columbia Mountains. Moose, hoary marmots and snowshoe hare were more common in samples from the Omineca Mountains. Seasonal analyses indicated significant differences between summer and winter season food habits in both the Omineca Mountains samples ($\chi^2 = 12.75$, df = 5, $P < 0.05$) and the Columbia Mountains samples ($\chi^2 = 18.97$, df = 7, $P < 0.01$), although sample sizes for summer are very small in both study areas (see Table 2). Comparison of scats collected at den sites and those collected at other locations during winter showed that caribou and hoary marmots were more prevalent in scats from den sites, whereas moose were more prevalent in scats from other locations (Omineca: $\chi^2 = 9.14$, df = 5, $P < 0.0001$; Columbia: $\chi^2 =$

Table 2. Percent occurrence of prey items in scat samples from the Omineca and Columbia Mountains by season (includes samples with confidence rankings A and B only). Numbers in brackets represent the total number of samples each prey species occurred in.

	Omineca Mountains		Columbia Mountains	
Prey species	Summer (N = 7)	Winter (N = 209)	Summer (N = 5)	Winter (N = 266)
Mountain goat	0 (0)	0 (0)	0 (0)	15.0 (40)
Moose	71.4 (5)	36.4 (76)	0 (0)	9.4 (25)
Caribou	0 (0)	35.4 (74)	0 (0)	32.0 (85)
Mule deer	0 (0)	0 (0)	0 (0)	1.9 (5)
Porcupine	0 (0)	0 (0)	20 (1)	36.8 (98)
Beaver	42.9 (3)	9.6 (20)	0 (0)	0 (0)
Hoary marmot	28.6 (2)	40.7 (85)	60 (3)	13.2 (35)
Snowshoe hare	0 (0)	12.0 (25)	0 (0)	0.4 (1)
Red squirrel	0 (0)	0.5 (1)	0 (0)	0 (0)
Flying squirrel	0 (0)	0 (0)	40 (2)	1.5 (4)

135.68, df = 7, $P < 0.0001$; Table 3). Snowshoe hare was found primarily in non-denning samples in the Omineca Mountains. Mountain goats and porcupines were found in the Columbia Mountains samples, but not in the Omineca Mountains samples, and porcupines were most prevalent in reproductive den samples in the Columbia Mountains. Additional wolverine food species, which were identified from bone and hair fragments or which appeared in trapper submitted stomach samples but not elsewhere, included deer mouse *Peromyscus maniculatus*, ruffed grouse *Bonasa umbellus*, an unidentified species of ptarmigan and varied thrush *Ixoreus naevius*.

Foraging event data (Table 4) were primarily from the winter season when kill and scavenging sites were easier to find. Moose were fed upon in both seasons. The majority of foraging events in winter in the Omineca Mountains involved moose. Feeding on moose was also common in the Columbia Mountains in the winter season, however, almost as many goat foraging events were recorded during this season. Wolverines were recorded foraging on caribou on 12 occasions, primarily in winter. Nine (eight in Omineca and one in Columbia) of these events were of wolverines killing caribou. Caribou killed by wolverines (one calf of unknown sex; eight adults: three bulls, one cow and four of unknown sex) for which long bones could be examined (three bulls, one cow) appeared to be in very poor condition. Bone marrow fat content ranged within 5-8%. Mech et al. (1998) suggest that bone marrow fat content of less than 70% in ungulates is debilitating. Foraging events on marmots were only recorded in summer and all were by female wolverines raising young.

Discussion

The differences we observed between scat and stomach samples suggest caution in interpreting food habit results from stomach samples of trapped wolverines. Our scat analyses concur with many previous studies and indicate that although wolverines are opportunistic foragers, ungulates are the dom-

Table 3. Percent occurrence of prey items in scats from reproductive dens and other winter sampling locations from the Omineca and Columbia Mountains (includes samples with confidence rankings A and B only). Numbers in brackets represent the total number of samples each prey species occurred in.

	Omineca Mountains		Columbia Mountains	
Prey Species	Reproductive den (N = 122)	Other (N = 86)	Reproductive den (N = 221)	Other (N = 45)
Mountain goat	0 (0)	0 (0)	17.6 (39)	15.6 (7)
Moose	16.4 (20)	65.1 (56)	1.8 (4)	46.7 (21)
Caribou	50 (61)	15.1 (13)	38.5 (85)	0 (0)
Mule deer	0 (0)	0 (0)	0 (0)	11.1 (5)
Beaver	9.8 (12)	9.3 (8)	0 (0)	0 (0)
Porcupine	0 (0)	0 (0)	40.3 (89)	17.8 (8)
Hoary marmot	67.2 (82)	3.4 (3)	15.8 (35)	0 (0)
Snowshoe hare	1.6 (2)	26.7 (23)	0 (0)	2.2 (1)
Red squirrel	0 (0)	1.2 (1)	0 (0)	0 (0)
Flying squirrel	0 (0)	0 (0)	0.5 (1)	6.7 (3)

Table 4. Number of foraging events recorded in the Omineca Mountains and Columbia Mountains by season (includes aerial telemetry observations, site investigations and snow trailing observations).

	Omineca Mountains		Columbia Mountains	
Food Item	Summer (N = 12)	Winter (N = 75)	Summer (N = 7)	Winter (N = 53)
Moose	4	48	0	17
Caribou	0	11	0	1
Mountain goat	0	0	2	13
Unidentified ungulate	0	0	0	8
Hoary marmot	7	0	5	0
Beaver	0	2	0	0
Porcupine	0	0	0	3
Red squirrel	0	1	0	0
Snowshoe hare	1	3	0	0
Black bear	0	2	0	0
Fisher	0	1	0	0
Unidentified small mammal	0	0	0	3
Ruffed grouse	0	2	0	0
Thrush	0	1	0	0
Unidentified songbird	0	1	0	1
Domestic cow	0	1	0	7
Garbage	0	2	0	0

inant food item. Moose were particularly prevalent in both scat and stomach samples and observed foraging events, and appear to comprise the bulk of wolverine diet. Moose was the most common prey item in all winter samples except those from reproductive dens. Although goats were available in small numbers in the Omineca Mountains there was no indication that wolverines fed upon goats. Opportunities for wolverines to forage on goats may have been limited by the terrain of the Omineca Mountains study area. Terrain within this study area was gentle relative to the more rugged Columbia Mountain study area and avalanche chutes were relatively uncommon. Most goats fed upon by wolverines in the Columbia Mountains were associated with avalanche kills (12 of 15 events), whereas fewer goats were killed by wolverines (3 of 15 events; unknown sex and age). Caribou, marmots and porcupines were more important to adult females with kits than to other sex and age classes. Adult females may be more likely to have caribou hunting and scavenging opportunities during this time than other sex and age classes as they are consistently found at higher elevations (Krebs et al. 2007). Caribou are only seasonally available in the Omineca Mountains study area (primarily winter). Caribou are classified as Threatened in the Columbia Mountains whereas they are classified as Special Concern in the Omineca Mountains (MCTAC 2002). Dependence on caribou for food by denning females may already be a conservation issue for both species. Wolverine predation may increase predation pressure on caribou and decreasing caribou numbers could negatively influence wolverine reproduction (Persson 2005).

The use of carrion by wolverine has an inherent trade-off between resources gained and risk of predation. Use of wolf, cougar or bear-killed ungulates by wolverine could result in direct conflict and mortality (Krebs et al. 2004). Denning females may reduce the risk of intra- and interspecific predation by foraging at higher elevations, spatially separate from other predators, including other wolverines. The presence of ungulate species (such as caribou and mountain goat) and marmots at high elevation provides an ecological niche for female wolverines in the mountainous regions of British Columbia.

Based on foraging observations and limited scat samples, marmots appear to be important in the diet of female wolverine during summer. During this time females are provisioning kits that are undergoing their greatest period of growth. The presence of marmot hair in scat samples from reproductive dens may indicate the use of previously cached carcasses (Magoun 1987) or predation on newly emerging marmots. Concern over the decline of alpine habitats and associated species (Beever et al. 2003, Moen et al. 2004) in climate change scenarios could have implications for wolverine conservation in the future.

Small mammals and birds, although consumed, appear to be a relatively unimportant component of wolverine diet in our study areas. Although gathering foraging event data for these potential food spe-

cies is difficult, scat and stomach data corroborate this statement. These prey items may be more prevalent during the summer when our sample sizes were small.

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