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The wolverine's niche: linking reproductive chronology, caching, competition, and climate

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Wolverines are demographically vulnerable and susceptible to impacts from climate change. Their distribution is correlated with persistent spring snow cover, but food-based explanations for this relationship have not been explored. We synthesize information on the timing of both wolverine reproductive events and food availability to improve our understanding of the behaviors, habitat features, and foods that influence reproductive success. Wolverine births are constrained to a brief period of the year and occur at an earlier date than other nonhibernating, northern carnivores. Our examination suggests that this timing is adaptive because it allows wolverines to take advantage of a cold, low-productivity niche by appending the scarce resources available during winter to the brief period of summer abundance. The wolverine's bet-hedging reproductive strategy appears to require success in 2 stages. First, they must fuel lactation (February–April) with caches amassed over winter or acquisition of a sudden food bonanza (e.g., winter-killed ungulates); otherwise, early litter loss occurs. Next, they must fuel the majority of postweaning growth during the brief but relatively reliable summer period of resource abundance. The 1st stage is likely dependent on scavenged ungulate resources over most of the wolverine's range, whereas the 2nd stage varies by region. In some regions the 2nd stage may continue to be focused on scavenging ungulate remains that have been provided by larger predators. In other regions the 2nd stage may be focused on predation by wolverines on small prey or neonatal ungulates. During all seasons and regions, caching in cold, structured microsites to inhibit competition with insects, bacteria, and other scavengers is likely a critical behavioral adaptation because total food resources are relatively limited within the wolverine's niche. Habitat features that facilitate caching, e.g., boulders and low ambient temperatures, are likely important and could be related to the limits of distribution. This ''refrigeration-zone'' hypothesis represents a food-based explanation for the correlation between wolverine distribution and persistent spring snow cover. Understanding regional differences in foods that fuel reproduction and underlying causes to the limits of distribution could be important for maintaining wolverine populations in the future.

Key words: cache, climate change, competition, distribution, delayed implantation, food, *Gulo gulo*, niche, reproduction, wolverine

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Wolverines (*Gulo gulo*) are demographically vulnerable, have experienced historical declines in some regions, and are susceptible to impacts from climate change (Aubry et al. 2007; Copeland et al. 2010; Persson et al. 2006). The wolverine is a species of conservation concern in some parts of its distribution. In Scandinavia, the species is considered vulnerable in Sweden and endangered in Norway (National Red List—Gärdenfors 2010; Kålås et al. 2010). In the lower 48 United States, the wolverine was recently designated as warranted for protection under the United States Endangered Species Act (ESA—United States Fish and Wildlife Service 2010). Climate change was the primary threat leading to ESA designation in the United States. To develop conservation strategies capable of ensuring wolverine persistence through the

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21st century, we must fully understand the factors that influence distribution and enable them to reproduce successfully.

Reproduction is a key component of fitness that is ultimately limited by the amount of energy that can be channeled toward offspring (Bronson 1989; Stearns 1992). In seasonal environments, timing the most energetically demanding periods of reproduction to occur when food resources are abundant can be a critical factor for individual fitness. For example, ungulate births typically occur within a narrow annual window related to a flush of nutrition (Geist 2002; Miller 2003), and even small differences in birth dates within this window can influence overwinter survival (Singer et al. 1997). On the other hand, species whose food resources are relatively constant are less constrained to specific time periods for reproduction, e.g., mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*—Anderson and Lovallo 2003; Pierce and Bleich 2003). The energy required for carnivores to reproduce (conception through weaning) can be >100 times the daily metabolic requirement (Oftedal and Gittleman 1989), and lactation is often the most demanding phase of the female's reproductive cycle. However, postweaning growth of offspring also requires higher levels of energy and may represent the constraint that determines the timing of reproduction (Bronson 1989; Lack 1968). Clearly, natural selection will favor individuals that time these critical and energetically demanding periods of reproduction to occur during the season of food abundance.

The timing of reproductive events in relation to food availability may be particularly critical for the wolverine. The wolverine's large feet are a morphological adaptation that allows it to travel easily over deep snow, and the species is distributed in circumpolar fashion across the tundra, boreal, and montane biomes (Copeland and Whitman 2003). Throughout its distribution, the wolverine displays extremely large home ranges, territoriality, low densities, and low reproductive rates (Copeland 1996; Inman et al. 2012; Krebs et al. 2007; Lofroth and Krebs 2007; Magoun 1985; Mattisson et al. 2011a; Persson et al. 2006, 2010). These adaptations are necessary for exploiting a cold, low-productivity niche where growing seasons are brief and food resources are limited (Inman et al. 2012). Starvation is a significant natural cause of wolverine mortality in some populations (Krebs et al. 2004). In addition, Persson (2005) experimentally demonstrated that wolverine reproduction in Scandinavia was limited by winter food availability. Taken together, these factors suggest that wolverines need to be exceptionally efficient in channeling available food resources into reproduction to persist within their niche.

The wolverine's reproductive chronology is unique in that birth occurs earlier than for other northern carnivores that do not hibernate (Fig. 1). However, our knowledge of the specific mechanisms that wolverines utilize to reproduce within their relatively unproductive niche is incomplete. For instance, although it is clear that wolverines are opportunistic and utilize a wide variety of foods (Banci 1994; Hash 1987; Lofroth et al. 2007; Magoun 1987), no attempt has been made to discern which foods specifically fuel the most energetically demanding periods of reproduction. Caching is a common behavior (Haglund 1966; Landa et al. 1997; Magoun 1987; Mattisson 2011; May 2007; Samelius et al. 2002), yet there has been no effort to determine how or why it could be a key in the reproductive process. At present, distributional limits of the wolverine are suggested to depend on where they can give birth and/or avoid physiologically prohibitive summer temperatures (Copeland et al. 2010) rather than where and how they can successfully compete for food. Clarifying our understanding of these fundamental aspects of the wolverine's ecology can help develop more effective conservation strategies for the species.

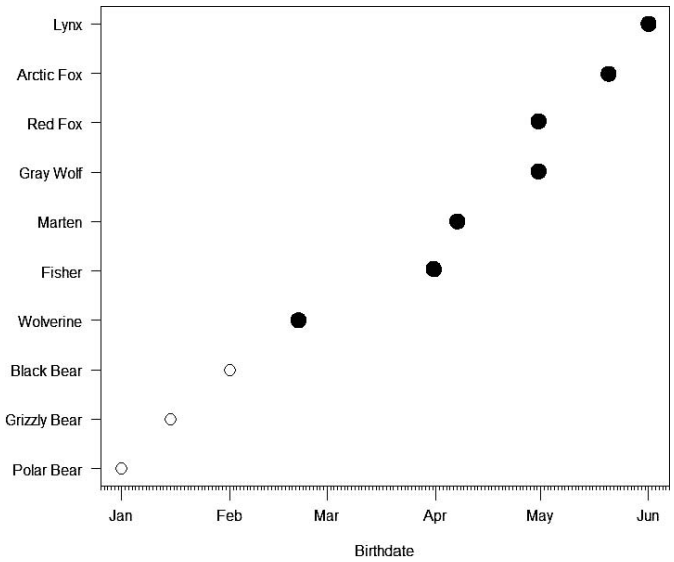


Fig. 1.—Median reported birthdates of northern carnivores (Amstrup 2003; Anderson and Lovallo 2003; Cypher 2003; Paquet and Carbyn 2003; Pelton 2003; Powell et al. 2003; Schwartz et al. 2003). Hollow circles indicate species that hibernate.

Given the adaptive significance of acquiring food resources for reproduction most efficiently, the wolverine's reproductive chronology can provide key insights for how the species exploits its niche. Although many authors have reported anecdotally on the timing of events associated with wolverine reproduction, no comprehensive, easily interpreted, chronological sequence has been published. Herein we consolidate the available information regarding the timing of events related to wolverine reproduction. We then attempt to identify specific mechanisms by which this chronology is adaptive for wolverines; we discuss behavioral adaptations necessary to occupy the species' niche, habitat features that may influence their distribution, and the potential influence of various food sources on reproductive success.

Materials and Methods

Because this review was intended to summarize information available from numerous sources, virtually all of which are based on small sample sizes obtained using different methodologies, we present the data used to define the extent and peak of each reproductive event along with our synopsis in the ''Results'' section. We estimated the extent and peak periods

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of reproductive events on the basis of similarities among studies and by weighting each study's contribution on the basis of sample size, technique, and whether observations were based on wild or captive wolverines. We also used personal knowledge related to the timing of reproductive events obtained during wolverine field studies that we conducted (Inman et al. 2012; Magoun 1985; Mattisson 2011; Persson 2003; Persson et al. 2006; Royle et al. 2011). We also reviewed the literature to determine time periods during the year when the species wolverines use as food are likely to be more available; we considered information on their birthing periods, higher than usual levels of mortality (e.g., ungulate deaths due to winter kill), and entrance/emergence dates for hibernating species. We then discuss these chronologies in light of other information about wolverines in an attempt to develop hypotheses regarding which foods, behaviors, and habitat features may be influential for wolverines.

Results

Mating season.—Mead et al. (1991) obtained blood samples and vaginal smears from 8 captive female wolverines throughout the year and reported 3 waves of ovarian activity related to sexual receptivity occurring during May to early June, mid-June to July, and August; vaginal cornification began increasing in May and maximal cornification and vulva enlargement occurred during June and July. Mead et al. (1991) reported that females were anestrus from September to April. Rausch and Pearson (1972) examined the carcasses of 417 female wolverines but were not able to define the proestrus period. The vast majority of the wolverines were killed between November and April; thus only 3 contained strong evidence of imminent (follicle) or recent (corpora lutea) estrous, all of which occurred from 16 to 28 June. Wright and Rausch (1955) found no evidence of ovarian activity in 2 lactating females killed 9 and 10 April. However, in northern Sweden 1 captured female had a swollen vulva as early as 2 April, another on 26 April, and several in early May (J. Persson, pers. obs.).

Wright and Rausch (1955) examined 8 adult male wolverines killed November–April for spermatogenesis; 0 of 5 killed in November–January contained sperm, whereas 1 of 2 in February and 1 of 1 in April did; in addition, sperm were present in 2 young males killed 31 March and 4 April. Danilov and Tumanov (1972) examined 2 males in mid-March that were both fertile. Liskop et al. (1981) detected spermatogenesis in 1 of 2 males killed in January, 2 of 5 in February, and 1 of 2 in March. Rausch and Pearson (1972) examined 43 pairs of male testes for weight, spermatogenesis, and the presence of epididymal sperm. Although they concluded that peak mating condition of males occurred during late May and June, they thought that mating may occur over a longer period. Given their statement that ''testes collected in late winter clearly showed an increase in weight, spermatogenesis, and the presence of epididymal sperm,'' their report suggests males were prepared to mate by at least March and April. Mead et al. (1991) measured changes in plasma testosterone levels and testes size in 7 captive males and suggested that males reach near-maximal testes size by early April and peak in June. Rausch and Pearson (1972), Mead et al. (1991), and Banci and Harestad (1988) all found evidence of testes beginning to increase in size by March. Results from both Rausch and Pearson (1972) and Mead et al. (1991) indicate that testicular regression begins in July and is likely completed by early August.

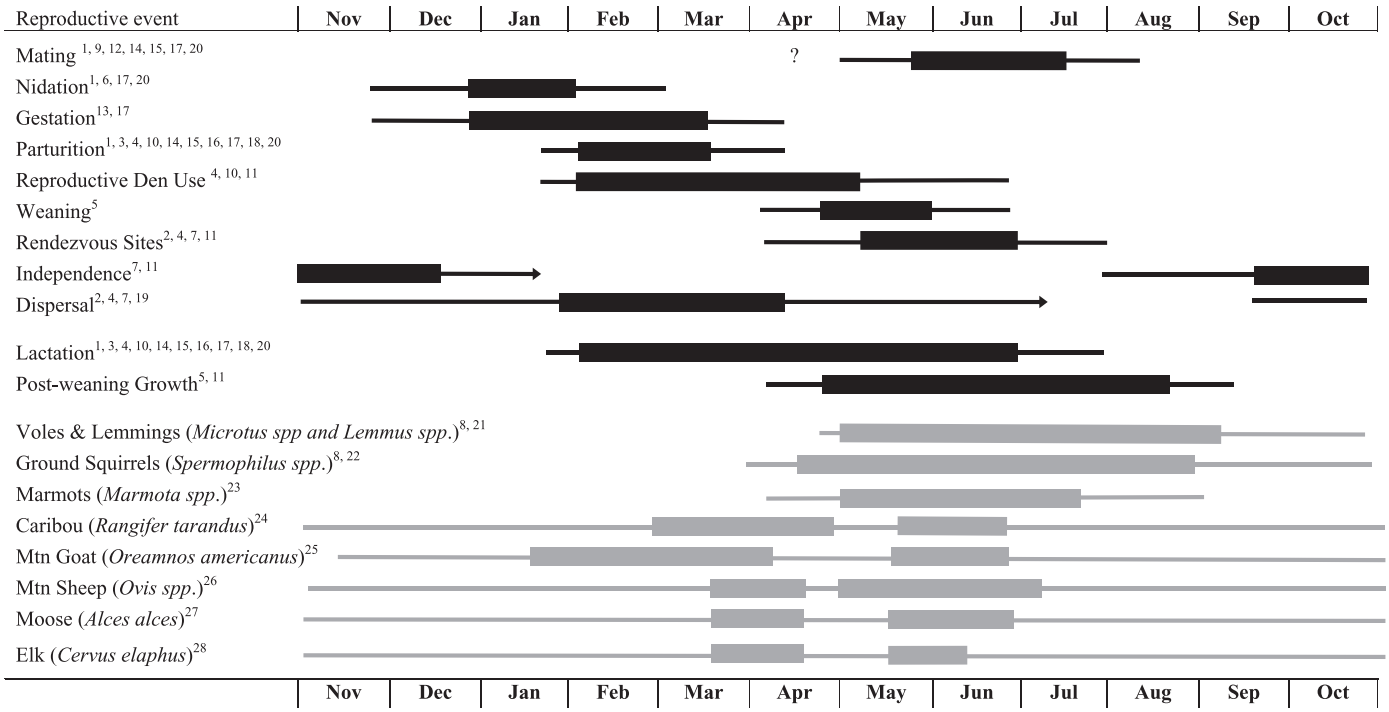
Observations of assumed mating by wild wolverines are limited to 7 cases occurring mid-April, 27 April, 15 May, 5, 9, 11 June, and 6 August (Krott and Gardner 1985; Magoun and Valkenburg 1983; J. Persson, pers. obs.). Seven matings occurred 7 June–14 July at a captive facility in Washington State (D. Pedersen, pers. comm.). Five of the matings occurred from 7 to 27 June. Four of the matings were by the same female in 4 different years. In Europe, observations of 69 matings in captivity took place from 17 May to 25 July, and 45% occurred during the first 2 weeks of June (Blomqvist 2001). Captive wolverines were observed to mate on 10 April and at the end of May in Sweden (Krott 1959). Other matings by captive wolverines were observed on 31 May (Mehrer 1975) and from 17 to 22 July (Mohr 1938). Mating pairs were not monitored continuously, so mating could have occurred on other days as well.

In summary, June appears to be the peak of a wolverine mating season that extends from at least May through early August (Fig. 2). Males appear to be prepared to mate by March, possibly as early as January, but the evidence for females being prepared before May is limited and somewhat contradictory.

Nidation.—Almost all information on nidation (and therefore, on gestation) is derived from trapper-caught wolverines and many dates of capture are likely approximate. Wolverines exhibit delayed implantation (Rausch and Pearson 1972; Wright and Rausch 1955). Wright and Rausch (1955) examined 7 adult female reproductive tracts and suggested that nidation occurs during January. Banci and Harestad (1988) sampled 56 individuals and found evidence of active pregnancy beginning as early as November. Rausch and Pearson (1972) found evidence of blastocysts, fetuses, or postpartum condition in 122 female wolverines and only 4% of carcasses obtained by the end of December contained a macroscopic fetus. Rausch and Pearson (1972) found that the number of reproductive tracts containing unimplanted blastocysts declined dramatically after January, suggesting that most nidation had occurred by the end of January. Unimplanted blastocysts were found by Rausch and Pearson (1972) and Liskop et al. (1981) as late as March. Given a 45-day gestation period (see below), implantation that occurred 1 March would result in a mid-April birth, but data on parturition suggest that such late births occur very rarely (see below). Wolverines may resorb fetuses (Banci and Harestad 1988) and it is possible that blastocysts could be present in March but remain unimplanted for the same physiological reasons that could lead to resorption.

Although mating occurs during spring/summer, active gestation may begin as early as November and as late as

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1. Banci and Harestad 1988
2. Copeland 1996
3. Davis 1967
4. Inman et al. 2007
5. Iverson 1972
6. Liskop et al. 1981
7. Magoun 1985
8. Magoun 1987
9. Magoun and Valkenburg 1983
10. Magoun and Copeland 1998
11. May 2007
12. Mead et al. 1991
13. Mead et al. 1993
14. Mehrer 1975
15. Mohr 1938
16. Pulliainen 1968
17. Rausch and Pearson 1972
18. Shilo and Tamarovskaya 1981
19. Vangen et al. 2001
20. Wright and Rausch 1955
21. Pugh et al. 2003
22. Yensen and Sherman 2003
23. Armitage 2003
24. Miller 2003
25. Côtè and Festa-Bianchet 2003
26. Krausman and Bowyer 2003
27. Bowyer et al. 2003
28. Raedeke et al. 2002

Fig. 2.—Range (thin line) and peak (thick line) time periods associated with wolverine (*Gulo gulo*) reproductive biology and availability of food items.

March, with the peak of implantation occurring during late December to early February (Fig. 2). Data on nidation are not available from the southern portion of wolverine range. If there are latitudinal differences in birth date, nidation date likely also differs.

Gestation.—Rausch and Pearson (1972) suggested an active gestation period of 30–40 days on the basis of 50% of females killed in February having implanted embryos and 64% of those killed in March being postpartum. Mead et al. (1993) suggested that active gestation occurs for approximately 50 days on the basis of elevated progesterone profiles of captive females. We used a 45-day gestation period to aid interpolation of other reproductive events (Fig. 2).

Parturition.—Wright and Rausch (1955) reported that parturition appears to occur in late March or early April on the basis of 7 adult female reproductive tracts. After examining 122 female reproductive tracts with evidence of blastocysts, fetuses, or postpartum condition, Rausch and Pearson (1972) reported that parturition occurred from January to March, and in 1 case (0.8%) as late as mid-April; peak parturition was February, but the authors did not specify whether this was late February or earlier. Banci and Harestad (1988) found evidence of postpartum condition in 6 females; 1 had given birth in January and 5 in February. Both Rausch and Pearson (1972) and Banci and Harestad (1988) reported that the percentage of females that had active pregnancies increased from December to February and decreased thereafter.

Pulliainen (1968) obtained information on parturition from 2 reproductive tracts and from wolverine bounty hunters who dug out 31 wolverine dens. Pulliainen (1968) reported 4 litters as ''blind,'' which are <5 weeks old (D. Pedersen, pers. comm.), during January and on 6 February, 20 March, and 25 March. Pulliainen (1968) also found embryos in reproductive tracts in late March and suggested that parturition occurs primarily during February and March. Magoun and Copeland (1998) estimated date of parturition by comparing tooth eruption, body size, or pelage coloration of the cubs with that of known-age, captive wolverine cubs; they reported dates of 16, 18, and 23 February in Idaho and 24 February, 1, 4, and 6 March in Alaska. Inman et al. (2007) used repeated very-high-frequency (VHF) radiotelemetry locations during the denning season combined with subsequent observations of cubs to estimate parturition dates (more specifically the beginning date for use of natal den site) in the Yellowstone region of Idaho, Montana, and Wyoming on 29 January and 5, 18 ($n = 2$), and 23 February; 1 additional female wearing a global positioning system (GPS) collar began using a natal den on 16 February. On the basis of GPS collar locations, parturition dates (initial natal den use) for females in northern Sweden were estimated to be 1, 8, 11, 12, 16 ($n = 2$), 18 ($n = 2$), 19, and 21 February (J. Persson, pers. obs.). In addition, females immobilized there on 2 February ($n = 3$), 9 February ($n = 1$), and 15 February

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($n = 2$) were pregnant (on the basis of palpation). Two females immobilized 23 February had given birth (were lactating).

The birth of 19 litters by 7 captive females occurred from 30 January to 18 March (D. Pedersen, pers. comm.). The peak in births occurred from 23 February to 6 March (11 of 19), with 4 before this period and 4 after. In February, 1 birth occurred in the 1st week, 2 in the 3rd week, and 6 in the last week. In March, 5 births occurred in the 1st week, 3 in the 2nd week, and 1 in the 3rd week. One female gave birth to 9 litters over a 10-year period; 8 of these births occurred from 23 February to 10 March and 1 birth occurred on 30 January. Sixty percent of 30 births at European zoos took place during the last 2 weeks of February; all occurred during the months of February (81%) and March (19%—Blomqvist 2001). Other captive females have given birth on 16 February (Davis 1967), 17 February (Mohr 1938), 26 February (Myhre and Myrberget 1975), and in March (Shilo and Tamarovskaya 1981).

In summary, the peak period for parturition appears to be February through mid-March. This period corresponds well with peak periods of nidation occurring from late December through early February and an approximate 45-day active gestation period. Births outside this period occur (late January and mid-March to mid-April), but appear to be rare (Fig. 2).

Reproductive den use.—The sites where female wolverines keep cubs before weaning have been distinguished as natal dens (birth location) and maternal dens (site used subsequent to natal den but before weaning—Magoun 1985; Magoun and Copeland 1998). Use of natal dens obviously begins no later than parturition; however, it is unknown whether females investigate or prepare the natal den before giving birth. Dates for abandonment of natal dens and initiation of maternal dens were difficult to establish. Natal dens have commonly been assumed to be used until cubs are old enough to be weaned; thus the 1st move away from the natal den would be to a rendezvous site. However, this has mainly been based on VHF radiotracking, which may not be accurate enough to detect short moves (~200 m) from a natal to a maternal den. Cubs in Idaho were moved between den sites at approximately 15–30 days of age (Magoun and Copeland 1998), and monitoring of females with GPS collars has shown that some females move to and between multiple den sites in March–April (J. Persson, R. Inman, pers. obs.). Magoun and Copeland (1998) reported that natal dens were abandoned in Alaska and Idaho when ''maximum daily temperatures rose above freezing for a number of days for the 1st time since denning commenced.'' These dates obviously differ by latitude, elevation, and year. Other factors such as parasites, defending against intraspecific predation, or disturbance could also influence den shifts. Overall, it appears that the timing of a shift from a natal den to a maternal den varies widely and that further research is needed to establish the prevalence, timing, causes, and function of these shifts. For the purposes of this paper we do not distinguish between these two types of dens but use the inclusive term ''reproductive dens'' to refer to dens used before weaning (Magoun and Copeland 1998). Movements away from these reproductive denning areas typically occurred during late April and early May in Sweden (J. Persson, pers. obs.), mid-May in Norway (May 2007), 18 April–5 May in northwest Alaska (Magoun and Copeland 1998), and 16 April–2 May in the Yellowstone region (Inman et al. 2007). Thus the reproductive den(s) are commonly used from early February through mid-May (Fig. 2).

Weaning.—Myhre and Myrberget (1975) estimated that cubs are weaned (beginning to eat solid foods) at 7–8 weeks on the basis of stomach contents, but ages of cubs were assigned by comparison with weight curves of captive cubs, which may gain weight more quickly than wild cubs. Iversen (1972) speculated that weaning occurs at 10 weeks of age on the basis of the timing of a metabolic break he measured in 3 captive wolverine cubs, the relationship of this metabolic break and weaning in other species, and age at weaning in other carnivores. Captive cubs also become interested in solid foods at about 10 weeks (D. Pedersen, pers. comm. and A. Magoun, pers. obs.). On the basis of an age of weaning of 10 weeks and our estimated parturition dates, most cubs would be weaned during late April and May. The age at which cubs no longer nurse is unknown, but nursing can occur until about 3.5 months (D. Pedersen, pers. comm.; A. Magoun, pers. obs.). Photographs of the abdomen of a wild wolverine indicated that lactation was still occurring on 13 May but regression of teat size for this female had occurred by the time she was photographed with motion-detection cameras again on 18 June (A. Magoun, pers. obs.), although the survival of the cubs was unknown. The following year, noticeable regression in teat size for this same female had occurred by the end of June and 2 cubs were photographed with the female on July 31. Thus, nursing appears to end during late May and June.

Rendezvous sites.—Rendezvous sites are locations used after weaning where the female leaves cubs and from which they will not depart without her; the female either brings food back to the cubs or returns to lead them to a food source (Magoun 1985). Differentiation of reproductive dens and rendezvous sites at the time of weaning is based on behavioral differences associated with weaning (Magoun and Copeland 1998). Once the cubs are weaned, their need for meat increases and the female probably needs to be away from the cubs more frequently than when she is nursing them. The need to hunt, along with the cubs' ability to travel short distances, allows the female to move cubs closer to foraging sites and cached food rather than bringing food back to a den. On the basis of parturition dates, time to weaning, and observed den abandonment, rendezvous site use begins to peak in early May (Fig. 2). Magoun (1985) observed female offspring groups and suggested that the cubs began traveling regularly with their mother, rather than remaining at rendezvous sites, by late June or early July.

Independence.—Magoun (1985) showed that cubs spend a considerable amount of time foraging on their own within their mother's home range during August. However, she was not able to observe mother–offspring interactions in the latter part of July so cubs may begin foraging independently as early

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as late July. Observations of 2 captive-reared cubs taken to a remote field area for behavioral observations indicated that excursions away from the mother may begin in late July but cubs are not accomplished hunters by then (A. Magoun, pers. obs.). May (2007) radiotracked family groups (mothers and cubs) from the beginning of May to 1 March and suggested that cubs were nearly full-grown and nutritionally independent from the mother by September. The period in which cubs begin to forage on their own probably varies with birth date and growth rate.

Dispersal.—Vangen et al. (2001) studied timing of exploratory movements and dispersal of 24 known-age juvenile wolverines and found that wolverines were 11 months old on average when they made their 1st exploratory movement outside their mother's home range. The range of age at dispersal was 7–18 months for males and 7–26 months for females; median ages were 10 months for males and 11 months for females (Vangen et al. 2001). Magoun (1985) reported 2 dispersal events occurring at 8–12 months and at 12 months of age; circumstantial evidence suggested that dispersal occurred as early as January and as late as May (10–14 months of age). Copeland (1996) reported that 2 males estimated to be 2 years of age made long-distance movements outside of their own home ranges; both disappeared from radio contact in February. Inman et al. (2012) reported that exploratory movements began at 11 months of age on average (range = 8–14 months, $n = 6$) and continued through at least 36 months of age for some individuals. Inman et al. (2012) reported that pulses of dispersal-related movements appeared to occur near the time of parturition. Peak periods of exploratory and dispersal movements seem to occur at 10–15 months of age but such movements may span a period of years (Fig. 2).

Food availability.—Wolverines are opportunistic foragers and food items include caribou/reindeer (*Rangifer tarandus*), moose (*Alces alces*), mountain goats (*Oreamnos americanus*), sheep (*Ovis* spp.), elk (*Cervus elaphus*), beavers (*Castor* spp.), marmots (*Marmota* spp.), ground squirrels (*Spermophilus* spp.), voles (*Microtus* spp.), lemmings (*Lemmus* spp.), hares (*Lepus* spp.), porcupine (*Erethizon dorsatum*), birds, bird eggs, insect larva, amphibians, and berries (Copeland and Whitman 2003; Dalerum et al. 2009; Lofroth et al. 2007; Magoun 1987; Mattisson et al. 2011b; Packila et al. 2007; Samelius et al. 2002; van Dijk et al. 2008).

Adult ungulates are generally thought to be taken in the form of carrion. However, wolverine predation on semidomestic reindeer (Bjärvall et al. 1990; Haglund 1966; Landa et al. 1997; Mattisson et al. 2011b), caribou (Gustine et al. 2006; Wittmer et al. 2005), and domestic sheep (Landa et al. 1999) can occur with some regularity. Wolverine predation on other adult ungulates, such as moose, occurs at least occasionally under specific conditions (Haglund 1974; Wittmer et al. 2005). In areas where most ungulates and larger predators move to winter range that is outside of the areas used by wolverines (Inman et al. 2012; Magoun 1985), scavengeable resources may be scarce during winter. In areas where larger predators and ungulates do not move to winter ranges outside of wolverine habitat, scavengeable ungulate resources are likely available at some roughly base rate throughout the year (Mattisson et al. 2011b). In all areas, late winter (March–April) probably represents higher than usual levels of adult ungulate mortality for reasons including ease of predation with deep snow conditions or weakened animals, avalanches, starvation, and return of migrant ungulate herds (Bowyer et al. 2003; Côtè and Festa-Bianchet 2003; Krausman and Bowyer 2003; Miller 2003; Raedeke et al. 2002). Haglund (1966) suggested that March and April were the part of winter when availability of reindeer as both carcasses and prey for wolverines peaked in Scandinavia. In tundra ecosystems, movements of large numbers of migratory caribou in the same period may provide a temporary increase in available carcasses (Dalerum et al. 2009; Magoun 1985).

Wittmer et al. (2005) found that caribou in British Columbia were more likely to die from predation during spring calving and in summer than during other seasons. Neonatal ungulates are vulnerable to predation by wolverines. For example, the wolverine was the main predator on caribou calves in British Columbia (Gustine et al. 2006). Caribou (reindeer), moose, mountain goats, elk, and mountain sheep give birth in May to early June (Bowyer et al. 2003; Côtè and Festa-Bianchet 2003; Krausman and Bowyer 2003; Miller 2003; Raedeke et al. 2002). In summary, ungulate biomass accessible to wolverines probably peaks during late winter to early summer because of overwinter mortality, migration, and the birthing period. Although ungulate resources are likely to be lower during winter within all regions, this difference is far more pronounced in regions where the vast majority of ungulates and their predators migrate out of wolverine habitat during winter.

Those species of ground squirrels that overlap with wolverine distribution in North America are obligate hibernators with an active season of approximately May–September (Yensen and Sherman 2003). Dates of emergence and immergence vary annually due to weather and snow cover and squirrels can emerge as early as March and immerge as late as November (Magoun 1987; Yensen and Sherman 2003). Ground squirrels rear 1 litter per year, and young become active above ground during June. Marmots are also obligate hibernators, and the general period of emergence is April and immergence is September (Armitage 2003). Burrows are critical resources for marmots that are used by many generations (Armitage 2003), possibly providing a reliable point source of food for wolverines. Young marmots are active above ground by June (Armitage 2003). Voles are active throughout the year but become more vulnerable to predation by wolverines after snow melting exposes them, typically in May (Magoun 1987; Pugh et al. 2003). Smaller prey are also available at a low but base rate throughout the year but likely have a significant peak during May through August when snowmelt exposes microtines, hibernating rodents emerge, and the nesting season of many birds peaks.

Wolverines cache foods frequently during both winter and summer and this behavior likely extends availability beyond the peak periods of mortality and wolverine predation. The

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behavior appears to be innate given that a captive cub demonstrated caching behavior at less than 3 months of age (A. Magoun, pers. obs.). Adult females cached ground squirrels and ptarmigan (*Lagopus* spp.) during summer in Alaska, and wolverines fed on cached ground squirrels during winter (Magoun 1987). Wolverines killed and cached geese and their eggs during June and July in Nunavut; however, some of these carcasses had rotted several days later (Samelius et al. 2002). May (2007) documented that wolverines partitioned and cached reindeer carcasses within a few nights during late winter/early spring, and that portions of up to 7 individual reindeer were located at a reproductive female's den site. Mattisson (2011) used GPS collar locations to investigate kill sites and found that wolverines of both sexes and during all seasons moved back and forth between carcasses and cache sites, removing large amounts of the carcass in a short time. At present it appears that caching occurs year-round and is utilized by both sexes; however, the degree to which specific time periods, sexes, or reproductive classes may differ is unknown.

Overall, calories available to wolverines probably reach a maximum from March to August (Fig. 2). Because weather factors that cause mortality of ungulates during winter vary greatly from year to year, annual consistency of accessible food is probably greatest during summer (May–August). The diversity of food sources is also likely greatest during summer (May–June). Major differences may occur by region during winter on the basis of whether one or more ungulate species and their predator(s) remain within wolverine habitat or migrate to areas of winter range where wolverines do not occur.

Discussion

Our examination suggests that caching is likely an important behavioral adaptation that complements the morphology and demography of the wolverine and allows it to occupy its niche. Even though the vast majority (>90%) of mature female wolverines are pregnant in a given year (Banci and Harestad 1988; Rausch and Pearson 1972), mean annual proportion of females reproducing appears to be about 50% or less (Copeland 1996; Inman et al. 2007; Magoun 1985; Persson et al. 2006). This suggests that resorption or early litter loss is common. Early litter loss may be more adaptive for wolverines because the cost of gestation is low and, unlike a hibernating bear, it is possible for a female wolverine to suddenly acquire a major energetic source for lactation such as an ungulate carcass. This is consistent with the bet-hedging strategy of mustelids (Ferguson et al. 1996). Winter can be a period of unpredictable and low food availability for wolverines (Magoun 1985; Persson 2005), and caching behavior is common, including by reproductive females (Magoun 1987; May 2007). Early litter loss may occur unless caches accumulated over the winter allow sufficient female condition for lactation. Thus caches likely fuel much of the period of early lactation and may be critical for neonate survival. Accordingly, habitat features that facilitate caching may be critical for wolverine reproduction, i.e., structure that prevents access by avian and large mammalian competitors along with cold temperatures that inhibit consumption by insects and bacteria.

Caches increase the predictability of food resources, reduce the energy spent searching for food during the demanding period of lactation, and decrease the time away from vulnerable newborns. Food caching can be considered functionally analogous to storage of body fat (McNamara et al. 1990), but without added body weight, which could be important for a species like the wolverine that is forced to move over large areas in search of food (Inman et al. 2012; Mattisson 2011). Bevanger (1992:9) first noted the relevance of ''nature's own natural fridges—swamps, snowdrifts, and rocky screes,'' as important places for wolverines to store food. Magoun and Copeland (1998) also suggested that den location could be related to areas where rearing young would be improved by better food storage during summer. We expect that the limits to wolverine distribution are ultimately related to the species' ability to avoid competition by existing in cold, low-productivity environments and accumulating (caching) the limited food resources present therein. As such, we propose a ''refrigeration-zone'' hypothesis as a food/competition-based explanation for the observed correlation between wolverine distribution and the area encompassed by persistent spring snow cover (Copeland et al. 2010). This concept fits well with other characteristics that have been measured for wolverines, i.e., their spatial ecology (Inman et al. 2012; Persson et al. 2010), low densities (Golden et al. 2007; Inman et al. 2012; Lofroth and Krebs 2007; Royle et al. 2011), low fecundity (Copeland 1996; Inman et al. 2007; Magoun 1985; Persson et al. 2006), and bioclimatic envelope (Copeland et al. 2010).

Although ungulate carrion as described above may be critical due to its use during lactation and beyond, the wolverine's reproductive chronology makes it difficult to dismiss summer foods, including nonungulate prey, as insignificant or even less significant. Juvenile wolverines gain most of their adult body size within 7 months of birth, and absolute weight gain during the postweaning period is greater than that from nidation to weaning (J. Persson, A. Magoun, pers. obs.). Thus, although lactation may be the most energetically demanding period for a reproductive female, the period of postweaning growth represents a significantly greater energetic demand from the environment by the family group. For wolverines, this period of growth occurs during summer (May–August). In addition, the longer the female continues to invest in the litter, the more she borrows significant physiological resources from the next potential litter to achieve success with the current litter (Persson 2005). Therefore, litter loss that occurs during summer results in both reproductive failure in the current year and reduced potential to reproduce the next year. Early litter loss is common, but starvation as the ultimate cause of juvenile mortality during summer is rare (Persson et al. 2009). This suggests that food availability is generally higher and more predictable and/or that juveniles are less sensitive to food shortage in summertime. Summer foods, whatever they may be, are also likely to be key to wolverine reproductive success.

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Table 1.—Percentage of wolverine (*Gulo gulo*) food habit observations made during summer (May-October) and winter (November–April).

	Summer			Winter				
Reference	*n*	No. ungulate items	No. nonungulate items	*n*	No. ungulate items	No. nonungulate items	Empty	Method
Rausch and Pearson 1972[a]	.	.	.	193	44	41	99	Gastrointestinal tracts
Newell 1978[b]	15	1	16	30	9	26	.	Scats
Hornocker and Hash 1981	.	.	.	56	40	36	.	Scats
Gardner 1985[b]	9	3	6	35	16	17	.	Summer observations, winter gastrointestinal tracts
Magoun 1987	33	6	27	82	30	67	.	Summer observations, winter scats
Banci 1987	.	.	.	411	186	360	126	Gastrointestinal tracts
Poole 1992[b]	.	.	.	173	149	83	.	Stomachs
Copeland 1996	33	24	24	84	69	73	.	Scats and foraging events
Landa et al. 1997[a]	.	.	.	347	335	210	.	Scats from dens
Lofroth et al 2007	12	5	11	475	305	269	.	Scats and stomachs
Lofroth et al 2007	19	6	13	128	106	22	.	Foraging events
Packila et al. 2007	13	6	8	48	36	10	.	Scats and foraging events
Total observations	134	51	105	2,062	1,325	1,214		
% of total observations	6%			94%				

[a] Primarily winter observations, but a small number may have occurred during May.
[b] As reported by Banci (1994).

Few studies of summer food habits exist for wolverines, largely because snow-tracking is not usually possible during this period. In fact, approximately 94% of food habit samples have been obtained during winter (Table 1). Therefore it is not surprising that the items that dominate winter foraging are often thought to be of greater significance (Banci 1994; Banci and Harestad 1988; Dalerum et al. 2009; Lofroth et al. 2007; Rausch and Pearson 1972). Persson's (2005) supplemental feeding experiment suggests that winter is usually a period of low food availability for wolverines. It is possible that winter foods may typically allow wolverines to survive this season and fuel lactation in years when availability is great enough. On the basis of the timing of reproductive events, summer foods appear to have an equally important role, and the limited information specific to summer diet indicates that predation on small prey occurs frequently in most areas (Gardner 1985; Lofroth et al. 2007; Magoun 1987; Packila et al. 2007). Total biomass obtained from small prey can be significant; 1 female was observed to eat 2 small mammals or ptarmigan chicks, an adult ptarmigan, a ground squirrel, and 2 eggs during a 2½-h period in June (Magoun 1987). In addition, wolverines have been documented as the main predator of woodland caribou calves during the calving season (Gustine et al. 2006), and predation on reindeer and other ungulate neonates occurs (Bjärvall et al.



Fig. 3.—This elk calf was killed by a female wolverine (*Gulo gulo*) on 16 June 2004 in southwestern Montana. She had moved parts of the carcass to a rendezvous site where she had a cub. She dragged the remainder of the carcass to another cache site under large boulders (right photo) where there was ice that was likely to be present until autumn. Structure and cold temperatures may be critical habitat features for cache longevity because they inhibit competition from avian, mammalian (e.g., bears), insect, and bacterial competitors.

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1990; Landa et al. 1997; Mattisson et al. 2011b; Fig. 3). Given these factors, it is difficult to rule out predation during summer, including nonungulate prey, as a major factor in reproductive success and population dynamics of wolverines. Therefore, cached ungulate carrion and summer foods both appear to play critical roles in reproductive success for wolverines.

Despite the wolverine's flexibility in utilizing a wide variety of food resources and obtaining them through both scavenging and predation, it may be important to consider regionally and seasonally specific food resources that influence reproduction. If managers assume that wolverines scavenge ungulate carrion provided by larger predators and only occasionally utilize small prey, they could logically conclude that ensuring adequate food supplies simply consists of maintaining significant ungulate herds along with large predators. Although this might hold true in some areas, failure to ensure adequate populations of small prey could lead to deficient energetic supplies for reproduction in other areas. Better information on summer food habits of wolverines is needed within each of the biomes where the species occurs. Information on female body condition throughout the year would also be valuable in understanding key resources and limiting factors.

Wolverines were recently listed as warranted for protection under the ESA based in large part on the threat of climate change reducing distribution and connectivity (McKelvey et al. 2011; United States Fish and Wildlife Service 2010). To develop conservation actions for the species, we must understand the direct cause or causes by which climate limits distribution. For instance, is there an average ambient temperature above which wolverines are physiologically compromised? Will females be unable to find a denning area with sufficient thermal cover for cubs if snowpack changes during spring? Will competition for food increase if snow conditions allow prolonged presence of terrestrial competitors and higher temperatures compromise the wolverine's ability to cache food away from insects and bacteria? Although these hypotheses are not mutually exclusive, our examination of the wolverine's reproductive chronology suggests that it is important to include summer foods and the influence of climate on competition for food as potential drivers of wolverine population dynamics. By doing so, the causes of projected declines due to climate change, should they occur, may be better understood and acted upon.

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