

# Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability

Jens Persson

**Abstract:** An individual has only a given amount of resources, and therefore an increase in one demographic trait results in a trade-off that necessitates a decrease in a different demographic trait. In general, the main factor determining an individual mammal's reproductive investment is food supply. This study addresses how female wolverine (*Gulo gulo* (L., 1758)) reproduction is limited. I tested two complementary hypotheses: (1) current reproduction is affected by the costs of reproduction in the preceding year and (2) current reproduction is affected by food availability in the current winter. I addressed the first hypothesis by comparing reproductive rates of females in relation to their reproductive effort in the preceding year. I experimentally tested the second hypothesis by comparing reproductive rates of food-supplemented females versus non-supplemented females. Reproduction incurred costs on female wolverines that affected future reproduction, and reproductive costs appeared to be related to the duration of parental care. Reproduction was higher for food-supplemented females than for non-supplemented females, even though all food-supplemented females had reproduced the preceding year. This study suggests that reproduction is limited by winter food availability and that additional food can compensate for reproductive costs. Thus, I suggest that female wolverine reproduction is determined by their condition in winter, which is a result of the combined effect of reproductive costs and winter food availability.

**Résumé :** Un individu possède une quantité limitée de ressources et donc toute amélioration d'une caractéristique démographique se traduit par un compromis qui requiert la réduction d'une autre caractéristique démographique. En général, le facteur principal qui détermine l'investissement reproductif d'un mammifère individuel est la provision de nourriture. La présente étude s'intéresse au contrôle de la reproduction chez les femelles du glouton (*Gulo gulo* (L., 1758)). Deux hypothèses complémentaires ont été testées : (1) la reproduction de l'année courante est affectée par les coûts de la reproduction de l'année précédente et (2) la reproduction de l'année courante est affectée par la disponibilité de nourriture pendant l'hiver de cette même année courante. La première hypothèse a pu être vérifiée par la comparaison des taux reproductifs des femelles en fonction de leur effort reproductif de l'année précédente. La comparaison des taux reproductifs de femelles qui reçoivent des suppléments alimentaires et de celles qui n'en reçoivent pas sert à vérifier expérimentalement la seconde hypothèse. La reproduction chez les gloutons femelles entraîne des coûts qui affectent les reproductions futures et ces coûts semblent reliés à la durée des soins parentaux. La reproduction est plus importante chez les femelles qui reçoivent des suppléments alimentaires que chez celles qui n'en ont pas, même si toutes les femelles qui ont reçu des suppléments se sont reproduites l'année précédente. Les résultats laissent croire que la reproduction est limitée par la disponibilité de nourriture en hiver et que de la nourriture supplémentaire peut contrebalancer les coûts reproductifs. Il semble donc que la reproduction des gloutons femelles soit déterminée par leur condition en hiver qui résulte de l'effet combiné des coûts reproductifs et de la disponibilité de nourriture en hiver.

[Traduit par la Rédaction]

## Introduction

Revealing which factors affect the number of offspring produced over the life span of individuals is important in understanding a species population dynamics (Lomnicki 1978; Stearns 1992). The number of reproductive events in iteroparous animals is a more substantial component of fitness than a given breeding event (Ruusilla et al. 2000). Variance in environmental factors makes it difficult for an individual to predict availability of resources, e.g., food, that are

needed for future reproductive investments. This leads to a central feature of life-history theory, that variation in demographic traits are circumscribed by the existence of trade-offs. Trade-offs are linkages between traits that constrain the simultaneous optimization of two or more traits (Stearns 1992). An individual has only a given amount of resources, and therefore an increase in one trait implies a decrease in another. Some of the most studied trade-offs are related to the cost of reproduction, e.g., trade-offs between current reproduction and future reproduction (Ericsson 2001).

Received 11 February 2005. Accepted 21 September 2005. Published on the NRC Research Press Web site at <http://ejz.nrc.ca> on 4 November 2005.

**J. Persson.**<sup>1</sup> Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.

<sup>1</sup>Present address: Grimsö Wildlife Research Station, Department of Conservation Biology, Swedish University of Agricultural Sciences, SE-730 91 Sweden (e-mail: [jens.persson@nvb.slu.se](mailto:jens.persson@nvb.slu.se)).

The impact of reproduction on an animal's physiological condition can be dramatic and have significant consequences for future reproduction, as well as survival, growth, and condition (Roff 1992; Stearns 1992). Several studies have revealed negative phenotypic correlations between components of reproductive success in mammals (e.g., Clutton-Brock et al. 1983; Berger 1989; Green and Rothstein 1991; Sydeman et al. 1991; Hogg et al. 1992; Marrow et al. 1996; Ruusilla et al. 2000). However, other studies of reproductive costs in mammals have not shown trade-offs (e.g., Murie and Dobson 1987; Festa-Bianchet 1989; Millar et al. 1992), and some have even shown positive associations between fitness components (Clutton-Brock 1991; Ericsson 2001). The most likely explanation for the latter is differences in individual reproductive potential (Clutton-Brock 1991; Festa-Bianchet et al. 1998). Other confounding variables that could obscure costs of reproduction are effects of parental phenotype or early environment on offspring phenotype and environmental differences affecting reproduction (Clutton-Brock 1991). The effect of varying environmental conditions is illustrated by reproductive costs being more pronounced or only occurring at high densities and (or) in harsh environments (Clutton-Brock 1991; Festa-Bianchet et al. 1998), showing that physiological costs of reproduction does not necessarily result in fitness costs of reproduction.

An individual's reproductive investments respond to population density and food supply (Stearns 1992; Sæther et al. 1996). Terrestrial vertebrate populations in temperate environments are frequently limited by food supply (Boutin 1990), and variability in food availability often causes annual variation in mammal reproduction (Bronson 1989). Accordingly, food availability affects reproductive rates in many carnivore species (Kirkpatrick 1988; Boertje and Stephenson 1992; White and Ralls 1993; Fuller and Sievert 2001). To support the energetic costs of late pregnancy and lactation, maternal food intake must increase and (or) the energy accumulated prior to reproduction or during early pregnancy must be mobilized (Loveridge 1986; Gittleman and Thompson 1988). The most energy-consuming activities related to reproduction are lactation and feeding young (Sadleir 1969; Bronson 1989; Clutton-Brock 1991), and the condition of the mother likely affects offspring survival (Tait 1980; Derocher and Stirling 1996).

Because of low sample sizes in previous studies of wolverine reproduction, there are very few data on which to assess reproduction processes in wolverines (*Gulo gulo* (L., 1758)), or to determine which ecological factors limit reproduction in adult female wolverines. The proportion of pregnant adult females ( $\geq 3$  years) in earlier studies have ranged from 73% to 92% (Rausch and Pearson 1972; Liskop et al. 1981; Banci and Harestad 1988), suggesting that most adult females mate every year. However, the proportion of females producing kits in studies of free-ranging wolverines is lower (Magoun 1985; Copeland 1996; Persson et al. 2006). In fact, low reproductive frequency compared with high pregnancy rate suggests that reproduction represents a high cost for female wolverines, so high that it might influence future reproduction. The reproductive effort for mustelids, such as wolverines, with delayed implantation is proportioned differently and may be even higher than that of other placental mammals (Harlow 1994). There are possible energetic ad-

vantages of prolonged gestation and short lactation over short gestation and prolonged lactation (Lilligraven 1975). But delayed implantation has short gestation and long lactation, if gestation is defined as the period of rapid development after implantation (Harlow 1994). For example, Harlow et al. (1985) estimated that the energetic cost to an American badger (*Taxidea taxus* (Schreber, 1777)) mother nursing two pups during a 40 day lactation period was 16 times that of gestation. Accordingly, the overall reproductive effort from implantation to weaning would be expected to be greater for mammals that have a short gestation and lengthy lactation period (Harlow 1994). Most wolverines give birth in February and early March (Pulliainen 1968; Blomqvist 2001), implying that implantation often occurs in early January. Kits (i.e., juveniles 0–1 year old) are weaned at 9–10 weeks of age (Iversen 1972) and appear to be independent of their mother in August at 5–6 months of age (Vangen et al. 2001).

Wolverines commonly cache large amounts of food (Banci 1994), which is typical for animals facing unpredictable or varying food resources (Roberts 1979; Lea and Tarpay 1986). Availability of food for wolverines in my study area is presumably dependent on movements of migrating semi-domesticated reindeer (*Rangifer tarandus* (L., 1758)) (Björvall et al. 1990) and is therefore unpredictable in winter. Reindeer exhibit seasonal migration, resulting in lower densities in early to late winter in the mountains where most wolverines reproduce in my study area, when other potential prey are relatively scarce, resulting in a temporary shortage of food.

In this paper I tested two complementary hypotheses of female wolverine reproduction: (1) reproduction is affected by the costs of reproduction the preceding year and (2) reproduction is affected by winter food availability. I tested the first hypothesis by comparing reproductive rates of females in relation to their reproductive effort in the preceding year. I also examined whether reproduction was influenced by the duration of parental care the preceding year, particularly whether costs of denning only (i.e., kits are lost before weaning) or weaning kits had differential effects. I experimentally tested the second hypothesis by comparing reproductive rates of food-supplemented females to that of non-supplemented females. Finally I evaluated the interactive effects of reproductive costs and winter food availability on the reproduction of female wolverines.

## Methods

### Study area

I carried out the study in and around Sarek National Park in the County of Norrbotten, in northwestern Sweden (Kvikkjokk: 67°00'N, 17°40'E). The approximate size of the study area was 7000 km<sup>2</sup>. The climate is continental with cold winters (−10 to −13 °C in January) and medium warm summers (13 to 14 °C in July). The annual precipitation is low in the eastern part of the area (500–1000 mm), but higher in the western part (around 2500 mm) (Påhlsson 1984; Björvall et al. 1990). The ground is usually snow-covered from October to May. The Sarek area is characterized by downy birch (*Betula pubescens* Ehrh.), Scots pine (*Pinus sylvestris* L.), and Norway spruce (*Picea abies* (L.)

Karst.) and consists of deep valleys, glaciers, and high plateaus with peaks up to 2000 m above sea level (a.s.l.) (Grundsten 1997). Downy birch forms the treeline and reaches a maximum of 600–700 m a.s.l. (Grundsten 1997). Semi-domesticated reindeer are managed extensively by the indigenous Sámi people. Breeding populations of brown bear (*Ursus arctos* L., 1758) and Eurasian lynx (*Lynx lynx* (L., 1758)) occur in the area. Moose (*Alces alces* (L., 1758)) is the only wild ungulate occurring in significant numbers, although in low densities. The approximate density of wolverines in the study area is 1.4/100 km<sup>2</sup> (based on the number of recorded natal dens; for details see Landa et al. 1998).

### Capture and instrumentation

A total of 20 radio-marked female wolverines >24 months old were monitored during the study period (1993–2001). On average, data were available for each female for 3.4 years (range 2–6 years). The wolverines were captured and immobilized with xylazine and ketamine during the 1993–1998 study period (Armeno et al. 1998), and with medetomidine and ketamine during the 1999–2001 study period. Adult wolverines were equipped with intraperitoneally implanted transmitters (Telonics<sup>®</sup> Imp/210/L, Imp/300/L or Imp/400/L; 30–90 g; Telonics<sup>®</sup> Inc., Mesa, Arizona) or collar-mounted radio transmitters (Telonics<sup>®</sup> Model 315; 150–200 g). See Persson et al. (2003) for details on capture and marking of kits. The study was approved by the Animal Ethics Committee for northern Sweden, Umeå. Animals handled in the study were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1993).

### Data collection

I measured reproduction in two complementary ways. First, I documented denning behaviour to reveal whether females reproduced or not. Second, I documented presence and number of offspring in May to early June to reveal whether females weaned kits. I refer to mid-February to early May as the denning season. Denning behaviour was determined primarily by intensive radio-tracking of females from aircraft and ground. Occasionally, wolverines exhibit very restricted movements concentrated around a food source, e.g., moose carcasses, resulting in a risk of confusing a food cache with a den. Den sites show typical characteristics (Magoun and Copeland 1998), which makes it possible to separate dens from food caches. Therefore, suspected dens were also visited on the ground to search for typical characteristics of a den (e.g., the same hole in the snow is used during an extended period and is surrounded by trails leading in and out of the hole). In no case did this disturbance result in den abandonment. The presence of kits and of litter size was determined from early May to early June either by snow-tracking, visual observation, and (or) by capturing family groups.

Females that were confirmed to reproduce, based on denning behaviour, but lost the kits before weaning were defined as unsuccessful denning females, and females documented to have kits in mid-May to early June were defined as weaning females. Reproductive females referred to both categories combined. Assuming birth date at 1 March, unsuccessful denning females had kits for 1–2.5 months, whereas weaning females had kits for at least 2.5 months.

Preliminary data (1993–1998) indicated an every 2nd year pattern in female wolverine reproduction, suggesting that reproduction was limited by food and (or) affected by reproductive costs. Thus, to test the effect of winter food availability and reproductive costs on reproduction I also performed a complimentary food-supplementation experiment. I compared the reproductive outcome of food-supplemented females with that of control (non-supplemented) females. I used the same four females all years for logistic reasons, i.e., their home ranges were accessible by snow machine in December. All food-supplemented females had reproduced (one denning, three weaning) the year preceding the experiment to ensure a conservative result (cf. cost of reproduction). The females were provided with road-killed moose and reindeer in early December to early January in 3 consecutive years (1998–2000). It is widely known that wolverines cache large amounts of food (Banci 1994). Therefore, the extensive food supplementation in December should enhance food availability over an extended period, i.e., at least until March. Each female was supplied with the equivalent of at least seven adult reindeer each winter. Use of carrion by the targeted females was confirmed with a combination of intensified radio-tracking and snow-tracking.

### Analyses

To determine if there is a cost of reproduction, I compared the reproductive rates in consecutive years ( $t$  and  $t + 1$ ) for females that had reproduced in year  $t$  with those that had not. This comparison included unsuccessful denning females in both years, but because some of their kits may have been lost early and some late in the denning period, reproductive effort was probably variable. Therefore, to be conservative I also analysed the data after eliminating unsuccessful denning females in year  $t$  and  $t + 1$ . Food-supplemented females were not included in the comparative test of reproductive costs.

I used three pairwise comparisons to investigate the relationship between cost of reproduction and duration of parental care by comparing frequency of reproduction and weaning in year  $t + 1$  between females in the following groups: (i) females that weaned a litter in year  $t$  and females that did not wean litters in year  $t$ , i.e., the latter category includes both unsuccessful denning females and females that did not reproduce; (ii) unsuccessful denning females from year  $t$  and weaning females from year  $t$ ; and (iii) unsuccessful denning females from year  $t$  and females that did not reproduce in year  $t$ .

In the experiment, I compared reproductive frequency (proportion of females reproducing), weaning frequency, and birth rate (kits/female per year) between food-supplemented females ( $n = 4$ ) and non-supplemented females (control group,  $n = 12$ ) that were monitored during the same time period (1999–2001). All food-supplemented females had reproduced in the year preceding supplemental feeding.

As the data did not meet the requirements of parametric tests, nonparametric tests were used in all analyses. Because of small sample sizes, I was more concerned with type II than type I errors. Therefore, all analyses were considered biologically significant when  $P < 0.10$ . Probability levels are two-tailed in all analyses of reproductive costs. Because preliminary data indicated effects of reproductive costs and (or)

food limitation, I used one-tailed probability levels in all analyses of the effects of food supplementation.

## Results

### Cost of reproduction

Females that did not reproduce in year  $t$  showed a higher reproductive frequency in year  $t + 1$  (0.71,  $n = 17$ ) than females that reproduced in year  $t$  (0.39,  $n = 31$ ) ( $\chi^2$ , corrected for continuity = 3.28,  $P = 0.07$ ). Moreover, females that did not reproduce in year  $t$  produced 3.2 times more offspring per female in year  $t + 1$  ( $1.12 \pm 1.16$  (mean  $\pm$  SD),  $n = 17$ ) than females that had reproduced in year  $t$  ( $0.35 \pm 0.80$ ,  $n = 31$ ) (Mann–Whitney  $U$  test,  $Z = 2.7$ ,  $P = 0.01$ ; Fig. 1).

When all unsuccessful denning females were excluded from the analysis, the proportion of weaning females was higher in year  $t + 1$  after no reproduction in year  $t$  (0.64,  $n = 14$ ) than it was in year  $t + 1$  after weaning in year  $t$  (0.19,  $n = 21$ ) (Fisher's exact test,  $P = 0.01$ ).

Finally, I investigated the relationship between reproductive effort in year  $t$  and year  $t + 1$  by ranking effort in the following way, i.e., no reproduction is 0, denning but no kits in May is 1, one kit in May is 2, two kits in May is 3, and three kits in May is 4. There was a negative relationship between birth rate in year  $t + 1$  and the total reproductive effort in year  $t$  (Spearman's rank correlation,  $r_s = -0.37$ ,  $P = 0.01$ ,  $n = 48$ ). In conclusion, the foregoing results show that reproduction incurs costs on wolverine females that affect reproduction the subsequent year.

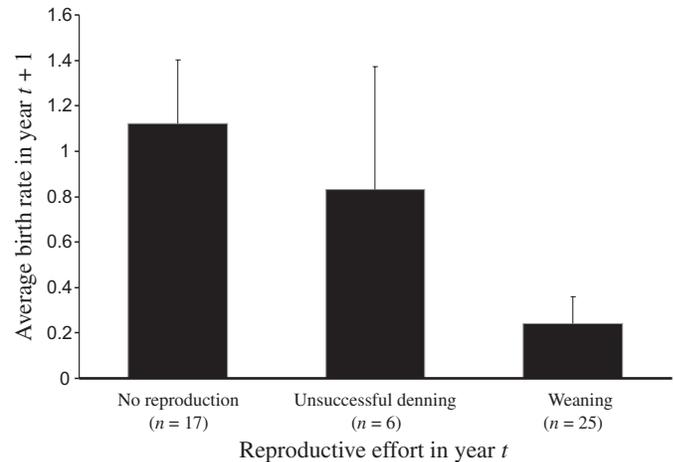
### Reproductive costs and duration of parental care

Both the proportion of reproducing females and the proportion of weaning females were significantly higher in year  $t + 1$  if they did not wean kits in year  $t$  (0.70,  $n = 23$  and 0.48,  $n = 23$ , respectively) than if they did wean kits in year  $t$  (0.47,  $n = 25$  and 0.16,  $n = 25$ , respectively), (Fisher's exact test,  $P = 0.02$  and  $P = 0.03$ , respectively). In contrast, there was no difference in reproductive frequency when females that did not reproduce (0.71,  $n = 17$ ) were compared with unsuccessful denning females (0.67,  $n = 6$ ) (Fisher's exact test,  $P > 0.99$ ). These results imply that reproductive costs are related to the duration of parental care.

### Effect of winter food availability on reproduction

All 4 food-supplemented females reproduced in 3 consecutive years (including the year preceding the start of the experiment), whereas only 2 of 11 (18%) non-supplemented females monitored  $\geq 3$  consecutive years (1993–2001) did the same (Fisher's exact test,  $P = 0.01$ ). A higher proportion of food-supplemented females reproduced (0.83,  $n = 12$ ) than did non-supplemented females (0.52,  $n = 21$ ) (Fisher's exact test,  $P = 0.08$ ). Also, a higher proportion of food-supplemented females weaned kits (0.58,  $n = 12$ ) than did females in the control group (0.29,  $n = 21$ ) (Fisher's exact test,  $P = 0.09$ ). Food-supplemented females showed a tendency to have higher birth rates ( $0.92 \pm 0.90$ ) than non-supplemented females ( $0.62 \pm 1.02$ ) (Mann–Whitney  $U$  test,  $P = 0.13$ ). Altogether, these results suggest that food availability in winter influences wolverine female reproduction.

**Fig. 1.** Average ( $\pm$ SE) birth rate for wolverine females in year  $t + 1$  in relation to reproductive effort in year  $t$ . Females that reproduced in year  $t$  are separated into females that lost their kits before weaning (“unsuccessful denning”) and females that weaned kits in year  $t$  (“weaning”).



## Discussion

The results in this study support the hypotheses that the cost of reproduction in the preceding year affects current reproduction and that food availability in winter also affects reproduction in wolverines. Therefore, the reproductive success of a wolverine female in a given year is partly determined by the combined effect of the preceding year's reproductive effort and winter food availability.

### Effects of previous reproduction on current reproduction

I have in this study confirmed that a wolverine female incurs costs in a year when she reproduces that affects reproduction in the subsequent year. Negative effects of the previous reproduction on current reproduction have also been shown for a small number of large mammal species (e.g., Clutton-Brock et al. 1983; Berger 1989; Ruusilla et al. 2000), but to my knowledge no corresponding studies have been performed on carnivores.

Energy expenditure at peak lactation commonly lies between 2.5 and 5 times that for non-reproductive female mammals (Clutton-Brock 1991). In carnivores, the estimated energy output in milk during 1 day at peak lactation is similar to or greater than the estimated energy content of the entire litter at birth (Ofstedal and Gittleman 1989). Energy deposition during pregnancy, expressed relative to maternal energy requirements, is low for most mustelids (Ofstedal and Gittleman 1989). Moreover, litter mass of wolverines (percentage of maternal mass) is low (2.7%) compared with the litter mass of most carnivores (0.1%–22%; Ofstedal and Gittleman 1989). In contrast, the basic metabolic rate of wolverines during their first months of life is higher than reported for most other mammals (Iversen 1972). Delayed implanters have short gestation and long lactation (Harlow 1994), and can therefore be expected to incur high costs of

lactation and provisioning young, relative to pregnancy, that would affect reproduction the following year.

My results suggest a relation between the duration of parental care and reproductive rate in the following year. First, there was a larger effect on subsequent reproductive frequency when only weaning was accounted for. Second, there was a significant difference in both reproductive and weaning frequencies when unsuccessful denning females were grouped together with non-reproductive females. In fact, the difference in the proportion of females that reproduced the following year was larger when unsuccessful denning females were included in the non-reproductive category than when unsuccessful denning females were grouped together with weaning females. Furthermore, although sample size was small, there was no statistical difference in reproductive frequency between years preceded by no reproduction (0.71) and years preceded by unsuccessful denning (0.67). Altogether, these results suggest that females that wean kits, i.e., lactate during the entire denning period and in most cases also provisioned young after weaning, incur higher costs than females that reproduced and lactate during a shorter time period (i.e., lose their kits before weaning).

Note that the relation between duration of parental care and reproductive rate the subsequent year is due to both lactation and provisioning of young. Juvenile survival from weaning to independence is about 0.78 (Persson et al. 2003), suggesting that most weaning females provisioned kits until independence. Young wolverines grow quickly after weaning and achieve adult size by 7 months of age (Magoun 1985). Rapid growth, before and after weaning, should place high energetic demands on mothers (Banci 1987), both when lactating and provisioning young, which could induce reproductive costs on fitness parameters.

### Effect of winter food availability on reproduction

Results from the food-supplementation experiment support the hypothesis that reproduction is influenced by food availability in winter. The proportion of food-supplemented females that reproduced for 3 consecutive years was 5.5 times higher than that for non-supplemented females over all years. Moreover, reproductive frequency and weaning frequency was higher for food-supplemented females than for non-supplemented females, and there was a strong tendency for a higher birth rate. These effects were seen despite the fact that all food-supplemented female years were preceded by a reproductive year (cf. reproductive costs).

In general, the birth of young must coincide with favourable conditions for optimum growth, and the timing of mating must allow for the necessary gestational development (Asa 1987). However, wolverines have delayed implantation, which makes timing of birth and mating independent (Mead 1989). Banci (1994) suggested that parturition of wolverines in winter is favoured by the availability of ungulate carrion and enhanced security cover for kits in winter. Yet, food availability for Scandinavian wolverines in winter is presumably dependent on migrating reindeer, whose movements are influenced by seasonal snow conditions and Sámi reindeer herding practices. Reindeer migrate in the late fall from most parts of my study area, and although variable in time and space, the return migration is often in early spring (Björvall et al. 1990), coinciding with the latter part of lactation for

wolverines. Therefore, reindeer are often rare in mid-winter in the area with highest densities of wolverines. To support the energetic costs of late pregnancy and lactation, maternal food intake must increase and (or) the energy accumulated prior to reproduction or during early pregnancy must be mobilized (Oftedal and Gittleman 1989). Wolverines cache food when it is abundant and subsequent consumption of this food may be important during periods of food shortage or to supplement the diet of growing young (Vander Wall 1990; Pasitschniak-Arts and Lariviere 1995). Food caching can be functionally analogous to storage of body fat (McNamara et al. 1990). I suggest that the availability of carrion in late fall and early winter, which can be cached for use over the entire winter, is an important determinant of female wolverine condition at the time of pregnancy and early lactation and determines the reproductive success of female wolverines.

### Relationship between reproductive costs and food availability

That food-supplemented females showed higher reproduction than non-supplemented females, despite the fact that they had all reproduced the preceding year, strongly suggests that a supply of extra food compensates for costs of previous reproduction. This is consistent with suggestions that costs of reproduction may depend on resource availability (e.g., Ruusilla et al. 2000). For instance, Koskela et al. (1998) found that litter-size enlargements in the bank vole (*Clethrionomys glareolus* (Schreber, 1780)) did not decrease the body mass of weanlings when females obtained extra food. Other studies have shown that observed effects of reproductive costs change with density (Clutton-Brock et al. 1983; Festa-Bianchet et al. 1995, 1998; Berube et al. 1996), proposing a causal relationship between available nutrition and reproductive costs. In accordance with this, the observed effects of reproductive costs and food availability on wolverine reproduction suggest that costs of previous reproduction and food availability interact to determine the condition of wolverine females, which in turn determine reproductive success.

### Conclusions

I suggest that reproductive success of wolverine females is ultimately determined by their condition at the time of implantation, pregnancy, and probably most importantly, during lactation. Moreover, condition of wolverine females during this critical phase is determined by combined effects of costs from the preceding year's reproduction and food availability in winter of the current year, where the effect of reproductive costs on reproduction is inversely related to winter food availability. Thus, the proximate factor in regulation of reproduction in wolverine females is the combined effect of reproductive costs and food availability.

Higher reproduction among food-supplemented females suggests that reproductive costs could be related to population density and that wolverine reproduction is limited by winter food availability in the study area. Hence, reproductive costs would lower reproduction at higher densities and low food availability, whereas higher food availability would compensate for reproductive costs in low-density populations. However, wolverines are territorial and winter food

availability in my study area is presumably quite variable. Therefore, I envision that temporal and spatial variation in availability of reindeer, owing to reindeer migration patterns, snow conditions, and the occurrence of other predators, could overshadow the immediate effects of changes in wolverine density per se. On the other hand, density might affect the potential for wolverines to adapt spatially to changing food availability, e.g., increasing or changing territories if they can, according to spatial variation in food availability. Thus, costs of reproduction may be more likely to be compensated for by high food availability at low densities than at high densities, if density is related to carrying capacity.

## Acknowledgments

I thank Tom Wiklund and Peter Segerström for their proficient work in the field, and Jon Arnemo for conducting the veterinary aspects of the study. I appreciate constructive comments on earlier drafts of the manuscript by Göran Ericsson, Audrey Magoun, Jon Swenson, and Henrik Andrén. The study was financed by the Swedish Environmental Protection Agency, World Wildlife Fund Sweden, and the Norwegian Directorate for Nature Management. I also acknowledge the Kempe Foundation for financial support.

## References

- Arnemo, J.M., Dypsund, P., Berntsen, F., Schulze, J., Wedul, S.J., Ranheim, B., and Lundstein, L. 1998. Bruk av implanterbare radiosendere på store rovdyr (Use of intraperitoneal radio-transmitters in large carnivores). *Nor. Veterinærtidsskr.* **110**: 799–803. [In Norwegian with English summary.]
- Asa, C.S. 1987. Reproduction in carnivores and ungulates. *In* *Psychobiology of reproductive behavior; an evolutionary approach*. Edited by D. Crews. Prentice-Hall Inc., Englewood Cliffs, N.J. pp. 258–290.
- Banci, V. 1987. Ecology and behaviour of wolverine in Yukon. M.S. thesis, Simon Fraser University, Burnaby, B.C.
- Banci, V. 1994. Wolverine. *In* *The scientific basis for conserving forest carnivores. American marten, fisher, lynx and wolverine in the western United States*. Edited by L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski. U.S. For. Serv. Gen. Tech. Rep. RM No. 254. pp. 99–123.
- Banci, V., and Harestad, A.S. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Ann. Zool. Fenn.* **25**: 265–270.
- Berger, J. 1989. Female reproductive potential and its apparent evaluation by male mammals. *J. Mammal.* **70**: 347–358.
- Berube, C.H., Festa-Bianchet, M., and Jorgenson, J.Y. 1996. Reproductive costs of sons and daughters in Rocky mountain bighorn sheep. *Behav. Ecol.* **7**(1): 60–68.
- Björvall, A., Franzén, R., Nordkvist, M., and Åhman, G. 1990. Renar och rovdjur. Naturvårdsverket förlag, Solna, Stockholm. [In Swedish.]
- Blomqvist, L. 2001. Management of captive wolverines *Gulo gulo* in Europe: studbook and guidelines to husbandry. Vol. 2. European Association of Zoos and Aquaria. VTT-Grafiska, Vimmerby, Sweden.
- Boertje, R.D., and Stephenson, R.O. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. *Can. J. Zool.* **70**: 2441–2443.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* **68**: 203–220.
- Bronson, F.H. 1989. *Mammalian reproductive biology*. The University of Chicago Press, Chicago.
- Canadian Council on Animal Care. 1993. *Guide to the care and use of experimental animals*. Vol. 1, 2nd ed. Canadian Council on Animal Care, Ottawa, Ont.
- Clutton-Brock, T.H. 1991. *The evolution of parental care*. Monographs in behavior and ecology. Princeton University Press, Princeton, N.J.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1983. The costs of reproduction to red deer hinds. *J. Anim. Ecol.* **52**: 367–383.
- Copeland, J.P. 1996. *Biology of the wolverine in central Idaho*. M.S. thesis, University of Idaho, Moscow.
- Derocher, A.E., and Stirling, I. 1996. Aspects of juvenile survival in polar bears (*Ursus maritimus*). *Can. J. Zool.* **234**: 527–536.
- Ericsson, G. 2001. Reduced cost of reproduction in moose (*Alces alces*) through human harvest. *Alces*, **37**(1), 61–69.
- Festa-Bianchet, M. 1989. Individual differences, parasites, and the cost of reproduction for bighorn ewes (*Ovis canadensis*). *J. Anim. Ecol.* **58**: 785–795.
- Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M., and Wishart, W.D. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. *Ecology*, **76**: 871–881.
- Festa-Bianchet, M., Gaillard, J.-M., and Jorgenson, J.T. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* **152**: 367–379.
- Fuller, T.K., and Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. *In* *Carnivore conservation*. Edited by J.L. Gittleman, S.M. Funk, D. MacDonald, and R.K. Wayne. Cambridge University Press, Cambridge. pp. 163–178.
- Gittleman, J.L., and Thompson, S.D. 1988. Energy allocation in mammalian reproduction. *Am. Zool.* **28**: 863–875.
- Green, W.C.H., and Rothstein, A. 1991. Trade-offs between growth and reproduction in female bison. *Oecologia (Berl.)*, **86**: 521–527.
- Grundsten, C. 1997. *The Laponian area — a Swedish world heritage site*. Swedish Environmental Protection Agency. Fälths Tryckeri AB, Stockholm.
- Harlow, H.J. 1994. Trade-offs associated with the size and shape of American martens. *In* *Martens, sables and fishers: biology and conservation*. Edited by S.W. Buskirk, A.S. Harestad, and M.G. Raphael. Cornell University Press, Ithaca, N.Y. pp. 402–422.
- Harlow, H.J., Miller, B., Ryder, T., and Ryder, L. 1985. Energy requirements for gestation and lactation in a delayed implanter, the American badger. *Comp. Biochem. Physiol. A*, **82**: 885–889.
- Hogg, J.T., Hass, C.C., and Jenni, D.A. 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behav. Ecol. Sociobiol.* **31**: 243–251.
- Iversen, J.A. 1972. Metabolic rate of wolverines during growth. *Norw. J. Zool.* **20**: 317–322.
- Kirkpatrick, R.L. 1988. Comparative influence of nutrition on reproduction and survival of wild birds and mammals — an overview. Caesar Kleberg Wildlife Research Institute, Texas A&M University, Kingsville.
- Koskela, E., Jonsson, P., Hartikainen, T., and Mappes, T. 1998. Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus*. *Proc. R. Soc. Lond. B Biol. Sci.* **265**: 1129–1134.
- Landa, A., Franzén, R., Tufto, T.B.J., Lindén, M., and Swenson, J.E. 1998. Wolverines in Scandinavia: population size and distribution. *Wildl. Biol.* **4**: 159–168.

- Lea, S.E.G., and Tapy, R.M. 1986. Hamster's demand for food to eat and hoard as a function of deprivation and cost. *Anim. Behav.* **34**: 1759–1768.
- Lilligraven, J.A. 1975. Biological considerations of the marsupial-placental dichotomy. *Evolution*, **29**: 709–722.
- Liskop, K.S., Sadleir, R.M.F.S., and Saunders, B.P. 1981. Reproduction and harvest of wolverine (*Gulo gulo*) in British Columbia. In Proceedings of the Worldwide Furbearer Conference, Worldwide Furbearer Conference, Frostburg, Maryland, 3–11 August 1980. Edited by J.A. Chapman and B.P. Pursley. Worldwide Furbearer Conference Inc., Frostburg, Md. pp. 469–477.
- Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. *J. Anim. Ecol.* **47**: 461–475.
- Loveridge, G.G. 1986. Bodyweight changes and energy intake of cats during gestation and lactation. *Anim. Technol.* **37**: 7–15.
- Magoun, A.J. 1985. Population characteristics, ecology and management of wolverines in north-western Alaska. Ph.D. thesis, University of Alaska, Fairbanks.
- Magoun, A.J., and Copeland, J.P. 1998. Characteristics of wolverine reproductive den sites. *J. Wildl. Manag.* **62**: 1313–1320.
- Marrow, P., McNamara, J.M., Houston, A.I., Stevenson, I.R., and Clutton-Brock, T.H. 1996. State-dependent life history evolution in Soay sheep: dynamic modelling of reproductive scheduling. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* No. 351. pp. 17–32.
- McNamara, J.M., Houston, A.I., and Krebs, J.R. 1990. Why hoard? The economics of food storing tits *Parvis* spp. *Behav. Ecol.* **1**: 12–23.
- Mead, R.A. 1989. The physiology and evolution of delayed implantation in carnivores. In *Carnivore behaviour, ecology, and evolution*. Edited by J.L. Gittleman. Vol. 2. Cornell University Press, Ithaca, N.Y. pp. 437–464.
- Millar, J.S., Derrickson, E.M., and Sharpe, S.T.P. 1992. Effects of reproduction on maternal survival and subsequent reproduction in northern *Peromyscus maniculatus*. *Can. J. Zool.* **70**: 1129–1134.
- Murie, J.O., and Dobson, F.S. 1987. The costs of reproduction in female Columbian ground squirrels. *Oecologia (Berl.)*, **73**: 1–6.
- Oftedal, O.T., and Gittleman, J.L. 1989. Patterns of energy output during reproduction in carnivores. In *Carnivore behaviour, ecology, and evolution*. Edited by J.L. Gittleman. Vol. 1. Cornell University Press, Ithaca, N.Y. pp. 355–378.
- Pasitschniak-Arts, M., and Larivière, S. 1995. *Gulo gulo*. *Mamm. Species*, **499**: 1–10.
- Persson, J., Willebrand, T., Landa, A., Andersen, R., and Segerström, P. 2003. The role of intraspecific predation in the survival of juvenile wolverines. *Wildl. Biol.* **9**: 21–28.
- Persson, J., Landa, A., Andersen, R., and Segerström, P. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *J. Mammal.* **87**. In press.
- Pulliaainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. *Ann. Zool. Fenn.* **5**: 338–344.
- Påhlsson, L. 1984. Naturgeografisk regionindelning av Norden. Nordiska ministerrådet, Stockholm. [In Swedish.]
- Rausch, R.A., and Pearson, A.M. 1972. Notes on the wolverine in Alaska and the Yukon territory. *J. Wildl. Manag.* **36**: 249–268.
- Roberts, R.C. 1979. The evolution of avian food-storing behavior. *Am. Nat.* **114**: 418–438.
- Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.
- Ruusilla, V., Ermala, A., and H. Hyvärinen. 2000. Costs of reproduction in introduced female Canadian beavers (*Castor canadensis*). *J. Zool. (Lond.)*, **252**: 79–82.
- Sadleir, R.M.F.S. 1969. The ecology of reproduction in wild and domestic animals. Methuen, London.
- Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Sydeman, W.J., Huber, H.R., Emslie, S.D., Ribic, C.A., and Nur, N. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. *Ecology*, **72**: 2204–2217.
- Sæther, B.-E., Engen, S., and Lande, R. 1996. Density dependence and optimal harvesting of fluctuating populations. *Oikos*, **76**: 40–46.
- Tait, D.E.N. 1980. Abandonment as a reproductive tactic—the example of grizzly bears. *Am. Nat.* **115**, 800–808.
- Vander Wall, S.B. 1990. Food hoarding in animals. University of Chicago Press, Chicago.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R., and Segerström, P. 2001. Characteristics of dispersal in wolverines. *Can. J. Zool.* **79**: 1641–1649.
- White, P.J., and Ralls, K. 1993. Reproduction and spacing patterns in kit foxes relative to changing prey availability. *J. Wildl. Manag.* **57**: 861–867.