From:	Jens Persson
To:	Grizzle, Betty
Subject:	Re: Request for time to discuss wolverine in N. America
Date:	Wednesday, March 8, 2017 12:10:43 AM
Attachments:	Can J Zool 2005 PerssonFemale wolverine (Gulo gulo) reproduction reproductive costs and winter food availability83,1453-145911.pdf ATT00001.htm Rauset15-0262.1.pdf ATT00002.htm

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Hi Betty!

Congratulations! To be half-Swedish :-)

Sorry again for slow reply. I have been in the field and other things. It will be different from next week.

Regarding your questions:

1) I have not seen any new studies about subspecies. And, to be honest, I have not paid so much attention to the older ones either. So I am not so familiar with that topic.

2) When it comes to denning success (or different parameters of reproduction), I would suggest the 2 papers from our studies here Persson 2005 and Rauset, Lo

Maybe we can get back to that question?

3) Those observations are unfamiliar to me. It is hard for me to have any thoughts about those without more information than this.

Sorry again for slow reply. It has been exceptionally busy last 2 months - but I hope I will be elaborate more if you have further questions after this week.

Vänliga hälsningar,

Jens

On 23 Feb 2017, at 17:32, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

Hi again - I am swamped with another project this week, but let me pose a few questions through email.

1) Have there been any new studies regarding the subspecies of *Gulo gulo*? As I understand the current taxonomy, there are two subspecies (here in North America, *G.g. luscus* and Eurasia, *G. g. gulo*) and that this was proposed in the Kurten and Rausch (1959) study (skull and teeth measurements). I have asked others about additional genetic studies to confirm this taxonomic classification, but everyone I contacted was unaware of any genetic studies to support this.

2) As you are aware, there is some debate on the need for snow, especially at den sites. I have reviewed several older physiological studies related to critical temperature, seasonal changes in fur, etc. But the importance of the availability of prey does not seem to be well-studied relative to denning success (in fact, denning success is not well documented in much of North America). How can prey availability be incorporated into an evaluation of den success (e.g., modeling) or den locations?

3) Related to physiology, one researcher here mentioned a few observations by a veterinarian during a necropsy, noting an enlarged heart and thyroid in that particular wolverine. Do you have any thoughts about these observations, and how they might relate to wolverine behavior?

Thanks so much! Oh, and in conversations with Bob Inman about his work in Scandinavia, he suggested that I mention to you that I am half Swedish! (I just discovered this through National Geographic DNA testing).

Betty

On Mon, Feb 20, 2017 at 1:29 AM, Jens Persson <Jens.Persson@slu.se> wrote:

> Hi Betty,
>
> I apologise for my slow reply!! I missed your e-mail earlier.
>
> If it is not too late now, I will be available this week (but not the week after).
>
> I you are still interested in this discussion, it might be good if you e-mail me more specific information

about things you would like to discuss.

Best wishes,

Jens

Jens Persson, PhD
Associate Professor
Grimsö Wildlife Research Station
Dept. of Ecology
Swedish University of Agricultural Sciences
SE-730 91 Riddarhyttan
Sweden
Phone: +46 581 697305

Websites:
www.wolverineproject.se (english)
www.jarvprojektet.se (svenska)
www.scandlynx.nina.no

> On 05 Jan 2017, at 18:26, Grizzle, Betty <betty_grizzle@fws.gov> wrote:
>
> Hello Jens - Bob Inman recommended you as a contact in Sweden for questions about the wolverine.
>
> A bit of background: I am a biologist with the U.S. Fish and Wildlife Service and have been assigned to work on our agency's listing determination for the wolverine (lower 48 states). As you are probably aware, a federal court vacated and remanded back to our agency our proposed rule (from 2014) to withdraw our previous proposed rule (2013) to list the species as threatened under the U.S. Endangered Species Act.
> We are preparing a new status review for the species and I have been tasked with preparing a status assessment report that will be used to support our next listing determination (either warranted for listing or another withdrawal).
>
> I have been busy reviewing background information and previous studies, as well as newer studies/publications, including the 2016 paper that you coauthored with Maria Aronsson, and would like to speak with you about habitat suitability modeling, among other topics.
>
> A phone call would be easier to discuss specifics, so please let me know if you are available next week. I am in California, so I believe you are about 9 hours ahead of me. I am generally at work by 7:15 am Pacific Standard Time, so perhaps first thing in the morning (my time) would be an appropriate time to reach you.
>
> Thank you for your time. I look forward to hearing from you,
> Betty
>
> --
>
> Betty J. Grizzle, D.Env.
> Fish and Wildlife Biologist
> U.S. Fish and Wildlife Service
> Carlsbad Fish and Wildlife Office
> 2177 Salk Ave, Suite 250
> Carlsbad, CA 92008

> 760-431-9440, ext. 215
> 760-431-5901 fax

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Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

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Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore

Geir Rune Rauset,[1,3] Matthew Low,[2] and Jens Persson[1]

[1]*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, 73091 Riddarhyttan, Sweden*
[2]*Department of Ecology, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden*

Abstract. Although the effects of individual age, resource availability, and reproductive costs have been extensively studied to understand the causes of variation in reproductive output, there are almost no studies showing how these factors interact in explaining this variation. To examine this interaction, we used longitudinal demographic data from an 18-year study of 53 breeding female wolverines (*Gulo gulo*), and corresponding environmental data from their individual home ranges. Females showed a typical age-related pattern in reproductive output, with an initial increase followed by a senescent decline in later years. This pattern was largely driven by four processes: (1) physiological/behavioral maturation between ages two and three; (2) age-related differences in the costs of reproduction resulting in an initial increase, and then a declining probability of breeding two years in a row as individuals aged; (3) resource availability (reindeer [*Rangifer tarandus*] carcass abundance; mostly Eurasian lynx [*Lynx lynx*] kills) in the months preceding parturition, which influenced the probability of having cubs, but only for individuals that had successfully bred in the previous year; and (4) resource availability also influenced the cost of reproduction in an age-dependent manner, as prime age females that had bred in the previous year were more responsive to resource availability than those at other ages. This study demonstrates that by examining how drivers of reproductive variation interact, we can get a much clearer understanding of the mechanisms responsible for age-related patterns of reproduction. This has implications not only for general ecological theory, but will also allow better predictions of population responses to environmental changes or management based on a population's age-structure.

Key words: apex predators; carry-over effects; food hoarding; Gulo gulo; *individual-based studies; intermittent breeding;* Lynx lynx; *multistate models;* Rangifer tarandus; *Sarek National Park, Sweden; sympatric scavengers; wolverine.*

Introduction

The production of young is a critical driver of population dynamics and determinant of individual fitness. Thus, understanding the causes of variation in reproductive output, both between and within individuals and populations, is a key component of evolutionary ecology (Roff 1992, Stearns 1992) and conservation biology (Richter et al. 2003, Low et al. 2007). Variation in reproductive output is primarily driven by three factors: (1) the current intrinsic reproductive potential of an individual (e.g., its physiological health or development; Forslund and Pärt 1995, Wilson and Nussey 2010), (2) the availability of resources necessary for successful reproduction (e.g., food or breeding sites; Fuller and Sievert 2001, Shaw and Levin 2013), and (3) trade-offs between current reproductive success and future reproductive potential (i.e., reproductive costs; Drent and Daan 1980, Reznick 1992, Stearns 1992). Because the impacts of resource availability and costs of reproduction may vary throughout the life of an individual (Forslund and Pärt 1995, Proaktor et al. 2007, Hamel et al. 2010*a*), an understanding of the changing relative contribution of these factors in determining age-specific reproductive patterns is necessary for developing and testing theory (e.g., senescence; Hamel et al. 2012) and the management of populations (Ferguson and Larivière 2002).

An important source of variation in reproductive output is when a sexually mature adult forgoes opportunities to breed, resulting in a pattern of reproduction known as "intermittent breeding" (Bradley et al. 2000). This is expected to evolve in long-lived organisms when the cost of not breeding is compensated for by future fecundity benefits (Stearns 1992, Shaw and Levin 2013), potentially becoming the most important determinant of reproductive variation in these taxa. An intermittent breeding strategy is more likely in variable environments, with the potential for "good" and "bad" years (Ferguson and Larivière 2002, Nevoux et al. 2010) where adults choose to breed based on environmental cues that predict resource availability prior to breeding (Shaw and Levin 2013). As such, adults may minimize the cost of reproduction by limiting breeding attempts

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[3] E-mail: geir.rauset@slu.se

when (1) resource abundance is low, if reproductive costs are regulated by environmental conditions, and/or (2) individual quality is low (e.g., by postponing the age of first breeding or reducing reproduction late in life; Shaw and Levin 2013, Zedrosser et al. 2013, Desprez et al. 2014). Despite general evidence that reproductive costs are modified by individual quality or age (Bérubé et al. 1999, Weladji et al. 2008) and that available resources may influence individual quality and reproductive costs (Laaksonen et al. 2002, Barbraud and Weimerskirch 2005, Robert et al. 2012), few studies have examined how these factors interact in explaining variation in reproductive output (but see Moyes et al. 2011, Robert et al. 2012).

Extended parental care, through provisioning dependent young, is energetically expensive (Clutton-Brock 1991), and thus expected to be influenced by age, resource availability, and trade-offs against future reproduction. Among female mammals with extended parental care, the cost of reproduction and its interaction between individual or environmental quality is mostly documented in herbivores and marine carnivores (Hamel et al. 2010*b*), with a scarcity of information on terrestrial carnivores (Proaktor et al. 2007). This is despite many mammalian carnivores having life history traits that should promote strong effects of reproductive costs on reproductive output: (1) a relatively short gestation, which results in the production of heavily dependent offspring that require extended and energetically demanding parental care (Millar 1977, Gittleman and Thompson 1988, Proaktor et al. 2007); (2) home ranges that (co)vary with quality among individuals (review in Mattisson et al. 2013); and (3) temporal variation in resource availability, with shifting environmental conditions and prey availability expected to drive individual fitness differences and relative costs of reproduction (Norris 2005, Harrison et al. 2011).

In this study we examined interactions between individual age, environmental resources, and reproductive costs in a large predatory mammal, the wolverine (*Gulo gulo*). The wolverine is an excellent study organism for examining how reproductive trade-offs are influenced by individual and environmental parameters because its reproductive strategy of delayed implantation allows females to influence embryo development (including termination) based on maternal condition (Ferguson et al. 1996), with condition influenced by previous reproductive output (Persson 2005) and seasonal fluctuations in prey availability (Mattisson et al. 2011*b*). Reproductive success in this species is not confounded by variation in male quality because parental care is exclusive to mothers. Also, the strong territoriality of females ensures that environmental variation in resource distribution can be linked to specific individuals based on their home range boundaries. Our study system is unusual for a large carnivore because of its duration (18 years), number of uniquely identified and aged breeding females ($n = 53$), ability to delineate home range boundaries from telemetry positions, and individual demographic and environmental data. Thus, we were able to examine the following: (1) Do female wolverines display age-related changes in reproductive output, and is this output primarily driven by changes in litter size or the probability of breeding? (2) To what extent does previous reproductive effort influence current reproduction, and are costs of reproduction responsible for age-related patterns in reproduction? (3) Do resource-linked environmental factors influence breeding probability; and do these effects differ depending on previous reproductive output (environmental quality × reproductive cost interaction), at different ages (environment × age interaction), and at different ages depending on breeding experience (environment × age × reproductive cost interaction)?

Methods

Study species and area

Wolverine reproduction is characterized by delayed implantation, short gestation, denning behavior, and extended maternal care (Inman et al. 2012*a*). Birth is generally earlier in wolverines than in other non-hibernating carnivores (Inman et al. 2012*a*), and the female cares for the cubs in a den during the snow season (Magoun and Copeland 1998, May et al. 2012), yielding dependent cubs at the onset of spring (Inman et al. 2012*a*). The cubs rely on maternal resources, including food and territory until age of dispersal (~11 months; Vangen et al. 2001). Wolverines display year-round intra-sexual territoriality (Persson et al. 2010, Mattisson et al. 2011*b*). During winter, ungulates constitute the main food source (van Dijk et al. 2008, Mattisson et al. 2011*a*), with wolverines displaying extensive food hoarding (Inman et al. 2012*a*). There is limited information on wolverine summer food (Inman et al. 2012*a*), but small rodent abundance is reported to positively influence wolverine reproduction (Landa et al. 1997), and ungulates can be important also during summer (Landa et al. 1999, Mattisson et al. 2011*a*).

The study was carried out in and around Sarek National Park in northern Sweden (67° N, 17° E). The area was characterized by large spatial and seasonal heterogeneity, with large altitudinal range (300–2000 m above sea level [asl]) encompassing distinct vegetation gradients within short distances. Vegetation at lower elevations mainly consisted of mixed conifer forest (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*), with mountain birch (*Betula pubescens*) predominating the tree line at 600–700 m asl. The alpine tundra above tree line was vegetated by dwarf birch (*Betula nana*) and willow (*Salix* spp.) shrubs, succeeded by lower growing heaths, grass and meadows, bare rock, and glaciers. Wolverines preferred habitats of mountain birch forest and alpine heaths in steep and rugged terrain (Rauset et al. 2013). The climate was continental with distinct seasons, and the ground was snow-covered from October until May. Mean onset of greenness in the

area was ~1 June, and primary production peaked (i.e., maximum normalized difference vegetation index [NDVI]; Pettorelli et al. 2005) around 15 July (ORNL DAAC 2012). The area included important spring to autumn grazing pastures for reindeer (*Rangifer tarandus*); during winter, most reindeer were moved to coniferous forests closer to the coast (Danell et al. 2006). Semidomesticated reindeer were the most important large prey for wolverines, of which a high portion was carrion from Eurasian lynx (*Lynx lynx*) kills (Mattisson et al. 2011*a*). Alternative small prey included mountain hare (*Lepus timidus*), Willow and Rock Ptarmigan (*Lagopus* spp.), Black Grouse (*Tetrao tetrix*), and Capercaillie (*Tetrao urogallus*), but it is unknown what role these played in the wolverine's diet. Rodents represent a substantial part of wolverines' summer diet in Scandinavia (Landa et al. 1997), and the densities of these fluctuate strongly between years (Ecke et al. 2010). The main source of mortality in subadult and adult wolverines in the study area was poaching (Persson et al. 2009). Annual adult mortality from natural (i.e., nonhuman) sources was low; the main mortality source in juvenile wolverines was intraspecific predation (Persson et al. 2009).

Wolverine reproduction and home range data

Wolverines were captured and immobilized (see Fahlman et al. 2008) and equipped with radio transmitters: very high frequency (VHF) or Global Positioning Satellite (GPS) collars, or intraperitoneal-implanted VHF transmitters. The capture and handling protocols (Arnemo et al. 2011) were approved by the Animal Ethics Committee for Northern Sweden, Umeå (protocol number A13-09). We recorded individual locations by radio-tracking VHF transmitters from the air or ground, or for GPS collars these were downloaded directly (e.g., from drop-offs or at recapture), downloaded by VHF to a receiver, or by Global System for Mobile communication (GSM). Location data were analyzed in ArcGIS 9.3 (ESRI 2008). We removed locations belonging to capture events, and those with accuracy >2000 m. We sampled the GPS records to only include one random location per individual per day.

During the denning period (Feb–May), we intensively radio-located and monitored adult females to evaluate whether they displayed behaviors that indicate a reproductive event (Persson et al. 2006). Because wolverine dens are often in deep snow (Magoun and Copeland 1998), we could not observe the number of cubs at parturition. However, after den abandonment (May–June), we located females and observed the number of cubs. Parallel to this, wolverine reproductions were monitored in the Swedish national monitoring program for large carnivores (Persson et al. 2015). This program observed no additional reproductive events among radio-marked individuals, indicating our methods were adequate. Thus, we could confidently say whether a female gave birth in a given year and how many cubs she weaned (first week of June). Since early litter loss is common in wolverines, females showing denning behavior, but no cubs at emergence in early June were classified as not reproducing. We marked all cubs we were able to capture, and those that did not disperse out of the study area were continuously monitored throughout their life. Thus, a high portion of the individuals were of known age.

We estimated individual home ranges, using a 90% kernel density estimator with a bivariate normal kernel function in the package AdehabitatHR (Calenge 2006) in R (R Development Core Team 2012). Kernel home range estimators are influenced by sample size; small sample sizes generally result in disproportionally large estimated home ranges (Börger et al. 2006). Therefore, we used bootstrapping simulations on real wolverine home range data sets containing >200 locations to explore the impact of sample size on the estimated home range sizes and compositions. From this we concluded that a minimum of 20 locations were needed to produce representative wolverine home range estimators, and excluded home ranges containing <20 locations. We extracted environmental representations for each individual home range.

Variation in resource availability and environmental conditions

To account for territory-specific annual variation in primary production, we used the integrated NDVI (normalized difference vegetation index; i.e., the sum of NDVI values over the year; Pettorelli et al. 2005) from 250 × 250 m cells throughout the study area. For food availability, we used the spatial distribution of reindeer carcasses (see Appendix; Mattisson et al. 2011*a*;) and an index of rodent density (specimens caught by 100 trap nights; Ecke et al. 2010). For reindeer carcass availability, we derived three variables relating to changing seasonal distributions of reindeer carcasses (winter/spring, Feb–May [$\text{reindeer}_{\text{SPR}}$]; summer, Jun–Sept [$\text{reindeer}_{\text{SUM}}$]; autumn/winter, Oct–Jan [$\text{reindeer}_{\text{WIN}}$]). These three periods were chosen because they represented different possible critical periods when carrion resources could influence the reproductive output of wolverines: Winter/spring is when females are lactating, summer is when females have dependent young, and autumn/winter is when females are gaining condition prior to parturition (see Appendix). The rodent density index was derived from the National Environmental Monitoring Program in Sweden for the site Stora Sjöfallet (Ecke et al. 2010). We pooled the eight rodent species, and observations during spring and fall into one annual rodent index. The rodent density index varied substantially between years (range 0.2–16.6, with a mean [±SE] of 4.1 ± 1.1), and was dominated by *Clethrionomys rufocanus* (52%), *Clethrionomys rutilus* (17%), *Microtus agrestis* (11%), and *Sorex araneus* (9%). To account for annual variation in winter severity, we used the mean winter (Nov–Mar) values of the North Atlantic Oscillation Index (NAO). In

our study area, positive winter values of the NAO represent warm and moist conditions with deep snow, which have negative impact on the winter condition of reindeer and possibly their vulnerability to predation from wolverines (Helle and Kojola 2008), but which also influence spring snow cover.

Reproductive output models

We estimated age of first reproduction (Persson et al. 2006), mean number of cubs by age and reproductive life span, based on 53 females (≥2 years) during 205 reproductive events, not including individuals of uncertain age, reproduction events with uncertain outcomes, and data from four individuals during years when they were included in a supplementary feeding experiment (Persson 2005). We analyzed age-related reproductive output, defined as number of weaned cubs after den abandonment in female wolverines using zero-inflated Poisson (ZIP) models in R package pscl (Zeileis et al. 2008). These include a binomial model to account for zeros that arise in addition to those modeled by the Poisson process (i.e., number of cubs produced per reproductive event). Thus, they were suitable for handling potentially different processes that determine the number of cubs produced: (1) maturity, as a binomial process, and (2) the number of cubs produced in a litter when a female is able to reproduce (a Poisson process). We initially modeled age-specific reproductive patterns by fitting different combinations of age terms (i.e., constant, linear, and quadratic) to both binomial and Poisson components. Based on this analysis, we then fitted variables describing year-specific effects and home range characteristics to the age-specific model with the highest support. Because not all environmental variables were available for all wolverines (e.g., lacking reliable home range measures), all models including resource availability were restricted to 41 individuals with 174 potential reproductive events (≥2 years). We did not include "year" in these models because there was no evidence of year effects on reproductive output when included in the highest ranked age model (year as categorical variable; $\Delta AIC_c = 21.9$, no single year effect with $P < 0.1$). Because we were primarily interested in within-individual age-related patterns, we needed to control for potential between-individual sources of heterogeneity that can bias cross-sectional population data (Forslund and Pärt 1995). Thus, in all models we included the age when the individual was first and last recorded in our data set (van de Pol and Verhulst 2006, Nussey et al. 2008). Normally these variables account for individual "quality" differences; however, in our data we did not expect these terms to be so easily interpreted because entry into the data set was partly determined by our ability to capture and collar an animal, and its exit often a result of poaching (Persson et al. 2009). Thus, these terms are more about statistical controls for individual entry and exit from the data to ensure any reproductive patterns relate to longitudinal effects on individuals as they age (Nussey et al. 2008).

To avoid multicollinearity, we evaluated suites of potential variables by Variance Inflation Factor (VIF; Zuur et al. 2009), and did not include variables with a correlation of $R^2 \geq 0.70$ or VIF ≥ 3 in the same model. We assessed model performance by AIC_c. We tested for count data overdispersion by the ratio (residual deviance)/df in the count process of the ZIP models, and by evaluating the dispersion parameter theta in corresponding ZINB models. To generate exact confidence intervals for the model predictions across the wolverines' life span (i.e., from ages 2–14), we reran the highest ranked model using a Markov chain Monte Carlo (MCMC) sampler (JAGS: Just Another Gibbs Sampler; Plummer 2003) called from R. For this we used 200 000 iterations with a 10 000 "burn in" and noninformative priors. Chains were checked for convergence using the Gelman and Rubin diagnostic and the 95% credible intervals extracted directly from the estimated posterior distributions of the model.

Reproductive cost models

We used multistate mark–recapture models in program MARK (version 5.1; White and Burnham 1999) to estimate the probability of breeding in year $t + 1$ for animals that were either breeders (state 1), or nonbreeders (state 2) in year t. A multistate modeling framework allows the estimation of transition probabilities specific to the initial breeding state of each animal each year (state transition [ψ]; i.e., nonbreeder to breeder [$\psi_{NB\rightarrow B}$] or breeder to breeder [$\psi_{B\rightarrow B}$]), in addition to the survival (Φ) and resighting (p) parameters, permitting a "cost of breeding" analysis (White et al. 2006, Moyes et al. 2011). The survival and resighting parameters were separately estimated for breeders and nonbreeders and had the same fixed structure for all analyses (Φ [state, age] p [state]) based on initial modeling where we compared different possible structures of the survival and resighting parameters (constant, state, age, state + age), while keeping the transition parameters general (i.e., state + full age-varying term: see also Low et al. 2010, Moyes et al. 2011). The age structure in the survival parameter was a simple two-stage factor (year 2 vs. older) because mortality in adult wolverines in the study area largely occurs through poaching, and in juveniles through intraspecific predation (Persson et al. 2009). Because of the substantial spatial variation in poaching associated with human land use and activity (Rauset 2013), this is likely to have a large confounding effect on age-related patterns in survival; hence, we did not model age-related survival patterns. The most general model (Φ [state, age] p [state] ψ [state, age]) was checked for goodness-of-fit using the median $\hat{c}$ variance inflation measure in MARK; this indicated there was no extra-binomial variation ($\hat{c} = 1.09 \pm 0.07$).

Because we were primarily interested in how individual and resource factors interacted with the cost of reproduction, we fitted explanatory variables separately to each transition state (i.e., $\psi_{NB\rightarrow B}$ and $\psi_{B\rightarrow B}$). This

allowed us to examine the strength of support for how each of these factors influenced wolverine reproductive output relative to whether the female had produced a den with cubs in the previous year. We first examined the influence of individual age on reproductive costs by modeling five different age structures: constant, two-stage (young vs. old), linear, quadratic, and full age-dependent. Based on AIC_c support, the highest ranked age parameter structure was then used as the basis of fitting the environmental covariates (see also Low et al. 2010). These environmental covariates included: (1) NDVI, (2) seasonal reindeer carcass availability ($reindeer_{SPR}$, $reindeer_{SUM}$, and $reindeer_{WIN}$; see Appendix for information on how these were calculated), (3) annual rodent density, and (4) winter NAO. We also included a second measure of reproductive cost as a covariate: (5) the number of cubs raised in year t (this was only fitted to the $\psi_{B\rightarrow B}$ parameter). We used these factors as variables because they were expected to influence food availability and female condition. Because NDVI and reindeer carcass availability were highly correlated ($r > 0.9$), we initially compared them in separate models and used the covariate with the strongest support (i.e., $reindeer_{WIN}$) for further model comparisons. Thus, when reindeer carcass availability is reported in the *Results* it can be effectively substituted for NDVI. All model comparisons were based on Akaike's information criterion with a second-order correction for sample size (AIC_c), with AIC weights used to determine the strength of support for each model, variable relative importance weights (0.7–1.0 indicating strong support, and <0.5 indicating weak or no support) and for deriving model-averaged estimates (Burnham and Anderson 2002).

Individual and environmental interactions

Because individual age may interact with environmental variables in determining the magnitude of the costs of reproduction (e.g., good environments may remove [or enhance] within-individual quality effects on reproductive costs), we examined whether the influence of $reindeer_{WIN}$ carcass availability, the only covariate identified in the multistate cost of reproduction analysis as having "strong support," on breeding probability varied with age. We used a sliding window approach within a multi-model inference framework (Mihoub et al. 2012) to assess the relative importance of this covariate on the probability of breeding at each age. The sliding window analysis involved creating a series of models where $reindeer_{WIN}$ carcass availability was constrained to only influence breeding probability estimates during specific periods of an animal's breeding life (a form of age-related "sensitivity" analysis for the covariate). Thus, the only element varying between the models was the period of the animals' life that reindeer carcass availability could influence the probability of breeding. This was possible in MARK through direct manipulation of the design matrix, where individual covariate values were assigned only to the ages of interest, leaving the covariate for all other ages set at "0" (i.e., noninformative; for a similar procedure see Low and Pärt 2009). A candidate set of 78 models for each transition state (i.e., 157 models in total including the "null" model) was created by varying the length of the window (i.e., from single-age estimates to estimates spanning all 12 possible reproductive transitions) and the starting position of the window, from transition at age 2–3 up to 13–14. We used a multi-model inference approach to account for model selection uncertainty in determining the strength of support for the variable at different ages. To do this, we first generated the AIC weight for each model within the candidate set and used these weights to calculate the relative importance of $reindeer_{WIN}$ carcass availability at each age. For example, to calculate the relative importance of the covariate on animals at five years of age for transition state $\psi_{B\rightarrow B}$, the AIC weights for all $\psi_{B\rightarrow B}$ models that contained this age group within the age window were added together (see also Mihoub et al. 2012). This allows a relative comparison for the strength of support in the data for the covariate of interest on each age group (cf. "relative variable importance" in Burnham and Anderson 2002). Because the starting position of each window influenced the possible lengths of the windows from that position (e.g., from age 2 the length could vary from 1 to 12, while from age 10 it could only vary from 1 to 4), this meant that ages were not evenly represented across the candidate model set. To remove this bias, we standardized the relative importance weights based on the number of models that included each age.

Results

We observed 53 wolverines during 205 potential reproductive events, from 2 to 14 years of age. Earliest breeding was at age 2 and the oldest at age 13. The age of primiparity was 3.4 ± 0.79 years (mean ± SD; range 2–5 years). There was a mean of 0.84 cubs per female per year (range 0–3 cubs); for animals with recorded denning behavior, this increased to 1.38 ($n = 149$, range 0–3).

Effects of age on reproductive costs and output

There was a clear relationship between the number of offspring produced and female age (Fig. 1). This age-specific relationship came from the combination of two processes: a binomial process where animals <3 years of age were extremely limited in their ability to reproduce, and a Poisson process that showed a decline in reproductive potential with age for animals ≥3 years (Fig. 1; Appendix: Tables A1, A2, and A3). Note that without the inclusion of the age-at-first-breeding and age-at-last-breeding parameters in the model, the general age effect in the count process was qualitatively similar (model with vs. without these parameters: −0.11 ± 0.04 vs. −0.09 ± 0.03, respectively), suggesting that any bias in age-related reproductive patterns arising from selective age-related appearance and disappearance

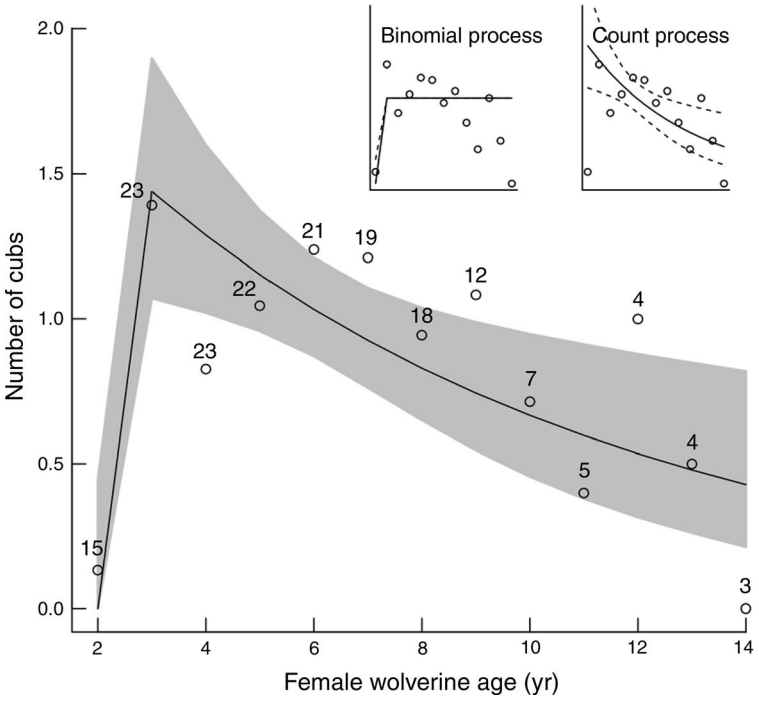


FIG. 1. Age-related reproductive output in female wolverines (*Gulo gulo*) based on 174 reproductive events from 41 individuals. Predictions represent the mean number of cubs weaned per individual and are derived from the highest ranked mixed-effects model in the Appendix: Table A2, with 95% credible intervals (shaded gray). Open circles represent the observed mean number of cubs per individual by age, labeled with age-specific sample sizes. The separate predictions from the binomial and count process components of the zero-inflated Poisson model are shown as insets.

of phenotypes was minor. By limiting the analysis to animals that gave birth, the age-related effect of litter size had little support (generalized linear mixed model [GLMM] with log-link: model without general age term $\Delta AIC_c = 0$; model + age = 0.7; model + age + age^2 = 2.6; AIC-weighted model-averaged estimates for age = 0.017 ± 0.032; age^2 = −0.0007 ± 0.002). This suggests that age-related reproductive patterns in wolverines ≥3 years old (Fig. 1) largely result from females becoming increasingly likely to skip breeding as they become older.

The increasing likelihood of skipping breeding with age was supported in the multistate analysis, and showed that this pattern resulted from age-related changes in the costs of reproduction. This is clearly seen by comparing the predicted transition probabilities ($\psi_{NB\rightarrow B}$ and $\psi_{B\rightarrow B}$) throughout the wolverine's life span (Fig. 2, Table 1; Appendix: Tables A4 and A5). Females that did not breed in the previous year ($\psi_{NB\rightarrow B}$) showed breeding probabilities that were similar to one another regardless of age, while females that did breed in the previous year ($\psi_{B\rightarrow B}$) showed a strong age-related breeding probability (Fig. 2).

Effects of environmental factors on reproductive costs and output

Reproductive output was positively influenced by reindeer carcass availability in the months prior to parturition (Oct–Jan [logit-link reindeer$_{WIN}$ = 1.42 ± 0.57 (mean ± SE)]; Table 1; Appendix: Tables A2, A3, and A5), meaning that females were more likely to give birth and suckle cubs in home ranges with greater food resource abundance at the time of fetal development. Summer NDVI was strongly correlated with winter reindeer carcass availability [$r = 0.94$] and its inclusion in the models gave qualitatively similar results as the reindeer covariate (Appendix: Table A2). As with female age, habitat quality/resource abundance interacted with the costs of reproduction, since support for the reindeer carcass covariate in the multistate analysis was restricted to females that had bred in the previous year (Table 1; Appendix: Table A5). There was some support for the number of cubs raised in the previous year having a negative influence on breeding probability in the current year, but little or no support for NAO and rodent density influencing breeding probability (Table 1; Appendix: Table A5).

Interactions between reproductive costs, individual age, and environmental factors

The sliding window analysis suggests that the three main determinants of reproductive output shown as important in this study (previous breeding history, female age, and winter reindeer carcass availability) interact in determining the probability of breeding (Fig. 3). By constraining reindeer$_{WIN}$ to only influence specific age windows, this showed evidence that some age classes

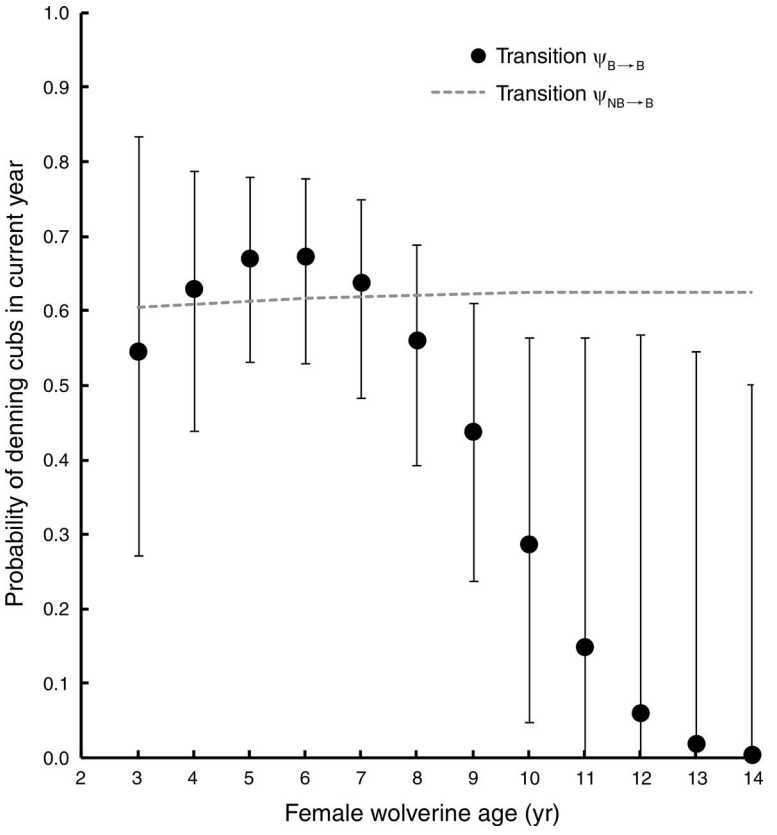


FIG. 2. Age-related changes in the probability of breeding for female wolverines ($n = 174$ reproductive events from 41 individuals) that had bred in the previous year ($\psi_{B\rightarrow B}$, black points) compared to females that had skipped breeding in the previous year ($\psi_{NB\rightarrow B}$, dotted line). Estimates are derived from model-averaging predictions from the candidate model set in the Appendix: Table A4, with 95% CIs shown for $\psi_{B\rightarrow B}$.

were more responsive to reindeer availability than others. For females that had bred in the previous year, restricting the influence of reindeer to only those years with a high probability of breeding again (from transition 3–4 years old to 7–8 years) showed stronger support over the model where reindeer_{WIN} explained all age groups ($\Delta AIC_c = 3.18$), with wolverines transitioning from 5–6 and 6–7 being the most responsive to this

TABLE 1. Factors influencing the breeding probability of a female wolverine (*Gulo gulo*) relative to her breeding status in the previous year.

	Breeder previous yr ($\psi_{B\rightarrow B}$)		Nonbreeder previous yr ($\psi_{NB\rightarrow B}$)	
Parameter	Estimate	VRI	Estimate	VRI
Intercept	0.57 ± 0.60	...	0.41 ± 0.32	...
Age	0.65 ± 0.34	1.0	0.02 ± 0.09	0.10
Age^2	−0.088 ± 0.039	1.0	−0.001 ± 0.002	0.03
Reindeer†	1.57 ± 0.60	0.94	−0.02 ± 0.03	0.16
Cubs ($t - 1$)	−0.44 ± 0.25	0.65	...	...
NAO	−0.45 ± 0.34	0.46	0.07 ± 0.15	0.11
Rodent density	0.18 ± 0.31	0.32	0.001 ± 0.12	0.09

Notes: Estimates (mean ± SE) and the variable relative importance (VRI) weights are AIC-weighted model-averaged estimates of determinants of the transition parameter from the candidate set of multistate mark–recapture models in the Appendix: Table A5. Parameters are: age (years), cubs (number of cubs raised in the previous year), winter reindeer carcass availability (years 2001–2011, centralized and standardized by 2 SD, i.e., "*z* scores"), annual winter North Atlantic Oscillation Index (NAO; *z* scores), and annual rodent density (*z* scores); with the probability of breeding calculated via a logit link. Ellipses indicate no data possible.

† Note that if the normalized difference vegetation index (NDVI) is substituted for reindeer carcass in Appendix: Table A5, the VRI weights for covariates from the $\psi_{B\rightarrow B}$ transition models were NDVI = 0.9, cubs = 0.56, NAO = 0.42, and rodent = 0.29.

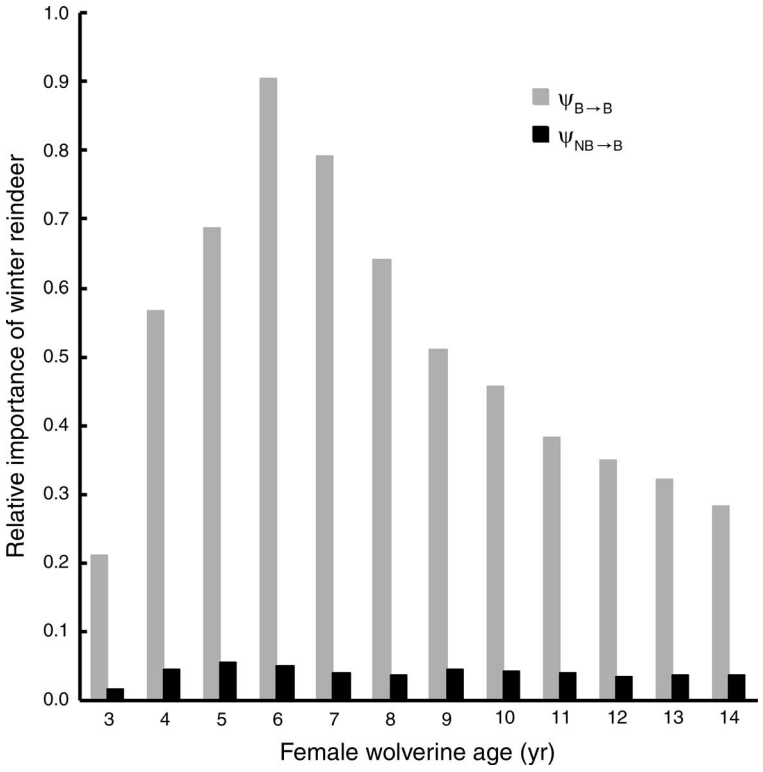


FIG. 3. Age-related changes in the relative importance of winter food resources (reindeer carcasses) in influencing the probability of breeding for female wolverines ($n = 174$ reproductive events from 41 individuals) that had bred in the previous year ($\psi_{B\rightarrow B}$, gray bars) compared to females that had skipped breeding in the previous year ($\psi_{NB\rightarrow B}$, black bars).

parameter (ΔAIC_c ages 6 and $7 = 0.0$ vs. ΔAIC_c all ages $= 4.19$; Fig. 3). This could be seen in the parameter estimates of the effect of $reindeer_{WIN}$ on the probability of reproduction for females aged 4–8 vs. the years outside this range (logit-link $reindeer_{WIN}$ estimates: 2.06 $\pm$ 0.71 vs. -0.23 ± 1.02, respectively [mean $\pm$ SE]). By AIC-weighting the strength of support for $reindeer_{WIN}$ on each age class, there was a strong age-dependent pattern for reindeer carcass availability influencing the probability of reproducing for those females that had bred in the previous year, but no apparent age-related decline for those that had skipped breeding in the previous year (Fig. 3).

DISCUSSION

Female wolverines showed typical age-related changes in reproductive output; i.e., an initial increase followed by a senescent decline in offspring production in later years. While such patterns have been reported in many taxa (Forslund and Pärt 1995, Caswell 2000, Gaillard et al. 2000), our study is one of the first to show how such age-related variation in reproductive output is driven by the interactions between female age, costs of reproduction, and resource availability (see also Robert et al. 2012). We identified four processes driving this variation. First, maturation occurs between two and three years of age, and is independent of resource availability (Fig. 1). Second, age-related differences in the costs of reproduction result in a declining probability of breeding two years in a row as individuals age (Fig. 2). Third, age-specific reproductive output is influenced by resource availability in the months preceding parturition, modulating the probability of breeding in a year following a successful breeding (Table 1). Finally, the influence of these resources on the cost of reproduction is also age dependent, as females at prime age are more responsive to resource availability than those at other ages (Fig. 3).

Maturation

By using a binomial and Poisson mixture model to predict reproductive output, we could disentangle two processes influencing failure to breed in wolverines. Failure to breed could arise from a simple binomial process linked to age; i.e., animals aged two or less very rarely breed, while older animals can breed, but may not because of an additional Poisson process linked to reproductive costs and resource availability. The sudden change in reproductive output from two to three years of age was not a result of delayed home range acquisition, and most likely due to age-related physiological or behavioral maturity and/or other improvements of competence (e.g., foraging ability; Forslund and Pärt 1995). Wolverines reach asymptotic growth before

primiparity (J. Persson, *unpublished data*); hence, it is unlikely that this pattern results from a simple trade-off between allocating resources for growth and reproduction (Zedrosser et al. 2009).

Interactions between individual age and reproductive costs

For individuals $\geq$3 years old, the age-related pattern in reproductive output was largely a result of changing probabilities of successfully breeding that were not only related to an individual's age, but also to a carry-over effect of the cost of reproduction from the previous year. Individuals that did not breed in the previous year had the same probability of breeding in the current year regardless of age, whereas individuals that had bred in the previous year showed strong age-dependent variation in the probability of breeding in the current year. This age-related sensitivity to the costs of reproduction appeared to be the main driver of the age-related patterns of reproductive output in this population.

Between four and seven years of age, there was no evidence of reproductive costs: All individuals had the same probability of successfully reproducing regardless of their reproductive status in the previous year. That prime-age females exhibit higher reproductive output regardless of previous reproductive status suggests that if within-individual age-related quality changes are ignored, they can mask detection of reproductive costs (Hamel et al. 2010*a*, Chambert et al. 2013). Variation in individual quality has been related to body condition (Reznick 1985, Bérubé et al. 1999), previous experience (Forslund and Pärt 1995), social rank, or age (Hamel et al. 2010*a*), but it is rare that measurements of multiple traits are available within one study (Wilson and Nussey 2010). In our study, the decline in reproductive output among older females appeared to be a result of reproductive senescence expressing itself as longer recovery times following a successful reproduction. One possibility is that reproductive costs accumulate over time, with individuals that start breeding later in life having a lower biological vs. chronological age compared to animals that begin breeding when young. There was some evidence for this based on the positive relationship between age at first reproduction and reproductive output. However, this pattern could also result from between-individual differences in quality unrelated to reproductive history. Senescence is not unexpected considering the bet-hedging life history of wolverines, where survival of adult females is the most important demographic parameter (Sæther et al. 2005, Persson et al. 2015). A conservative reproductive strategy is thus favorable, where older females do not trade current reproduction against their own survival.

Interactions between resource abundance and reproductive costs

Wolverines are adapted to seasonally and annually shifting resource availability (Ferguson and Larivière 2002); thus, it was not surprising to find an effect of seasonal resource abundance influencing the decision to breed (Nevoux et al. 2010, Shaw and Levin 2013). The distribution of reindeer carcasses during early winter positively influenced reproductive output by reducing the cost of reproduction for females that had successfully bred in the previous year. This importance of early-winter food corresponds with the timing of the decision to maintain or terminate embryonic development. Embryonic resorption or early litter loss has little cost, and thus consequences for future reproduction, compared to litter loss during or after lactation; implying that decisions to skip or abandon breeding should be made based on early-winter resources. Early-winter resources will also be available for the female, because of food hoarding, during late pregnancy and early lactation, when reindeer are generally rare (Persson 2005). This is also when the young are most vulnerable and the female is restricted in her hunting movements. Subsequently, coinciding with the latter part of lactation, reindeer are much less likely to become a limiting resource because of favorable hunting conditions in deep snow and late winter deaths and spring migration of reindeer (Haglund 1966, Persson 2005, Mattisson et al. 2011*a*). Notably, a large proportion of reindeer carcasses result from lynx kills (64%), suggesting that this top predator facilitates wolverine reproduction (cf. Mattisson et al. 2011*a*).

Because summer primary production (NDVI) was highly correlated with winter reindeer carcass abundance, and thus could not be included in the same models, it is possible that it also contributes to resource effects on individuals attempting to breed two years in a row. Increased primary production positively influences the abundance of various small prey, and there are indications that small prey constitute major summer food items for wolverines (Inman et al. 2012*a*). An increase in small prey availability reduces maternal effort during summer, either through easier hunting for the female during rearing, earlier independence of cubs, and/or reduced strain on stored resources (Persson 2005). The number of cubs raised the previous year had a moderate support for influencing the decision to breed again; this ongoing reliance of cubs on their mother's resources would be one explanation for such an effect.

Interactions between individual age, resource abundance, and reproductive costs

Resource abundance may simultaneously influence reproductive costs and exacerbate differences in within-individual quality related to aging, so that costs of reproduction may only become evident in harsh environments (Clutton-Brock 1991, Laaksonen et al. 2002, Tavecchia et al. 2005, Robert et al. 2012), with very young or old individuals disproportionately burdened by reproductive costs when resources are limited (Hamel et al. 2010*a*, Robert et al. 2012, Chambert et al. 2013). Here we found that, not only did the effects of resource abundance specifically influence the breeding

decisions of wolverine females that had bred in the previous year, but also that these effects were more influential on individuals during their peak reproductive years. This pattern is likely to be attributable to two factors: (1) Females that did not breed in the previous year have had time to fully recover their condition, and (2) females not in their prime age that had bred the previous year are less able to recover their condition quickly enough regardless of resource abundance. This suggests that females in their prime age that bred in the previous year are more influenced by resource abundance in the current year because they have a high enough intrinsic quality to overcome the costs of reproduction in years with high resource availability (or individual variation in unmeasured traits; Wilson and Nussey 2010).

By considering the interactions between individual age, reproductive costs, and resource abundance, we are provided an unusually detailed insight into the factors driving variation in reproductive output: a key component for understanding population dynamics and viability (see also Robert et al. 2012 for similar insights into seabirds). In addition, our study provides a stronger foundation for science-based management of this solitary carnivore. Several wolverine populations are intensively managed (Brøseth et al. 2010, Inman et al. 2013) and monitored (Brøseth et al. 2010, Ellis et al. 2014, Gervasi et al. 2014), requiring a basic knowledge of age-specific reproduction and reproductive costs. Also, our finding that reindeer carcass abundance was strongly linked to offspring production, but only in prime-aged individuals (cf. Robert et al. 2012), suggests that population responses to environmental variation will depend on the age-structure of the population, prey availability, and interspecific carnivore interactions, all of which may vary with species and ecosystem management. These examples demonstrate that studies able to consider interactions between drivers of population dynamics have much to offer not only ecological theory, but also practical population management.

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Supplemental Material

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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).

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J. Persson.[1] Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.

[1]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).

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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 (≥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 advantages of prolonged gestation and short lactation over short gestation and prolonged lactation (Lilligraven 1975). But delayed implanters have 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 Tarpy 1986). Availability of food for wolverines in my study area is presumably dependent on movements of migrating semi-domesticated reindeer (*Rangifer tarandus* (L., 1758)) (Bjärvall 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^2. 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; Bjärvall 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.)

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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^2 (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 (Arnemo et al. 1998), and with medetomedine and ketamine during the 1999–2001 study period. Adult wolverines were equipped with intraperitoneally implanted transmitters (Telonics® Imp/210/L, Imp/300/L or Imp/400/L; 30–90 g; Telonics® Inc., Mesa, Arizona) or collar-mounted radio transmitters (Telonics® 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)

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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, $n = 31$) (χ^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 ± 1.16 (mean ± SD), $n = 17$) than females that had reproduced in year t (0.35 ± 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.

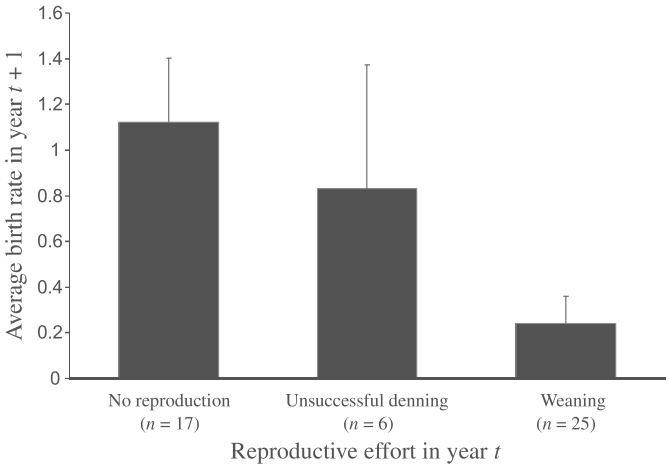
Reproductive costs and duration of parental care

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 ≥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 ± 0.90) than non-supplemented females (0.62 ± 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 (+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 (Oftedal and Gittleman 1989). Energy deposition during pregnancy, expressed relative to maternal energy requirements, is low for most mustelids (Oftedal 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%; Oftedal 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

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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 (Bjärvall 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

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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.

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