

# Life and Death in Wolverines

Linking Demography and Habitat for Conservation

Geir Rune Rauset

*Faculty of Natural Resources and Agricultural Sciences*

*Department of Ecology*

*Uppsala*

Doctoral Thesis

Swedish University of Agricultural Sciences

Uppsala 2013

Acta Universitatis Agriculturae Sueciae

2013:15

Cover: Svirja and her cub in Sarek National Park  
(photo: Jon M. Arnemo)

ISSN 1652-6880

ISBN 978-91-576-7772-3

© 2013 Geir Rune Rauset, Uppsala

Print: SLU Service/Repro, Uppsala 2013

## Life and Death in Wolverines – Linking Demography and Habitat for Conservation

### Abstract

Developing trustworthy conservation planning for endangered species requires a deep understanding of the variations of their populations in both space and time. I used individual-based long-term location and demographic data on wolverines (*Gulo gulo*) in Northern Sweden, and data on reproductions from the national monitoring systems of Norway and Sweden, to analyze how wolverine demography in Scandinavia is affected by variation in habitat and management policies. Wolverines showed age-related patterns of reproduction and reproductive costs, which were influenced by seasonal resources. The top predator Eurasian lynx (*Lynx lynx*) increase scavenging opportunities on reindeer (*Rangifer tarandus*) carrion, and wolverines and lynx selected for the same habitats when sharing prey base and sources of adult mortality. Illegal killing was a main source of adult mortality in brown bears (*Ursus arctos*), lynx and wolverines in northern Sweden, and the risk of being illegally killed was in general higher in national parks and on reindeer calving grounds, and lower in forest and steep terrain. At population level, the reproductive range of wolverines was set by latitude and elevation; presence of reindeer and lynx, rugged terrain and higher primary production had a positive effect; whereas human dominated habitats negatively influenced the frequency of reproductions. Different management policies influenced the frequency of wolverine reproductions; in Sweden this was 2 times higher than in Norway. Finally, I show that in Sweden, adult female wolverines were illegally killed at lower rates than males. Thus, the Swedish carnivore conservation payment system, which pays for wolverine reproductions, protects the demographic segment that is most important for population growth. Carnivores impose negative impact on rural economies and herding cultures in Scandinavia, and there will be need for continued monitoring combined with economic incentives to ensure carnivore-human co-existence. The approach of linking life histories to habitat has the potential for in-depth studies of mechanisms shaping spatial and temporal variation in populations, and should be implemented in future adaptive management for species persistence.

*Keywords:* Habitat, reproduction, survival, mortality, life-history, niche, management, Scandinavia, human-carnivore conflicts, conservation payment

*Author's address:* Geir Rune Rauset, SLU, Department of Ecology, Grimsö Wildlife Research Station, SE-730 91 Riddarhyttan, Sweden

*E-mail:* geir.rauset@slu.se

*Ein god realist skal ha seg eit slag i trynet kvar dag.*

John Seljeseth

# Dissertation

Time: 1 March, 2013, 13:00

Place: Loftets hörsal, Ulltuna, Uppsala

Chairman: **Lena Gustafsson**, SLU, Uppsala

External examiner: **John Fryxell**, University of Guelph, Canada

Evaluation committee: **Jos Milner**, University of Aberdeen, UK  
**Karl-Olof Bergman**, Linköping University  
**Fredrik Widemo**, The Swedish Association for  
Hunting and Wildlife Management  
**Tord Snäll** (reserve), SLU, Uppsala

Main supervisor: **Jens Persson**, SLU, Grimsö

Assistant supervisor: **Henrik Andrén**, SLU, Grimsö  
**Guillaume Chapron**, SLU, Grimsö

# Contents

<b>List of Publications</b>	<b>7</b>
<b>1 Introduction</b>	<b>9</b>
1.1 The wolverine	10
1.2 The Scandinavian wolverine population	11
1.2.1 Population history	11
1.2.2 Wolverine management	12
1.3 Objectives	14
<b>2 Methods</b>	<b>15</b>
2.1 Study area	15
2.2 Capture and immobilization	16
2.3 Location data	16
2.4 Reproduction	16
2.5 Mortality	17
2.6 Monitoring data	17
2.7 Environmental data	18
2.8 Habitat selection	19
2.9 Risk of mortality and mortality rates	19
2.10 Modeling reproduction and reproductive costs	20
2.11 Modeling species distribution	20
<b>3 Results and Discussion</b>	<b>23</b>
3.1 Habitat selection in wolverines and lynx	23
3.2 Spatial variation in brown bear, lynx and wolverine survival	24
3.3 Age-specific reproduction and reproductive costs in female wolverines	26
3.4 Environmental predictors of reproductions among Scandinavian wolverines	27
3.5 Effects of the Swedish conservation performance payment system	28
<b>4 Concluding remarks</b>	<b>29</b>
4.1 Future perspectives	31
<b>References</b>	<b>33</b>
<b>Acknowledgements</b>	<b>39</b>

## List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Rauset, G.R., Mattisson, J., Andrén, H., Chapron, G., Persson, J. (2012). When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia* [Online first] DOI 10.1007/s00442-012-2546-y.
- II Rauset, G.R., Samelius, G., Segerström, P., Swenson, J.E, Andrén, H., and Persson, J. National Parks as refuges for illegal killing of large carnivores. (manuscript).
- III Rauset, G.R., Low, M., and Persson, J. Age-specific reproduction and reproductive costs in female wolverines (manuscript).
- IV Rauset, G.R., Andrén, H., Mattisson, J., Brøseth, H., and Persson, J. Environmental predictors of the Scandinavian wolverine population (manuscript).
- V Persson, J., Rauset, G.R., and Chapron, G. Paying for coexistence: Assessing the performance of a large carnivore conservation performance payment system (manuscript)

Papers I is reproduced with the permission from Springer.



# 1 Introduction

Developing trustworthy conservation planning for endangered species requires a deep understanding of the variations of their populations in both space and time. Those variations are increasingly affected by human activities, both indirectly through loss and fragmentation of habitat or climate change and directly through hunting or poaching (Diamond, 1984), especially in large carnivores (Ray *et al.*, 2005). There is a substantial and increasing body of ecological research on habitat selection or demographic parameters. For example, presence/absence or radio-tracking data have been used to develop habitat selection models and to compute age-specific demographic rates. Relative to this, there are fewer, but with an increasing number of, attempts to provide a unifying approach merging these two critical aspects of animal ecology: habitat and demography (Gaillard *et al.*, 2010).

In particular, researchers often pay little or no attention to the differences in birth and death rates that occur in different habitats (Garshelis 2000, but see e.g. McLoughlin *et al.*, 2007; Johnson *et al.*, 2004). Combining studies of demography and habitat could give precise knowledge of both what determines population growth in different areas and identify demographic suitability of different habitats (Falcucci *et al.*, 2009; Nielsen *et al.*, 2006). Suitability can be defined as the ability of a habitat to sustain life and support population growth (Garshelis, 2000). To assess a species' needs, researchers commonly study habitat use and infer selection and preference. Such studies are often based on records of presence of individuals or populations; however, presence and/or density can often be misleading as indicators of what areas are suitable for a species (Hobbs & Hanley, 1990; VanHorne, 1983). In fact, the assumption that one can infer habitat suitability from studies of habitat selection is a serious flaw (Garshelis, 2000). The best measure of habitat quality is to test its effect on demographic parameters.

## 1.1 The wolverine

Wolverines (*Gulo gulo*) inhabit a Holarctic range (Copeland *et al.*, 2010; Pasitschniak-Arts & Larivière, 1995) defined by a bioclimatic envelope of spring snow and low summer temperatures (Copeland *et al.*, 2010). Their reproductive chronology and extensive food hoarding suggest that they are specifically adapted to exploit a cold, unproductive niche where resources are scarce and interspecific competition is limited (Inman *et al.*, 2012a; Inman *et al.*, 2012b). Wolverines are sensitive to human disturbance in terms of development and roads (May *et al.*, 2012; Krebs *et al.*, 2007; May *et al.*, 2006).

Wolverine females exhibit low reproductive rates, with long inter-birth intervals (Persson *et al.*, 2006). Wolverine reproduction is characterized by delayed implantation, short gestation length, reproductive denning behavior, and continuing maternal care following weaning (Inman *et al.*, 2012a). The timing of birth is earlier in wolverines than in other non-hibernating northern carnivores (Inman *et al.*, 2012a), and the female cares for the cubs in reproductive dens during the snow season (May *et al.*, 2012; Magoun & Copeland, 1998), yielding dependent young at the onset of spring (Inman *et al.*, 2012a). The cubs rely on maternal resources, including food and territory until age of dispersal (in average 11 months; Vangen *et al.*, 2001b). The most important demographic parameter for population growth in wolverines is survival of adult females. Wolverines display year-round intra-sexual exclusive territoriality (Mattisson *et al.*, 2011c). Their body mass is 10 and 14 kg for females and males respectively.

The wolverine is an opportunistic predator and facultative scavenger that often depend on scavenging (Mattisson *et al.*, 2011a; Dalerum *et al.*, 2009; van Dijk *et al.*, 2008). It is well adapted to find ungulate carcasses, which are often cached for later consumption (Haglund, 1965). Although the wolverine is a less skilled hunter (Haglund, 1965) it can be a significant predator on juvenile ungulates (Gustine *et al.*, 2006; Landa *et al.*, 1999; Bjärvall *et al.*, 1990). During winter, ungulates in terms of both prey and carrion constitute the main food source (Inman *et al.*, 2012a; Mattisson *et al.*, 2011a; van Dijk *et al.*, 2008; Haglund, 1966), and the presence of other large predators might increase food availability in form of increased scavenging opportunities (Koskela *et al.*, 2012; Mattisson *et al.*, 2011a; van Dijk *et al.*, 2008). A vital adaptation among wolverines to their cold and seasonal environments is extensive food hoarding (Inman *et al.*, 2012a), and increased resources during the pre-breeding season in terms of ungulate carrion is reported to reduce wolverine reproductive costs (Persson, 2005). There is limited information on wolverine summer food (Inman *et al.*, 2012a), but rodent abundance is reported to positively influence wolverine reproduction (Landa *et al.*, 1997).

## 1.2 The Scandinavian wolverine population

### 1.2.1 Population history

The Scandinavian wolverine population decreased during the 20<sup>th</sup> century due to intense persecution encouraged by a bounty system (Flagstad *et al.*, 2004; Persson *et al.*, 2003). When the bounty system was implemented, denning females with offspring were especially exposed to harvest, because bounties were paid per individual, and animals in den sites were easier to find and kill (Haglund, 1965). Increased accessibility following the introduction of snowmobiles accentuated the decline in the 1960s when the population size was at its lowest (Haglund, 1965). Despite the introduction of total legal protection in 1969 and 1973 in Sweden and Norway respectively, the recovery of the population was very slow (Björvall & Ullström, 1985). When large scale monitoring was first established in 1996 the population estimates were 265 and 147 individuals in Sweden and Norway respectively (Landa *et al.*, 1998). Subsequently, the number of registered reproductions has increased with 3.8 % per year and the estimated population size was 552-790 and 308-426 (90% CI) individuals in 2010 (Persson & Brøseth, 2011, Fig.1) with the population expanding into previously unoccupied areas (Aronsson & Persson, 2012).

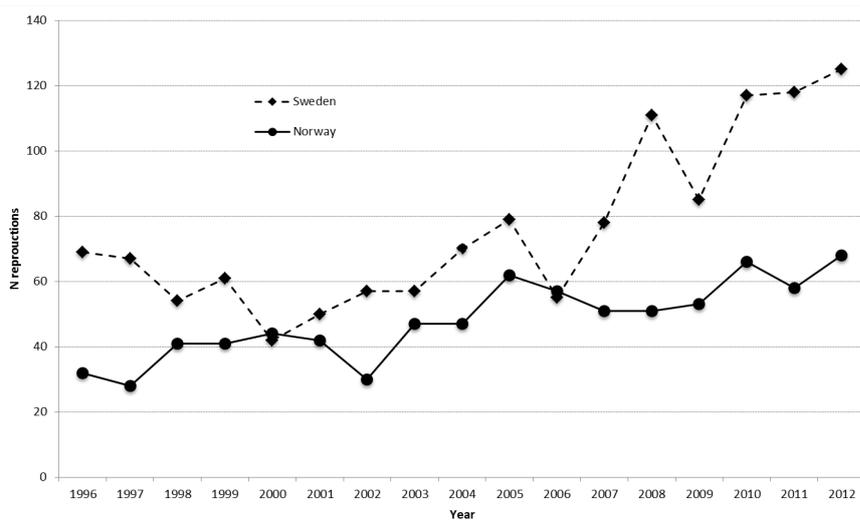


Figure 1. Number of wolverine reproductions in Norway and Sweden during 1996-2012.

### 1.2.2 Wolverine management

The Scandinavian wolverine management represents an interesting case since we have two countries sharing a population, while having diverging management policies regarding population goals, harvest regimes, and economic incentives for human-carnivore coexistence. Norway allows a public hunt with a generous quota, and conduct extensive lethal control of wolverines (Brøseth *et al.*, 2010, Fig. 2). National population goals are distributed into regional management zones, and in southwestern Norway (Fig. 3) the present policy is a “zero-tolerance” regarding wolverine reproductions to minimize conflicts with sheep husbandry. In Sweden there is no public hunt, and only limited lethal control has been allowed (Fig. 2). Instead, poaching is the main source of human-caused mortality in Sweden (Persson *et al.*, 2009).

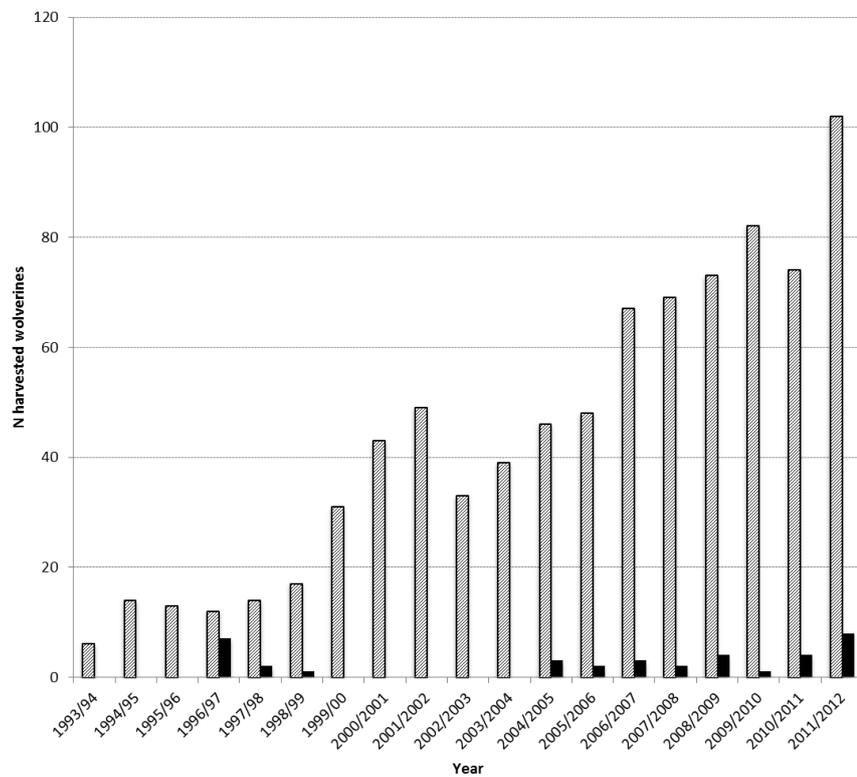


Figure 2. Annual harvest of wolverines in Norway (dashed bars) and Sweden (black bars).

Wolverines and semi-domestic reindeer (*Rangifer tarandus*) in Scandinavia represent an extreme case of predator-livestock coexistence, and a unique conservation challenge. The wolverine is red-listed (in Norway as endangered [EN]; Swenson *et al.*, 2010, in Sweden as vulnerable [VU]; Gärdenfors, 2010), and largely dependent on semi-domestic reindeer (Persson 2005; Mattisson *et al.* 2011a). Semi-domestic reindeer are private property owned by indigenous Sámi people, and depredation by wolverines and other predators on reindeer creates conflicts between carnivore conservation and sustainability of an important part of an indigenous culture (Hobbs *et al.* 2012). The two countries have implemented different economic incentives to facilitate human-carnivore coexistence. In the Swedish reindeer husbandry area, a conservation performance payment system is implemented based primarily on the number of reproductions (Zabel & Holm-Müller, 2008; Swenson & Andrén, 2005). Depredation on all livestock in Norway, mainly sheep (Landa *et al.*, 1999) and semi-domesticated reindeer (Mattisson *et al.*, 2011b), and other livestock than reindeer in Sweden is compensated directly in relation to depredation events (Swenson & Andrén, 2005).

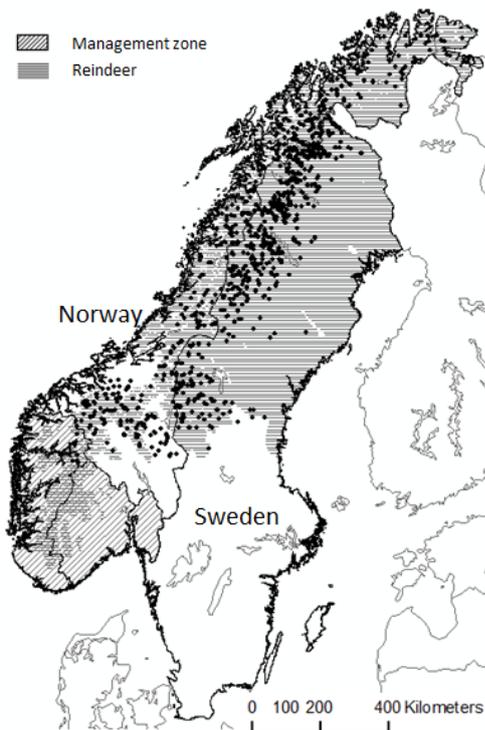


Figure 3. Norway and Sweden with all documented wolverine reproductions (n=1442) during 2001-2011 (dots).

### 1.3 Objectives

The aim of this thesis was to investigate how wolverine demography in Scandinavia is affected by variation in habitat (here defined in its broadest sense; including vegetation classes, landscape features, species interactions, human land use), and different regional and national management policies. To do this, I used individual-based long-term location and demographic data (mortality and reproduction) from a study area in Northern Sweden. In addition, I used data on wolverine reproductions from the national monitoring systems of Norway and Sweden. The main questions were:

- Paper I: Do species ecology or interspecific interactions result in differential habitat selection in sympatric Eurasian lynx and wolverines?
- Paper II: Can human activity and land use explain spatial variation in risk of mortality in brown bears, lynx, and wolverines?
- Paper III: Do individual wolverines show age-, habitat-, or year-specific patterns of reproductive output and reproductive costs?
- Paper IV: Which environmental variables explain the spatial distribution of wolverine reproductions in Scandinavia?
- Paper V: How is wolverine survival influenced by the Swedish carnivore performance payment system?

## 2 Methods

### 2.1 Study area

The study was mainly carried out in Jokkmokk and Arjeplog municipalities in northern Sweden (Fig. 4;  $67^{\circ}N$ ,  $17^{\circ}E$ ). The area is characterized by large spatial and seasonal heterogeneity, and spans gently rolling hills and valleys at about 300 m a.s.l. to high mountainous plateaus and peaks up to 2 000 m a.s.l., encompassing distinct vegetation gradients within short distances. Vegetation at lower elevations mainly consist of mixed conifer forest (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*) interspersed by numerous bogs and lakes, followed by mountain birch (*Betula pubescens*) forest which form the tree line at 600-700 m a.s.l. The alpine tundra above tree line is vegetated by dwarf birch (*Betula nana*) and willow (*Salix spp.*) shrubs, succeeded by lower growing heaths, grass and meadows, bare rock and glaciers. The climate is continental with distinct seasons, and the ground is usually snow-covered from October until May. Mean onset of greenness in the area was  $\sim$  1 June, and the primary production peaked around 15 July (MODIS, 2012).

The study took place in and adjacent to the largest national parks in Sweden; Sarek, Stora Sjöfallet and Padjelanta. Sarek and Stora Sjöfallet were among the nine Swedish national parks founded in 1909 as the first in Europe. Together with other protected areas, the three national parks form the 9 400 km<sup>2</sup> Laponia UNESCO world heritage site; one of the largest protected area networks in Europe. The justification for UNESCO world heritage designation included its nature qualities and indigenous Sámi reindeer herding culture. The area constitutes important spring-to-fall grazing areas and spring calving grounds for semi-domestic reindeer. During winter the reindeer herds were moved to coniferous forest closer to the coast (Danell *et al.*, 2006), but some reindeer remained also during the winter season.

Human infrastructure, agriculture and road density was very low, both inside and outside the park. Snowmobile access and hunting inside the NPs is restricted to reindeer herders and park rangers.

## 2.2 Capture and immobilization

Individual wolverines were immobilized (adults were darted from helicopter or from the ground and juveniles were captured by hand; Fahlman *et al.*, 2008) and equipped with radio transmitters, either Very High Frequency [VHF] collars, Global Positioning Satellite [GPS] collars, or intraperitoneally-implanted VHF transmitters. The continuously updated capture and handling protocols (Arnemo *et al.*, 2011) were approved by the Animal Ethics Committees in Sweden and fulfill the ethical requirements for research on wild animals.

## 2.3 Location data

We located individual animals either by manually radio tracking VHF transmitters from fixed-wing airplane, helicopter, or from ground, or by automated GPS location sampling. The GPS locations were downloaded directly from the collars (e.g. from drop-off collars or collars retrieved at recapture), downloaded by VHF signals to a receiver, or automatically transferred by Global System for Mobile Communication [GSM]. Location data were analyzed in ArcGIS 9.3™ (©1999-2004 ESRI Inc).

## 2.4 Reproduction

During the denning period (Jan-May), we radio located and monitored adult females intensively to evaluate whether they displayed denning behaviors that indicate a reproductive event. Because wolverines mostly have dens consisting of large tunnel systems in deep snow (May *et al.*, 2012; Magoun & Copeland, 1998) we were not able to observe the number of cubs originally given birth to by the denning female wolverines. In the period succeeding the abandonment of dens (May-June), we located potential mothers and visually observed the number of cubs accompanying her. We also marked all the cubs we were able to capture, and those that did not disperse out of the area were continuously monitored throughout their life. Thus, a high portion of the individuals were of known age, as they were captured as juveniles following their marked mother.

## 2.5 Mortality

We attempted to determine the cause of death for all individuals that died while carrying a functional radio-transmitter. The animals we found dead were examined carefully in the field and sent to the Swedish National Veterinary Institute for necropsy. However, in some cases the cause of death could not be reliably determined and were classified as unknown. Studying illegal killing of carnivores is extremely challenging; there is a strong incentive to conceal it because it is illegal and those responsible risk jail sentences (Liberg *et al.*, 2012; Persson *et al.*, 2009; Andrén *et al.*, 2006). We documented 22 cases when large carnivores were definitively killed illegally; e.g. the body was found shot, animals with collars removed but with functioning radio implants or smashed or cut-off/out and attempted hidden radio-transmitters (Persson *et al.*, 2009; Andrén *et al.*, 2006). In addition there were several occasions where we lost contact with an animal, and whose fate was difficult to determine. We know that people may remove or destroy radio-transmitters on animals they kill illegally, but telemetry units may also malfunction and young individuals may disperse from the study area (Samelius *et al.*, 2012; Vangen *et al.*, 2001a; Swenson *et al.*, 1998). We therefore classified animals we lost contact with as “likely illegally killed” or of “unknown fate”, based on several criteria (Persson *et al.*, 2009; Andrén *et al.*, 2006).

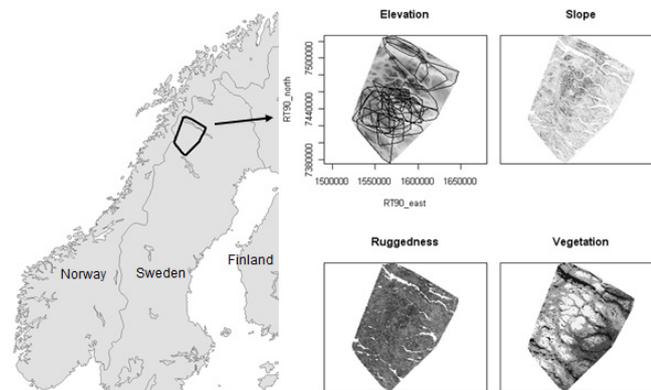
## 2.6 Monitoring data

We used official annual survey data on wolverine reproductions (2001-2011) and lynx family groups (2003-2011) from the Swedish Environmental Protection Agency and County Administration Boards in Sweden and the Norwegian Directorate for Nature Management and State Nature Inspectorate (SNO) in Norway.

The wolverine survey is performed from March to June and registered reproductions are based on documentation of den sites, tracks of females with cubs or visual observations of cubs after den abandonment (c.f. Landa *et al.*, 1998). Documentation of a den site requires observations of concentrated activity of tracks for >3 weeks. Possible den sites with activity <3 weeks are revisited after snowmelt to document signs of a den (e.g. several beds, large amounts of scats, cub hair, prey remains; Brøseth & Andersen, 2009). The majority of reproductions are documented at or close to the den site. Thus, spatial coordinates of reproductions provide a strong indication of the activity center of wolverine females during the denning period. The number of wolverine reproductions is assumed to give a representation of all wolverines in the population (Landa *et al.*, 1998).

## 2.7 Environmental data

For the analysis of habitat-specific survival we applied three continuous topographical raster maps: elevation, terrain ruggedness, and slope, one categorical vegetation raster, and two vector maps representing human land use: national parks and calving grounds of semi-domesticated reindeer (Table 3). Elevation was obtained from a 50 m x 50 m digital elevation map (Geographical Data Sweden [GSD], National Land Survey of Sweden). We calculated terrain ruggedness and slope from the elevation map using the tool “Vector Ruggedness Measure” (VRM; Sappington *et al.*, 2007 in ArcGIS 9.3™ ©1999-2004 ESRI Inc.). Vegetation was obtained from a 25 m x 25 m vegetation map (Swedish Land Cover [SMD], National Land Survey of Sweden). The national parks data was obtained from a Nature Conservation Area vector map (Geographical Data Sweden 2008), and the reindeer calving grounds were based on a map from the county administrations in Sweden (GIS data Länsstyrelserna© 2000-2008, SWECO). A spring snow cover index was provided from Copeland *et al.*, (2010). We used the mean integrated normalized difference vegetation index (NDVI) through the green season (June-Sept) on a 250 x 250 m scale to represent spatial and annual variation in primary production as a proxy for the distribution of alternative small prey (ORNL DAAC, 2012). To account for annual variation in winter severity, we used the mean winter (Nov-March) values of the North Atlantic Oscillation Index (NAO). A rodent index was derived from the National Environmental Monitoring Programme in Sweden for the site Stora Sjöfallet (see e.g Hörnfeldt, 2004).



*Figure 4.* Map of the study area in northern Sweden with environmental variables. The elevation layer plot includes coordinate axis in the RT90 25gonV datum and the 100 % minimum convex polygon home ranges of 10 lynx individuals and 16 wolverine individuals.

To avoid multicollinearity among many potentially correlated environmental variables, we tested for direct covariance between pairs of variables by Pearson's residuals and also evaluated suites of potential variables by Variance Inflation Factor (VIF; Zuur *et al.*, 2009 in the R package "AED"; Zuur, 2010). We did not include variables with a  $VIF \geq 3$  in the same models.

## 2.8 Habitat selection

We explored lynx and wolverine habitat selection (Paper I) using K-select analysis (Calenge *et al.* 2005), which is designed for hind-casting studies of habitat selection using individual radio-tracking data. The method is tightly linked to the concept of a multidimensional niche, and is able to analyse selection among several potentially correlated habitat variables. For each individual animal, differences between used and available habitat (i.e. selection) in a multidimensional ecological space define the marginality vector; its length reflects selection strength and its direction indicates which habitat variables are selected. The projection of the marginality vector on a factorial axis (i.e. the score) represents the selection along that axis. A non-centred principal component analysis (PCA) of the marginality vectors on the habitat variables, weighted by the proportion of relocations of each animal, returns a linear combination of habitat variables for which the average marginality is greatest. For details on the K-select, see Calenge *et al.* (2005).

## 2.9 Risk of mortality and mortality rates

To estimate habitat-specific risk of mortality among individuals of the three species (Paper II), we applied the Andersen-Gill (A-G) formulation of the Cox proportional hazards (CPH) model (Andersen & Gill, 1982). The hazard function represents the instantaneous probability of mortality, conditional upon the subject having survived to the beginning of the interval. A-G is the counting process analogue of CPH, using robust standard errors clustered within units. A-G allows for left- and right-censoring of data, time-varying continuous and categorical covariates, multiple events, and discontinuous intervals of risk (Johnson *et al.*, 2004). Each interval between succeeding relocations was treated as a unique interval of risk, and was attributed the environmental and demographic covariates belonging to the end point of the interval (Johnson *et al.*, 2004).

We estimated cause-specific mortality rates for adult males and females (Paper V) as described by Heisey & Fuller (1996) in R (R Development Core Team 2012). We used the *wildl* package in R rather than the most commonly

used *cmprsk* (Gray 2012) package because the former handles properly left truncation while the latter one does not (Pintille 2006).

## 2.10 Modeling reproduction and reproductive costs

We analyzed age-related patterns of reproductive output (here defined as number of confirmed cubs) in female wolverines using zero-inflated Poisson (ZIP) models in R package *pscl* (Zeileis *et al.*, 2008). These models include a binomial process to model excess abundance of zeros, in addition to the count 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: (i) the ability of individual females to produce a litter (e.g. maturity; as a binomial process) and (ii) the number of cubs produced in a litter when a female is able to reproduce.

To investigate the effect of individual heterogeneity for the ZIP model predictions, we reran the highest-ranked model using an MCMC sampler (JAGS: Just Another Gibbs Sampler; Plummer, 2003) called from R. For this we used 50 000 iterations with a 5 000 ‘burn in’ and non-informative priors. Chains were checked for convergence using the Gelman and Rubin diagnostic in R and the 95% credible intervals extracted directly from the estimated posterior distributions of the model.

We used multistate mark-recapture models in program MARK (version 5.1; White *et al.* 2006) to estimate the probability of breeding in year  $t + 1$  for animals that were either: (i) breeders, or (ii) non-breeders in year  $t$ . A multistate modelling framework was used because it allows the estimation of transition probabilities specific to the initial breeding state of each animal in each year (state transition ( $\psi$ ) i.e. non-breeder to breeder or breeder to breeder) in addition to the survival ( $\Phi$ ) and resighting ( $p$ ) parameters, permitting a ‘cost of breeding’ analysis (see chapter 9 in White 2011). Survival and resighting parameters were separately estimated for breeders and non-breeders and had the same fixed structure for all analyses ( $\Phi$  (state)  $p$  (state)).

## 2.11 Modeling species distribution

To model the range and number of wolverine reproductions all years combined, we applied zero-inflated models (i.e. ZIP/ZINB; Zuur *et al.*, 2009) in the R package *pscl* (Zeileis *et al.*, 2008). These models consist of a binomial part (0 or 1; which contrary to a logistic regression gives the probability of zeroes) and a count part (0, 1, 2, etc.), which allow for the handling of excess number of zeroes and zeroes deriving from different processes (Zuur *et al.*,

2009). We interpreted the binomial part of these models to predict the range of the reproductive part of the Scandinavian wolverine population, and the count process to predict the frequency of reproductions within this range. This allowed us to include data from the entire Scandinavian land area in the models; we did not have to set an arbitrary geographical boundary for potential wolverine habitat to ensure the specificity of model predictions.

To model annual probability of wolverine reproduction we developed generalized linear mixed models (GLMM; Bolker *et al.*, 2009), with binomial error distributions and the logit link function (i.e. logistic regression), in the R library *lme4*.



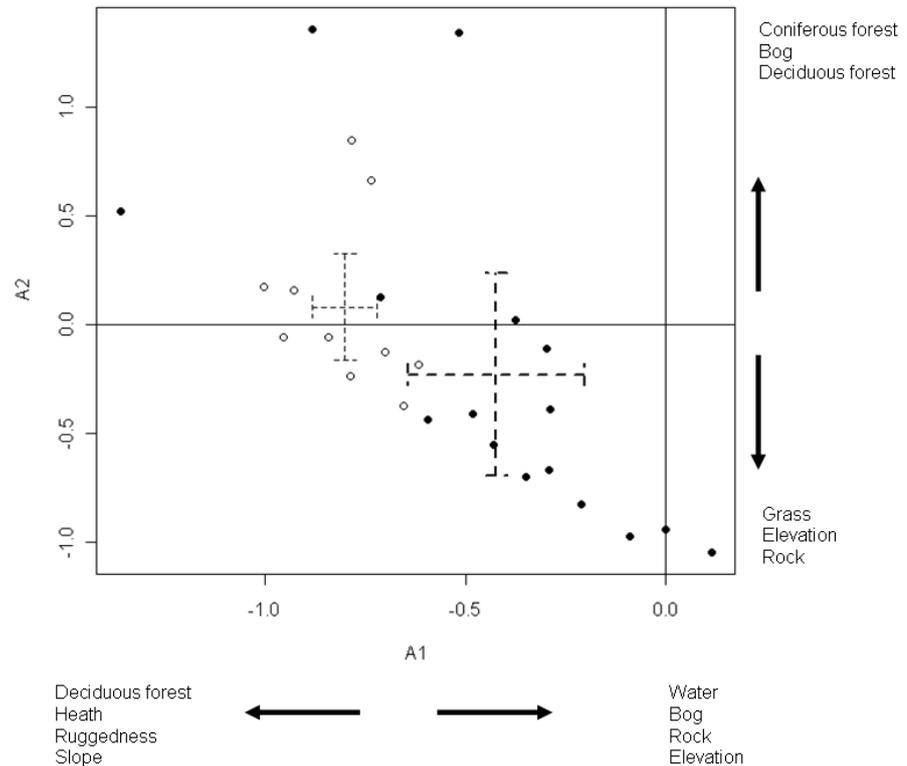
## 3 Results and Discussion

### 3.1 Habitat selection in wolverines and lynx

In this study we show that both lynx and wolverines selected for steep and rugged terrain in mountainous birch forest and in heaths independent of scale and available habitats. Still, lynx selected stronger for their preferred habitats when forming home ranges (Fig. 5) and selected the same habitats within their home ranges independent of home range composition. Wolverines displayed a greater variability when selecting home ranges (Fig. 5) and habitat selection also varied with home range composition. Both species selected for habitats that promote survival through limited encounters with humans, but which also are rich in prey, and selection for these habitats was accordingly stronger in winter when human activity was high and prey density was low.

The general results, with selection for the same habitats in both species, contradict the low overlap between suitable habitats for the two species in southern Norway (May *et al.* 2008). However, in southern Norway both sources of mortality (i.e. different human hunting techniques) and main prey differ between the species (May *et al.* 2008; Basille *et al.* 2009; Brøseth *et al.* 2010).

We suggest that the observed differences between the species result primarily from different foraging strategies (i.e. an obligate predator vs. an opportunistic predator and scavenger), but may also depend on differences in ranging and resting behaviour, home range size, and relative density of each species. Our results support the prediction that sympatric carnivores with otherwise diverging niches can select for the same resources when sharing main sources of food and mortality.



*Figure 5.* Result of the K-select analysis of selection for home ranges (second order selection) of lynx and wolverines in northern Sweden. The first axis A1 represents selection along the first principal component, comprising 49 % of the mean habitat selection (marginality), whereas A2 represents 24 %. The origin of space (0,0) represents the mean available habitat in the study area, which is the same for all individuals. Dots represent the end point of the marginality vector for each individual. The length of this vector represents selection strength, and the direction of the vector which habitats are selected. Open dots represent lynx individuals, and filled dots represent wolverine individuals. Bars represent 95% CI of mean marginality for the two species.

### 3.2 Spatial variation in brown bear, lynx and wolverine survival

This study confirmed illegal killing as an important source of mortality for sub-adults and adults of all three carnivore species (Bischof *et al.*, 2009; Persson *et al.*, 2009; Andrén *et al.*, 2006). There was an increased mortality risk for all species during the late snow season, due to an increased accessibility for humans on snowmobiles as the days are getting longer and the snow more suitable for snowmobiling (Persson *et al.*, 2009; Andrén *et al.*, 2006). In addition, brown bears were poached in fall during the bear and moose hunting season. Both national parks (NPs) and reindeer calving grounds represented an increased risk of being killed illegally, whereas forested and steep areas

represented decreased risk. The increased risks of illegal killing inside the NPs were not compensated by reduced risk of mortality from other causes (Table 1). We suggest that the increased risk of mortality in large carnivores associated with these national parks results from 1) the large areas where reindeer herders have exclusive access on snowmobile lowers the risk for perpetrators to be caught when illegally killing large carnivores, due to lowered public attention and surveillance and 2) many important reindeer calving grounds are located inside these parks. Thus, the Laponia World Heritage Site presently has a negative effect on the persistence of Scandinavian large carnivores, contrary to expectations and the historical intention of the park to secure a refuge for the brown bear. That these NPs seem to provide refuges for those who illegally kill carnivores is, however, not an effect of the NPs *per se*, but rather the snowmobile restrictions that are intended to limit human disturbance on wildlife and reindeer inside the NPs. The ecological baseline represented by these protected areas (PA) has thereby changed since their founding (Götmark & Nilsson, 1992), not through human development and habitat depletion (Liu *et al.*, 2001), but first of all as a result of technological innovations (i.e. snowmobiles; Andrén *et al.*, 2006). Thus, a critical reserve size based on historical data can be a poor predictor of carnivore persistence; the Laponia PA network is more than twice as large as the suggested critical reserve size for grizzly bears in North America (Woodroffe & Ginsberg, 1998).

Table 1. Parameter estimates ( $\beta \pm SE$ ) for the effect of national parks in Andersen-Gill models for the risk of being illegally killed, the risk of mortality from other sources, and the total mortality. The effects of the different strata were corrected for and therefore always included. A positive parameter estimate represents an increased risk of mortality within the national park. The  $\Delta AIC$  column represents the change in AIC when removing the effect of national parks from the model.

Mortality source	$\beta \pm SE$	$\exp(\beta)$	$\Delta AIC$
<i>Brown bear</i>			
Illegal	1.04 $\pm$ 0.46	2.8	2.9
Other	-0.46 $\pm$ 0.47	0.63	-0.96
Total mortality	0.23 $\pm$ 0.31	1.3	-1.3
<i>Lynx</i>			
Illegal	0.93 $\pm$ 0.46	2.5	2.3
Other	-0.31 $\pm$ 0.72	0.73	-1.8
Total mortality	0.55 $\pm$ 0.37	1.7	0.29
<i>Wolverine</i>			
Illegal	0.84 $\pm$ 0.36	2.3	3.5
Other	-0.084 $\pm$ 0.31	0.92	-1.9
Total mortality	0.38 $\pm$ 0.23	1.4	-0.26

### 3.3 Age-specific reproduction and reproductive costs in female wolverines

We showed that wolverines produced up to six litters during their lifespan at a mean of 0.84 (range 0-3, n = 249) cubs per potential reproductive event. Female wolverines showed strong age-specific reproduction, with a large increase occurring between 2 and 3-year-olds (most likely resulting from maturity effects), followed by a slow decline as a function of age (most likely reproductive senescence). The number of cubs produced per year was correlated with early winter (pre-breeding) resources (i.e. distribution of reindeer carrion) and summer primary production (i.e. normalized difference vegetation index NDVI). Notable is that the sympatric lynx presumably have a positive effect on wolverine reproduction, as lynx-killed reindeer provided the major part of reindeer carrion in our study area (Mattisson *et al.*, 2011a). Reproductive costs also showed an age-related pattern (Fig 6), with the probability of breeding in successive years peaking at 5-6 years of age and being strongly correlated with summer primary production. Interestingly, individuals at prime age that successfully reproduced also had a higher probability of weaning cubs the succeeding year than those that did not reproduce (Fig. 6). Thus, the cost of reproduction was only expressed in young and old individuals. The influence of annual variables was much lower than what was explained by age and spatial variation. We also identified substantial individual heterogeneity in reproduction among female wolverines.

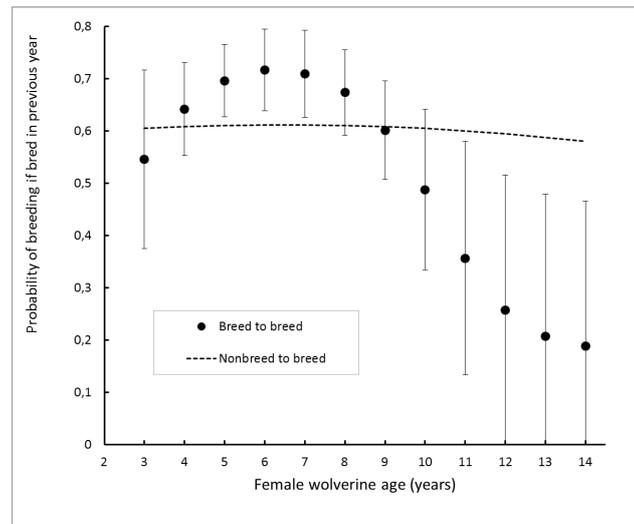
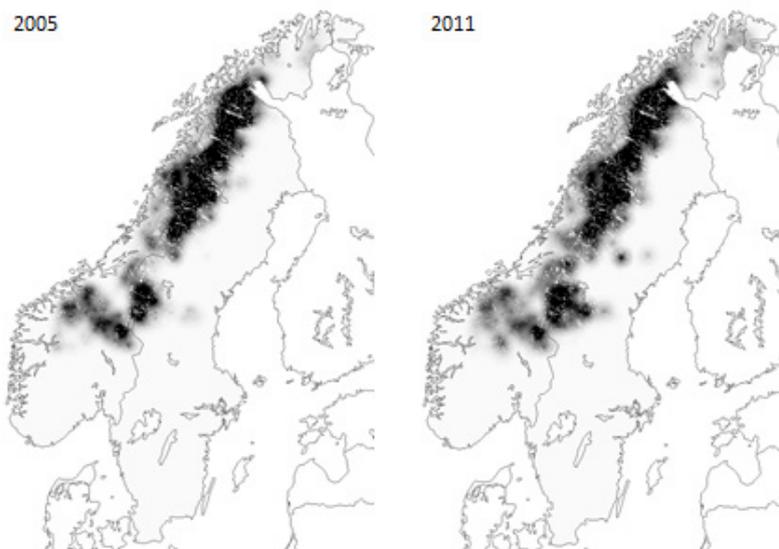


Figure 6. The probability to breed for female wolverines in relation to age for individuals that bred in previous year (point with 95 % CI) and for individual that not bred in previous year (dotted line).

### 3.4 Environmental predictors of reproductions among Scandinavian wolverines

We showed that the coarse scale range of wolverine reproductions in Scandinavia was defined by latitude and elevation, where latitude sets the southern limit and elevation confines the wolverine reproductions to mainly occur in alpine areas of the Scandinavian Peninsula. Within these areas wolverine occupancy was positively influenced by rugged terrain, mountain birch forest, and higher primary productive areas, and negatively affected by human dominated habitat. Wolverine range overlapped with their primary winter prey, reindeer, and the frequency of reproductions was enhanced by the presence of a top predator, the Eurasian lynx.

Management policies strongly affected reproductive success: in Sweden the frequency of reproductions were 2 times higher than in otherwise similar habitats in Norway, and in a “zero-tolerance” management zone in southwestern Norway the probability of reproduction was reduced 25 times compared to outside.



*Figure 7.* The predicted annual probability of wolverine reproductions in 2005 and 2011, based on the best logistic regression model.

This population was increasing in size and range during the study period (Fig. 1). The models of annual probabilities of wolverine reproduction therefore fluctuated (Fig. 7), with distance to earlier reproductions as an important variable, and with an observed effect of this up to mean dispersal distance in wolverines.

The Scandinavian wolverine population experienced a historical bottleneck in the mid 1900's following human campaigns of persecution, where areas characterized by remoteness and ruggedness were essential refuges for successful reproductions. The population later recovered, but its range is still mainly limited to wilderness-like areas with low human development.

### 3.5 Effects of the Swedish conservation performance payment system

We found that the Swedish conservation performance payment system did not put an end to illegal killing of wolverines. However, it leads to the demographic segment of the population used as the performance indicator in the scheme, adult female wolverines, having a significantly lower illegal mortality than adult males. In other words, Swedish authorities get what they have paid for.

Hence, we have moved from legal harvest with bounties, where females presumably were legally killed at higher rates than males (until 1969; see 1.2.1 Population history), to a system where females are illegally killed at lower rates than males (from 1996). We suggest that this lower poaching rate presumably explains the demonstrated increase (3.8 % per year) and expansion of the population since the scheme was introduced. Our evaluation illustrates that conservation performance payment schemes should be carefully designed and monitored to work.

Our model shows that a wolverine population can be quite resilient to relatively high rate of male mortality before declining, although highly skewed sex ratio of the adult populations could trigger unexpected dynamics that we did not incorporate.

## 4 Concluding remarks

Relating life history traits to habitats is critical for understanding habitat processes and ultimately the management of species of conservation concern (Franklin *et al.*, 2000).

The approach of linking wolverine demography to habitat has proven valuable for the Scandinavian wolverine population, both in linking habitat and individual fitness, but also in including results from local study areas into occupancy models at population level. This study reveal key knowledge for understanding both variation in wolverine life history and spatial variation in the population, where vital factors include habitat and landscape features, species interactions, and the effect of human land use and management policies.

Wolverines showed strong age-specific patterns of reproduction and reproductive costs (Paper III). I suggest that age-related variation in reproduction is more common among carnivores with similar life history, *bet-hedgers*, than what has previously been shown. Though survival of adult females is the most important parameter for population growth, reproduction can have large consequences for population dynamics if it is more variable (Charlesworth, 1994; Stearns, 1992), and age-specific fecundity should be implemented into population models. Wolverine reproduction was strongly influenced by seasonal resources (Paper III), which supports the suggestion from Inman *et al.*, (2012a) that summer food availability might play a role for reproductive costs in wolverines. Winter diet in wolverines mainly comprises ungulates (Koskela *et al.*, 2012; Mattisson *et al.*, 2011a; Dalerum *et al.*, 2009; van Dijk *et al.*, 2008), as prey or carrion, and the spatial distribution of reindeer carcasses influenced reproductive output (Paper III). This close relationship was also manifested in the influence of reindeer occupancy on the reproductive range of the Scandinavian wolverine population (Paper IV). As most of the

available ungulate carrion was provided by a top predator, the lynx (Mattisson *et al.*, 2011a), the presence of lynx presumably influence wolverine reproductive output positively (Paper III) and positively influenced the frequency of reproductions in Scandinavia (Paper IV). Thus, the top predator lynx facilitate the conservation of the facultative scavenger wolverine (Mattisson *et al.*, 2011a). This result diverges from earlier findings of wolverine and lynx overlap in southern Norway (May *et al.*, 2008), and also from other studies of large carnivores with interspecific competition and intra-guild predation (Creel *et al.* 2001; Linnell & Strand, 2000). Interspecific competition presumably plays a significant role of shaping wolverine niches/distribution throughout its range (e.g. Inman *et al.*, 2012b). However, when sharing prey base (Mattisson *et al.*, 2011a) and being subject to the same sources of adult mortality (Paper II), lynx and wolverines in general selected for the same habitat features (Paper I). Thus, I support general advises of considering species interactions when studying habitat selection (McLoughlin *et al.*, 2010) and also habitats-specific fitness.

The study confirms illegal killing as a main source of mortality among large carnivores in northern Sweden (Paper II; Bischof *et al.*, 2009; Persson *et al.*, 2009; Andrén *et al.*, 2006). There was a substantial variation in risk of mortality in brown bears, lynx and wolverines depending on landscape features and human land use, with some species differences that could be attributed their ecology (Paper II). National parks and reindeer calving grounds were in general associated with a higher risk of being illegally killed, whereas forest and steep areas were associated with lower risks (Paper III). This contradicts the general paradigm of conserving large carnivores through land preservation (Woodroffe & Ginsberg, 1998). Therefore, I warn against passive reserve management, and support continuously evaluating reserves conservation performance through monitoring. At population level, national parks were uninformative predictors of wolverine reproductions, which suggest that protected areas have minor effects on the conservation of large carnivores in Scandinavia (Paper IV). Linnell *et al.* (2001) also pointed to the fact that many carnivore populations in North America and Europe have been stable or increasing also outside protected areas and despite high human population densities. This leaves us with managing the conflicts between large carnivore ecology and rural economies and cultures themselves, which usually includes managing both policies and human behavior (Paper V). At population level, we see that different management policies dramatically influenced wolverine reproductions: in Sweden the frequency of reproductions was 2 times higher than in otherwise similar habitats in Norway, and in a “zero-tolerance” management zone in southwestern Norway the probability of reproduction was

reduced 25 times compared to outside, thus efficiently preventing permanent colonization of otherwise primary wolverine habitat. For Swedish wolverine conservation, the introduction of total legal protection in 1969 and later introduction of conservation performance payment system from 1996 have not stopped illegal killing of wolverines (Paper II, Paper V, Persson *et al.*, 2009), but resulted in a remarkable change on mortality patterns. Adult females, the segment of the population that is most important for population growth, were less likely to be illegally killed than males (Paper V). This indicates a promising potential for future implementation of conservation performance payment in other systems, especially where livestock is not the main prey.

#### 4.1 Future perspectives

This study shows that long-term individual-based data facilitate in-depth studies of mechanisms explaining variation in life histories and spatial distribution of populations. I emphasize the benefits of longevity data in ecology and conservation biology. However such data is scarce and waiting for such data to be collected for long-lived species with low reproductive rates might simply result in documenting the decline rather than providing recommendations for the conservation problem (Nielsen *et al.*, 2006). I further emphasize the promising prospects for empirical studies linking habitat and demography, and there are an increasing number of such studies that focus on the relationship between performance and habitat at various spatial scales (Gaillard *et al.*, 2010).

This thesis represents the first attempts on linking variation in wolverine demographic parameters to habitat features, and there is an obvious potential for expanding and improving the analytical approaches. Gaillard *et al.* (2010) identified four scales of habitat-performance relationships along a continuum of spatio-temporal dimension:

Individual energy gain → individual performance → population growth  
→ species persistence

Following this perceptual model, several potential approaches emerge. In Paper II, I employed a location-specific risk assessment in large carnivores, yielding information of spatial variation in risk at a level lower than home range, whereas potential energy acquisition was evaluated by the home range composition (Paper III). A natural next-step is to link each animal location to food abundance (e.g. probability of carrion) for modeling foraging decisions (Stephens & Krebs, 1986) and thereby achieve better measures of individual energy acquisition. A step-based model of foraging decisions could be linked with spatial variations in risk of mortality, facilitating a “holistic” approach in

spatial modeling, with the potential to reveal trade-offs between foraging and survival.

Scaling up to population level, the natural development from here will be a ranking of different habitats based on demographic contribution and include in regional population models (e.g. Falcucci *et al.*, 2009; Nielsen *et al.*, 2006). The fitness contributions of different areas, e.g. depicted as fitness maps, would be a valuable tool for management, both for assessing status and as a base for management actions e.g. by combining carnivore fitness maps and reindeer husbandry herding plan, we could identify areas of different conflict potential for conflict mitigation. Combined with continuous monitoring within an adaptive management framework this would contribute to sound management premises for species persistence.

## References

- Andersen, P.K. & Gill, R.D. (1982). Cox's Regression Model for Counting Processes: A Large Sample Study. *The Annals of Statistics* 10(4), 1100-1120.
- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R. & Segerström, P. (2006). Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biological Conservation* 131(1), 23-32.
- Arnemo, J.M., Evans, A. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Available at: <http://www.rovviltportalen.no/content.ap?thisId=500039688>
- Aronsson, M. & Persson, J. (2012). *Järv i skogslandet*. Technical report to WWF. Swedish University of Agricultural Sciences.
- Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A. & Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78(3), 656-665.
- Björvall, A., Franzen, R., Nordkvist, M. & Åhman, G. (1990). *Renar och rovdjur (Reindeer and predators, In Swedish)*. Solna, Sweden: Naturvårdsverket förlag.
- Björvall, A. & Ullström, S. (1985). *Däggdjur: Alla Europas arter*: W & W. ISBN 91-46-14896-5.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24(3), 127-135.
- Brøseth, H. & Andersen, R. (2009). Vurderinger knyttet til overvåking av ynglelokaliteter hos jerv i Sverige og Norge. (Evaluation of the monitoring of active wolverine dens in Sweden and Norway), NINA Rapport 437. Norwegian Institute for Nature Research, Trondheim, Norway
- Brøseth, H., Flagstad, O., Wardig, C., Johansson, M. & Ellegren, H. (2010). Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. *Biological Conservation* 143(1), 113-120.
- Charlesworth, B. (1994). *Evolution in Age-Structured Populations*. New York, NY, USA: Cambridge University Press.
- Copeland, J.P., McKelvey, K.S., Aubry, K.B., Landa, A., Persson, J., Inman, R.M., Krebs, J., Lofroth, E., Golden, H., Squires, J.R., Magoun, A., Schwartz, M.K., Wilmot, J., Copeland,

- C.L., Yates, R.E., Kojola, I. & May, R. (2010). The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88(3), 233-246.
- Creel, S., Spong, G., & Creel, N.M. (2001) Interspecific competition and the population biology of extinction-prone carnivore. In: Gittleman J.L. *et al.*, (eds) *Carnivore Conservation*. The Press Syndicate of the University of Cambridge, Cambridge, pp. 35-60,
- Dalerum, F., Kunkel, K., Angerbjorn, A. & Shults, B.S. (2009). Diet of wolverines (*Gulo gulo*) in the western Brooks Range, Alaska. *Polar Research* 28(2), 246-253.
- Danell, A.C., Andrén, H., Segerström, P. & Franzen, R. (2006). Space use by Eurasian lynx in relation to reindeer migration. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 84(4), 546-555.
- Diamond, J.M. (1984). "Normal" extinctions of isolated populations. In: Niticki, M.H. (Ed.) *Extinctions*. pp. 191-246. USA: Chicago University Press.
- Fahlman, Å., Arnemo, J.M., Persson, J., Segerström, P. & Nyman, G. (2008). Capture and Medetomidine-Ketamine anesthesia of free-ranging wolverines (*Gulo gulo*) *Journal of Wildlife Diseases* 44(1), 133-142.
- Faluccci, A., Ciucci, P., Maiorano, L., Gentile, L. & Boitani, L. (2009). Assessing habitat quality for conservation using an integrated occurrence-mortality model. *Journal of Applied Ecology* 46(3), 600-609.
- Flagstad, O., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P. & Ellegren, H. (2004). Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18(3), 676-688.
- Franklin, A.B., Anderson, D.R., Gutierrez, R.J. & Burnham, K.P. (2000). Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70(4), 539-590.
- Gaillard, J.M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010). Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365(1550), 2255-2265.
- Garshelis, D.L. (2000). Delusion in habitat evaluation: measuring use, selection, and importance. In: Boitani, L., & Fuller, T.K. (Eds.) *Research Techniques in Animal Ecology: Controversies and Consequences*. pp. 111-164. New York, USA: Columbia University Press.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* (165), 1-32.
- Gärdenfors, U. (2010). *The 2010 Red list of Swedish species*. Swedish University of Agricultural Sciences: Swedish Species Information Centre
- Götmark, F. & Nilsson, C. (1992). Criteria Used for Protection of Natural Areas in Sweden 1909-1986. *Conservation Biology* 6(2), 220-231.
- Haglund, B. (1965). *Järv och varg*. Stockholm: P.A. Norstedt & Söners Förlag.
- Haglund, B. (1966). De stora rovdjurens vintervanor I. (Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow). *Viltrevy* 4, 81-310.
- Hobbs, N.T. & Hanley, T.A. (1990). Habitat evaluation - do use availability data reflect carrying-capacity *Journal of Wildlife Management* 54(4), 515-522.

- Hörnfeldt, B. (2004). Long-Term Decline in Numbers of Cyclic Voles in Boreal Sweden: Analysis and Presentation of Hypotheses. *OIKOS* 107(2), 376-392. Data available online on: <http://www2.vfm.slu.se/projects/hornfeldt/index3.html>.
- Inman, R.M., Magoun, A.J., Persson, J. & Mattisson, J. (2012a). The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93(3), 634-644.
- Inman, R.M., Packila, M.L., Inman, K.H., McCue, A.J., White, G.C., Persson, J., Aber, B.C., Orme, M.L., Alt, K.L., Cain, S.L., Fredrick, J.A., Oakleaf, B.J. & Sartorius, S.S. (2012b). Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76(4), 778-792.
- Johnson, C.J., Boyce, M.S., Schwartz, C.C. & Haroldson, M.A. (2004). Modeling survival: Application of the Andersen-Gill model to Yellowstone Grizzly Bears. *Journal of Wildlife Management* 68(4), 966-978.
- Koskela, A., Kojola, I., Aspi, J. & Hyvärinen, M. (2012). The diet of breeding female wolverines (*Gulo gulo*) in two areas of Finland. *Acta Theriologica*, 1-6.
- Krebs, J., Lofroth, E.C. & Parfitt, I. (2007). Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7), 2180-2192.
- Landa, A., Gudvangen, K., Swenson, J.E. & Roskaft, E. (1999). Factors associated with wolverine *Gulo gulo* predation on domestic sheep. *Journal of Applied Ecology* 36(6), 963-973.
- Landa, A., Strand, O., Swenson, J.E. & Skogland, T. (1997). Wolverines and their prey in southern Norway. *Canadian Journal of Zoology* 75(8), 1292-1299.
- Landa, A., Tufto, J., Franzen, R., Bo, T., Linden, M. & Swenson, J.E. (1998). Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia. *Wildlife Biology* 4(3), 159-168.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B-Biological Sciences* 279(1730), 910-915.
- Linnell, J.D.C. & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions* 6(4), 169-176.
- Linnell, J.D.C., Swenson, J.E. & Andersen, R. (2001). Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4, 345-349.
- Liu, J.G., Linderman, M., Ouyang, Z.Y., An, L., Yang, J. & Zhang, H.M. (2001). Ecological degradation in protected areas: The case of Wolong Nature Reserve for giant pandas. *Science* 292(5514), 98-101.
- Magoun, A.J. & Copeland, J.P. (1998). Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62(4), 1313-1320.
- Mattisson, J., Andrén, H., Persson, J. & Segerström, P. (2011a). Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *Journal of Mammalogy* 92(6), 1321-1330.
- Mattisson, J., Odden, J., Nilsen, E.B., Linnell, J.D.C., Persson, J. & Andrén, H. (2011b). Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can

- ecological research contribute to the development of a fair compensation system? *Biological Conservation* 144(12), 3009-3017.
- Mattisson, J., Persson, J., Andrén, H. & Segerström, P. (2011c). Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology* 89(2), 79-89.
- May, R., Gorini, L., van Dijk, J., Brøseth, H., Linnell, J.D.C. & Landa, A. (2012). Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. *Journal of Zoology* 287(3), 195-204.
- May, R., Landa, A., van Dijk, J., Linnell, J.D.C. & Andersen, R. (2006). Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. *Wildlife Biology* 12(3), 285-295.
- May, R., van Dijk, J., Wabakken, P., Swenson, J.E., Linnell, J.D.C., Zimmermann, B., Odden, J., Pedersen, H.C., Andersen, R. & Landa, A. (2008). Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. *Journal of Applied Ecology* 45(5), 1382-1391.
- McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Moorter, B.V., Saïd, S. & Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* 88(12), 3192-3201.
- McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology* 79(1), 4-12.
- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation* 130(2), 217-229.
- ORNL DAAC, O.R.N.L.D.A.A.C. (2012). MODIS subsetted land products, Collection 5. In. Available on-line [<http://daac.ornl.gov/MODIS/modis.html>] from ORNL DAAC, Oak Ridge, Tennessee, U.S.A. Accessed Oct 8, 2012
- Pasitschniak-Arts, M. & Larivière, S. (1995). *Gulo gulo*. *Mammalian Species* 499, 1-10.
- Persson, J. (2005). Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83(11), 1453-1459.
- Persson, J. & Brøseth, H. (2011). *Järv i Skandinavien – status och utbredning 1996-2010*. (NINA Rapport).
- Persson, J., Ericsson, G. & Segerström, P. (2009). Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142(2), 325-331.
- Persson, J., Landa, A., Andersen, R. & Segerström, P. (2006). Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87(1), 75-79.
- Persson, J., Willebrand, T., Landa, A., Andersen, R. & Segerström, P. (2003). The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. *Wildlife Biology* 9(1), 21-28.
- Plummer, M. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. In: *Proceedings of Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna, Austria, March 20–22 2003.
- Ray, J., Redford, K.H., Steneck, R. & Berger, J. (2005). *Large Carnivores and the Conservation of Biodiversity*. Washington, D.C. , USA: Island Press..

- Samelius, G., Andrén, H., Liberg, O., Linnell, J.D.C., Odden, J., Ahlqvist, P., Segerström, P. & Sköld, K. (2012). Spatial and temporal variation in natal dispersal by Eurasian lynx in Scandinavia. *Journal of Zoology* 286, 120-130.
- Sappington, J.M., Longshore, K.M. & Thompson, D.B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71(5), 1419-1426.
- Stearns, S.C. (1992). *The evolution of life histories*: Oxford University Press, Oxford.
- Stephens, D. & Krebs, J.R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Swenson, J.E. & Andrén, H. (2005). A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. In: Woodroffe, R., *et al.* (Eds.) *People and Wildlife: Conflict or coexistence?* pp. 323-339. New York: Cambridge University Press..
- Swenson, J.E., Bjørge, A., Kovacs, K.M., Syvertsen, P.O., Wiig, Ø. & Zedrosser, A. (2010). *Mammalia*. - In: Kålås, J.A., Viken, S. and Skjelseth, S. (eds.) *The 2010 Norwegian Red List for Species*. Norwegian Biodiversity Information Centre, Norway.
- Swenson, J.E., Sandegren, F. & So-Derberg, A. (1998). Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67(5), 819-826.
- van Dijk, J., Gustavsen, L., Myrsetrud, A., May, R., Flagstad, O., Brøseth, H., Andersen, R., Steen, H. & Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology* 77(6), 1183-1190.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerström, P. (2001a). Characteristics of dispersal in wolverines. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 79(9), 1641-1649.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerström, P. (2001b). Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79(9), 1641-1649.
- VanHorne, B. (1983). Density as a Misleading Indicator of Habitat Quality. *The Journal of Wildlife Management* 47(4), 893-901.
- Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* 280(5372), 2126-2128.
- Zabel, A. & Holm-Muller, K. (2008). Conservation performance payments for carnivore conservation in Sweden. *Conservation Biology* 22(2), 247-251.
- Zeileis, A., Kleiber, C. & Jackman, S. (2008). Regression models for count data in R. *Journal of Statistical Software* 27, 1-25.
- Zuur, A. (2010). AED: Data files used in Mixed effects models and extensions in ecology with R (in Zuur *et al.* 2009). *R package version 1.0*.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*: Springer Science + Business Media, New York, USA (Statistics for biology and health).



## Acknowledgements

Sjå på mauren og bli vis, sa kong Salomo. Nokon tek slike råd litt for bokstavleg, og set seg med ræva godt planta i ein kontorstol år ut og år inn for å studere ein annan iherdig arbeidande kompis «på distans». Og kva sit ein igjen med - ei lita løpse med uforståelege skriblerier (dog med fint bilete på framsida)..

Det er ikkje nokon andre som kan skuldast for mine tilsynelatande meiningslause val her i verda, dei gjer eg sjølv. Derimot må eg få takke alle som gjennom livet, og spesielt dei siste fem åra, har gjort tilveret mitt rikare og meiningsfullt.

Først og fremst vil eg takke familien min, og sjølvsagt **systemene, mamsen og papsen**. Å få vekse opp med fjord og fjell rundt seg, og tidleg få interesse for friluftsliv, jakt og fiske, det er ikkje alle forunt. Og ikkje minst at de lærde meg gleda over bøker, det er forresten ikkje alle som lærer seg å lese gjennom ei fuglebok. Det er ingen tvil om at mine tidlege interesser for natur og friluftsliv har vore ein grunnstein for meg gjennom livet, og vore avgjerande i seinare livsvalg

At eg derimot skulle havne inn på vilforskings-sporet var ikkje sjølvsagt. Det var **Jon Swenson** og **Sven Brunberg** fekk meg inn på den vegen, og det er eg evig takknemleg for. De har skapt eit unikt miljø, som alltid vil alltid stå som eit førebilete. Takk óg til alle andre i björnjänget **Andrea, Günther, Ole-Gunnar, Jonas, Veronica, Andrés, Mia** og alle andre som gjorde somrane i Kvarnberg og Tackåsen til ein fest, og sjølvsagt storjägare **Walter**.

Og så fekk eg endeleg stige inn i Lo&järv-prosjektet - vilken ära och vilken tur! Må berømme **Jens** og **Henrik** for det djerve steget å inkludere ein norsk femtekollonist i sine rekker. No skal det seiast at dei snart oppdaga feilen dei hadde gjort og resolutt sette inn fatale tiltak for å rette opp den fatale feilen.

Så kvad **Stefan** langbrok : «att tolka i Sarek är säkert och visst en fara för liv och för lemmar».

Og det skal også tjene handledaren til ære, at ein ikkje sørgde for lenge over halvgjort verk, men sidan fann betre selskap å dra iveg med for å lage nye kluster.

Ei stor takk til Sarek-prosjektet *in persona*, **Peter**! Få har vel slik kunnskap og innsikt i rodjurens liv som deg, og eg er deg evig tekknemlig for alt eg har lært. Takk til gode

kollegaer og turkompisar i felt: **Einar, Jenny, Gustaf, Jens, Henrik, Jon, Alina** - you name them - for ein fantastisk gjeng å vere ute med! Det har også blitt mange ufroggløymelege stunder i Skaite med felespel, bastu og gode lag.

Bak det unike data-settet eg har fått boltre meg i ligg det eit stort tolmod og ein vilje til å halde på til ein får resultatet. Det er eit enormt feltarbeidet som er lagt ned gjennom tidene, både med fangst og peiling. Takk til alle gamle og nye karar: **Robban, Tom, Jon, Terje, Morten, Fredde, Per** og mange fleire - både for feltinnsats for å halde prosjektet levande.

Ei spesiell takk til **Peter** og **Solbritt** med familien i Vajki. Her har vi alle blitt tatt hjerteleg imot, med store smil og hjerter, og fått servert fantastiske måltid med alle skogen, fjellets og trädgårdens herligheter.

Gjennom dei siste fem åra har eg hatt gleda og privilegiet å jobbe på Grimsö. Hjerteleg takk til gode **kollegaer og vener på Grimsö** for eit fantastisk arbeidsmiljø – men det blir umogeleg å takke alle, då tar det aldri slutt... Eg vil likevel nevne mine doktorand-kollegaer **Camilla, Jenny, Jonas, Anna, Bobban, Lovisa og Malin**. Og kanskje spesielt **Örjan**, som generøst overlet den beste baracken i Morskoga til meg.

Kva skulle forresten laurdagskveldane i Bergslagsskogen vore utan Settlers-gjengen, og det eminente vertskapet på Laggars **Johan&Johanna?**

Many thanks to the **Inman family**, it's been a privilege to meet you all. Hope to visit you soon. And Bob, you really stood up as a brilliant example, your dissertation left me with a serious hangover and some extra inspiration to finish my last week of writing.

Eg vil takke forskarskolan på Ekologi-institutionen med **Helena** og **Åsa** for mange bra kurs, og sjølvsagt spesielt for Argentaturen. Takk **Ale** og **Celina** for ein fantastisk ekskursjon! Og takk **Matt** for stort tolmod ved siste analysene.

Men kva skulle det blitt av somrane om ein måtte sitje inne på kontoret? Inderleg takk til Scandlynx Nord med **John & John, Thomas, Jenny** for å skaffe meg fantastisk sommarjobb, og ikkje minst **Viggo, Olaf, Sigmund** og dei andre for formidle praktisk kunnskap om gaupe og jerv.

Hjertleg takk til **Ole-Gunnar, Jonas** og **Jens K** for «riktiga björntjänster» når de ordna feltarbeid og og fine dagar i urskogen i Udtja. Inderlig takk til familien Stokke: **Rune, Elli-Kari, Nils-Anders og Jonas**. Spesielt til Rune for fine betraktningar, og for demonstrasjon av Formell-klassa innan elding. Nuorrsjo, sjeldan har ein sove så godt ute. Takk til alle andre - **Therese, Pablo, Lasse, Lars-Thomas**.

Eg må få takke **Lars** Krempig for at han tilbake i 2001 viste bilete frå sitt tidlegare feltarbeid i Svenske Jervprosjektet i Sarek, og dermed sådde frøet til mi spesielle interesse for dette prosjektet, for at han og **Inger** organiserte mitt første jerv-feltarbeid med sporing av jerv i Alta

Takk til **Anders** Östergren og Länsstyrelsen i Västerbotten for at eg fekk følge med ein mästare ut på järvinventering, og for venleg overberenheit når eg spydde konstant i to timar under mitt livs mest ubehagelege helikoptertur. Berømm og takk til **Johan** Nyqvist for hans initiativ til utbetring av den svenske jervinventeringen i skogslandet.

Den som eg opp i all denne vennlegheita ikkje vil takke er **Espen** som overlet superbikkja **Hedvig** til meg hausten 2010, slik at den går inn i historia som den minst produktive..

Ein spesiell takk til mine dyktige veiledarar:

Min veiledar in absentia **Chappen**, som tappert initierte og halvvegs dreiv gjennom mitt livs mest eksklusive litteraturkurs, og som dagleg krydrar verden med sine spissformulerte og alternative synspunkt.

**Henrik** som sikkert styrte opp mitt vaklande doktorandprosjekt når et røynte på, og som enno har denne enestående evnen til barnslig nyfikenheit og glede over ein god modell eller figur.

**Jens** - jærvmannen sjølv - som med stort tolmod vegleda den eigenrådige doktoranden, som smurde skrive-maskineriet med whisky når det gjekk trøgt, og som snart endeleg kan puste letta ut.. Men som også må innrømme eit lite nederlag: sjølv etter fem år har du ikkje klart å lære med å seie det magiske ordet «wolverinologist».

Og sist men ikkje minst (i alle fall etter si eiga oppfatning) må eg få takke mi kjære **Jenny**. Først for at du let deg sjarmere av min laust samanraska doktorandsøknad, og for seinare også av meg. Og sidan har du halde ut med meg i tjukt og tynt, ein einestående prestasjon. Takk!





I





## When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores

Geir Rune Rauset · Jenny Mattisson ·  
Henrik Andrén · Guillaume Chapron ·  
Jens Persson

Received: 26 April 2012 / Accepted: 23 November 2012  
© Springer-Verlag Berlin Heidelberg 2012

**Abstract** Differentiation in habitat selection among sympatric species may depend on niche partitioning, species interactions, selection mechanisms and scales considered. In a mountainous area in Sweden, we explored hierarchical habitat selection in Global Positioning System-collared individuals of two sympatric large carnivore species; an obligate predator, the Eurasian lynx (*Lynx lynx*), and a generalist predator and scavenger, the wolverine (*Gulo gulo*). Although the species' fundamental niches differ widely, their ranges overlap in this area where they share a prey base and main cause of mortality. Both lynx and wolverines selected for steep and rugged terrain in mountainous birch forest and in heaths independent of scale and available habitats. However, the selection of lynx for their preferred habitats was stronger when they were forming home ranges and they selected the same habitats within their home ranges independent of home range composition. Wolverines displayed a greater variability when selecting home ranges and habitat selection also varied with home range composition. Both species selected for habitats that promote survival through limited encounters with humans, but which also are rich in prey, and selection for these habitats was accordingly stronger in winter when human activity was high and prey density was

low. We suggest that the observed differences between the species result primarily from different foraging strategies, but may also depend on differences in ranging and resting behaviour, home range size, and relative density of each species. Our results support the prediction that sympatric carnivores with otherwise diverging niches can select for the same resources when sharing main sources of food and mortality.

**Keywords** Interspecific interaction · Human disturbance · Eurasian lynx · Wolverine · Reindeer

### Introduction

Areas of range which overlap in species with otherwise diverging habitat associations provide opportunities for testing hypotheses of mechanisms in habitat selection. Though habitat is a complex concept it can be functionally defined (Gaillard et al. 2010) as the suite of resources (food and shelter) and environmental conditions (abiotic and biotic) that determine the presence, survival and reproduction of a population. Habitat selection, i.e. the disproportional habitat use in relation to the available range of resources, is closely linked to the ecological niche (sensu Hutchinson 1957; Hirzel et al. 2002) and several methods have been proposed to analyse habitat selection in a multi-dimensional space. The fundamental assumption in habitat-selection studies is that in heterogeneous environments, individuals capable of identifying and occupying favourable patches will have a selective advantage, favouring the evolution of habitat-selection strategies (Boulinier et al. 2008). In such heterogeneous environments, habitat selection is a hierarchical process (Hall et al. 1997), and several studies have described habitat selection to vary across

---

Communicated by Ilpo Kojola.

---

G. R. Rauset (✉) · H. Andrén · G. Chapron · J. Persson  
Department of Ecology, Grimsö Wildlife Research Station,  
Swedish University of Agricultural Science,  
730 91 Riddarhyttan, Sweden  
e-mail: geir.rauset@slu.se

J. Mattisson  
Norwegian Institute for Nature Research,  
7484 Trondheim, Norway

Published online: 14 December 2012

 Springer

scales, e.g. in ungulates response to predation risk and food availability (Rettie and Messier 2000; Anderson et al. 2005; Kittle et al. 2008; Hebblewhite and Merrill 2009). Rettie and Messier (2000) hypothesised that the most important factors limiting populations, e.g. survival through avoidance of predation or disturbance, are selected at a coarser scale.

Patterns of habitat selection may depend on factors other than resource availability, including interactions such as competition and predation, mutualism and parasitism (McLoughlin et al. 2010). Sympatric carnivores are often expected to differentiate in space and habitat use through the effects of intra-guild competition and interference (Linnell and Strand 2000; May et al. 2008). The subordinate species is then constrained from using the most suitable resources, resulting in its use of less suitable habitat and spatial segregation between species (Belant et al. 2010). In such systems, habitat-selection studies often fail to assess true habitat preference of the subdominant species (i.e. to reflect the intrinsic behavioural selection process), as habitat use is quantified in relation to habitat occurrence rather than availability (Beyer et al. 2010). In addition, habitat selection can be density dependent, and change with shifting distributions depending on abundance of territorial species (Boyce et al. 2002).

In this paper we explore hierarchical habitat selection in two sympatric predators, the Eurasian lynx (*Lynx lynx*) and the wolverine (*Gulo gulo*) having widely diverging population ranges and fundamental niches. The wolverine is considered a carnivore of remote arctic and alpine tundra, as well as boreal forest (May et al. 2006; Copeland et al. 2007). Conversely the Eurasian lynx is considered to be strongly associated with forested habitats even in mountainous areas (Breitenmoser et al. 2007). May et al. (2008) reported only 5 % overlap in the distribution of suitable habitats between the two species, the lowest overlap among the four large carnivores in their study area in southern Norway. However, in our study area in northern Scandinavia individual home ranges of the species overlap at close to 100 % (Mattisson et al. 2011c).

Both lynx and wolverines establish and defend intra-sexual territories, year-round and throughout their adult life (Breitenmoser-Würsten et al. 2007; Persson et al. 2010; Mattisson et al. 2011c). These territories have to provide all resources needed for individual biological functions: survival, foraging, reproduction and the sustenance of offspring until the age of dispersal. Survival of adult females is the most critical parameter influencing population growth in both species (Sæther et al. 2005, 2010). Anthropogenic causes of mortality, primarily poaching, are dominant in both species (Andrén et al. 2006; Persson et al. 2009). The frequency of poaching of lynx and wolverines in northern Sweden is higher during the snow season due to

an increased accessibility for humans on snowmobiles (Andrén et al. 2006; Persson et al. 2009). The two species share the same prey base and are both predators on semi-domestic reindeer (*Rangifer tarandus*), the main large prey in the area (Pedersen et al. 1999; Mattisson et al. 2011a, b). However, their foraging ecology differs considerably. Lynx are efficient and obligate predators that rarely scavenge (Haglund 1966; Pedersen et al. 1999; Odden et al. 2006; Mattisson et al. 2011b), and thus depend on a regular supply of available prey. Contrary to this, wolverines are facultative scavengers that, although capable of killing adult reindeer, to a high degree utilise ungulate carrion (Haglund 1966; van Dijk et al. 2008; Mattisson et al. 2011a). The wolverine is also a food hoarder (Samelius et al. 2002), and is able to divide large ungulate carcasses into portable pieces and store them in snow, earth, and water for several months (Haglund 1966). Different foraging strategies, e.g. stalking prey versus opportunistic searching for prey and carrion, may result in different ranging behaviours with corresponding differences in habitat-selection patterns. The body mass ratio of wolverines to lynx is almost 1:2, with implications for their energetic needs (Andrén et al. 2011), and this relationship is also reflected in larger home ranges in lynx (Mattisson et al. 2011c). Although wolverines find and use most reindeer killed by lynx, Mattisson et al. (2011c) found no evidence of a temporal attraction or avoidance between the species.

Based on ecological theory and species biology presented above we predict that:

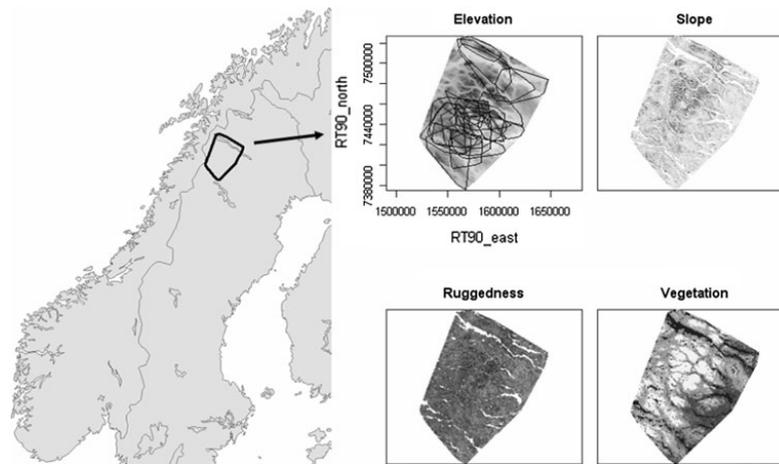
1. Wolverines and lynx select the same habitats and landscape features in general when subject to the same mortality factors and sharing a prey base.
2. The specialist predator lynx shows stronger selection for preferred habitats than the generalist wolverine.
3. The wolverine shows higher plasticity when forming home ranges than does lynx because of its foraging ecology, its lower body mass and lower energetic requirements.
4. Habitat selection in both species is stronger during the snow season when levels of human disturbance and poaching are higher and the density of prey is lower.
5. The strength of habitat selection is negatively related to home range size in both species.

## Materials and methods

### Study area

The study was carried out in and around Sarek National Park in northern Sweden (Fig. 1; Kvikkjokk: 67°00'N, 17°40'E). The area is characterized by deep valleys starting

**Fig. 1** Map of the study area in northern Sweden with environmental variables. The elevation layer plot includes coordinate axis in the RT90 25gonV datum and the 100 % minimum convex polygon home ranges of ten lynx individuals and 16 wolverine individuals



at about 300 m a.s.l. and high mountainous plateaus with peaks up to 2,000 m a.s.l., encompassing distinct vegetation gradients within short distances. The main vegetation at lower elevations consists of mixed conifer forest (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*) interspersed by numerous bogs and lakes, followed by hillsides and high elevation valleys of mountain birch forest (*Betula pubescens*) which form the tree line at 600–700 m a.s.l. The higher parts of the hillsides include low alpine tundra with dwarf birch (*Betula nana*) and willow shrubs (*Salix* spp.), succeeded by lower growing heaths, grass and meadows, to peaks and high plateaus of bare rock and glaciers. The climate is continental, and the ground is usually snow covered from November until May. The area includes important spring–autumn grazing pastures for semi-domestic reindeer, but some reindeer remain also during the winter season. Infrastructure in the area is limited to two dead-end roads in the outskirts, some minor permanent settlements, a few cabins, and a hydropower plant. The area hosts a limited amount of tourists, mainly in July and August and March and April.

#### Study animals and data collection

Between 2002 and 2006, we equipped ten lynx (seven females, three males) and 16 wolverines (12 females, four males) with store-on-board Global Positioning System (GPS) collars weighing ~300 g (Televilt Posrec C300; TVP positioning, Lindsberg, Sweden) during a total of 64 periods (i.e. battery life of a collar). The animals were immobilized with a mixture of ketamine and medetomidine, following pre-established protocols (Arnemo et al.

2011) by shooting a dart from a helicopter or from the ground, then captured. The handling protocols have all been approved by the Animal Ethics Committee for northern Sweden and fulfil the ethical requirements for research on wild animals.

We programmed all collars to acquire a GPS location every third hour (8 locations/day). GPS locations were stored within the collar and were accessible after retrieval of the collar. The collars were fitted with a drop-off function programmed to release them when the battery of the GPS unit was depleted. All lynx and wolverines were fitted with an intraperitoneally implanted VHF transmitter to facilitate long-term monitoring of individual animals.

During 7,087 monitoring days, GPS collars recorded 12,401 successful locations for wolverines and 25,218 for lynx, representing a location success of 50 % for wolverine and 80 % for lynx. Location data were distributed over the entire year. The GPS records were analysed in ArcGIS 9.2 (1999–2004 ESRI) and we removed locations belonging to capture events, and one single event of extra-territorial foray (a total 0.2 % of the original data set). The data records did not include positional dilution of precision values, but we excluded all 1D fixes (0.3 % of the data set) from the analysis.

Prior to analysing the habitat selection, we tested individual GPS records for temporal autocorrelation, i.e. a lack of independence among successive observations, using the Schoener's index and the Swihart and Slade index in the Home Range Tools for ArcGIS (Rodgers et al. 2007). As a consequence of the autocorrelation tests we performed the habitat-selection analysis both on the original data set and on a reduced data set where we systematically removed

four out of five GPS locations, resulting in location intervals of one GPS location every 15 h.

#### Environmental data

For the analysis of habitat selection we applied three continuous topographical layers of elevation, terrain ruggedness, and slope, and one categorical vegetation layer. Elevation was obtained from a  $50 \times 50$ -m digital elevation map (Geographical Data Sweden, National Land Survey of Sweden). We calculated terrain ruggedness and slope from the elevation map using the tool Vector Ruggedness Measure (VRM) (Sappington et al. 2007) in ArcGIS 9.2 (1999–2004 ESRI). We set the VRM neighbourhood size to three, resulting in a local scale ruggedness index based on nine neighbouring cells, and log-transformed the ruggedness index. Vegetation was obtained from a  $25 \times 25$ -m vegetation map (Swedish Land Cover, National Land Survey of Sweden), which was aggregated into a  $50 \times 50$ -m raster to fit the cell size of the topographical layers. The 34 vegetation classes represented within our study area were reclassified into seven vegetation classes (Table 1). We chose to include water bodies as a vegetation class because they are ice- and snow-covered for about half of the year, and used by both wolverines and lynx. Glaciers were included in the rock vegetation class as small glaciers do not functionally differ much from other barren vegetation in winter, and Skarin et al. (2008) found no evidence of reindeer avoiding these glaciers in spring and late summer. Bogs were classified as a separate vegetation class as they were not related to any of the other habitats. The aggregation of the  $25 \times 25$ -m vegetation raster into a  $50 \times 50$ -m raster changed the proportions among the seven main vegetation classes by only 0.01–0.09 %.

Available habitat at study area level was defined by buffering the area enveloping all valid GPS relocations [100 % minimum convex polygons (MCP)] by 10 km, corresponding to the approximate radius of a female

wolverine home range. The resulting area of available habitat was 10,840 km<sup>2</sup>.

#### Habitat selection

We explored lynx and wolverine habitat selection using *K*-select analysis (Calenge et al. 2005), which is designed for hindcasting studies of habitat selection using individual radio-tracking data. Thus the method is well suited for exploring patterns in data, but not intended for habitat modelling and mapping. The method is tightly linked to the concept of a multidimensional niche, and is able to analyse selection among several potentially correlated habitat variables. For each individual animal, differences between used and available habitat (i.e. selection) in a multidimensional ecological space define the marginality vector; its length reflects selection strength and its direction indicates which habitat variables are selected. The projection of the marginality vector on a factorial axis (i.e. the score) represents the selection along that axis. A non-centred principal component analysis of the marginality vectors on the habitat variables, weighted by the proportion of relocations of each animal, returns a linear combination of habitat variables for which the average marginality is greatest. Thus this method nicely handles multicollinearity (i.e. the inclusion of several correlated covariates in the same model), a recurring problem in many a habitat-selection study. Restricting the number of principal components to the ones explaining most of the variation (e.g. to a factorial plane of two principal components) allows for a visual investigation of each individuals selection, a feature which is often highly appreciated, e.g. when comparing patterns of individual or species selection. A drawback when reducing the number of principal components is a loss in the variation explained by the model. For details on the *K*-select, see Calenge et al. (2005).

*K*-select analyses were carried out in a hierarchical manner by varying mean availability of the different habitats. For the selection of home ranges, corresponding to second-order habitat selection (Johnson 1980), availability for all individuals was defined by the study area. For within-home range habitat selection, corresponding to third-order selection, availabilities were defined by the individual home ranges estimated by 95 % MCP. Species' differences in habitat-selection strengths at level two and three were tested by differences in mean marginality (i.e. individual selection strength) when projected onto a factorial plane defined by the first two principal component axes, and also by mean marginality when projected on the first and second factorial axes separately. We used  $F_{\max}$  (Sokal and Rohlf 1981) to test whether variability in marginalities differed between the species. Functional responses in third-order habitat selection (Mysterud and

**Table 1** Reclassifications of vegetation classes [Swedish Land Cover (SMD) National Land Survey of Sweden] and the proportion of each class within the study area in northern Sweden

SMD_recode	SMD_reclass (original class ID)	%
1	Coniferous forest (43–50, 54–56)	9
2	Deciduous forest (40–42)	12
3	Heaths, thickets (52, 53)	28
4	Grassland, meadows (4, 30, 32, 51, 63–64)	18
5	Bare rock, glaciers (6, 10–11, 59–62)	20
6	Bogs, marshes (70–72)	3
7	Lakes, open water (80–82)	10

Ims 1998) were tested by marginality projected onto the two axes separately in relation to availability along the corresponding axes. Individual selection strength (marginality vector length) of both second- and third-order selection was tested against individual home range size.

Seasonal differences in habitat selection were assessed both for second- and third-order selection by separating individual location records into summer (June–October) and winter season (November–May), based on the snow cover in the study area. Because the home ranges of both species are relatively stable year-round (Danell et al. 2006; Persson et al. 2010), we defined habitat availability for third-order selection by annual 95 % MCP. For *K*-select analysis we employed only individuals having a sufficient number of locations (>100) in both seasons. We tested for mean individual seasonal differences in habitat selection in a pair-wise manner (summer vs. winter) for the two species separately.

All analyses were performed using R (R Development Core Team 2009) and the *K*-select analysis was done with the R package “adehabitat” (Calenge 2006).

## Results

### Selection for individual home ranges

When performing *K*-select analyses on both the original data set and on the reduced data set, consisting of 1/5 of the original data, we only observed negligible differences, and therefore we have chosen to present the results from the analyses on the original data set. The two first principal component axes of the *K*-select analysis accounted for 49 and 24 % of the mean individual selection (i.e. eigenvalues of 0.49 and 0.24 in the multivariate analysis) and were kept in the visual representation and further analysis. The vegetation classes of water, bog, rock, and elevation had positive loadings for the first principal component axis (A1), whereas deciduous forest, heath, slope and ruggedness had negative loadings (Table 2). The second principal component axis (A2) had a high positive loading for coniferous forest but also deciduous forest, bog and water had positive loadings; whereas heath, grass and to a lesser extent rock had a negative loading (Table 2).

Both lynx and wolverines selected negatively along A1 (i.e. mean marginality along A1 was significantly lower than zero; Fig. 2), which means that they select for rugged and steep areas in deciduous forest and in heaths, but there was no mean selection along A2 (Fig. 2). Selection strength (marginality vector length) did not differ between the species (Wilcoxon rank sum test,  $W = 94$ ,  $P = 0.48$ ). However, lynx showed a stronger selection along A1 than wolverines did (logistic regression, Wald's test  $z = 2.31$ ,  $P = 0.021$ ). Selection along A2 was not different between

**Table 2** Loadings of habitat variables on the first two axes (A1, A2) of the *K*-select analyses of wolverine and lynx habitat selection in northern Sweden

Habitat variable	Selection for home range		Within-home range selection	
	A1	A2	A1	A2
Elevation	0.268	-0.253	0.407	-0.137
Slope	-0.300	-0.099	-0.214	-0.162
Ruggedness	-0.317	-0.126	-0.188	-0.162
Coniferous forest	0.014	1.019	0.166	-0.214
Deciduous forest	-0.746	0.245	-0.780	0.279
Heath	-0.353	-0.148	-0.408	-0.066
Grass	0.018	-0.386	0.057	-0.017
Rock	0.486	-0.180	0.609	-0.172
Bog	0.612	0.407	0.344	0.109
Water	0.808	0.235	0.726	0.312

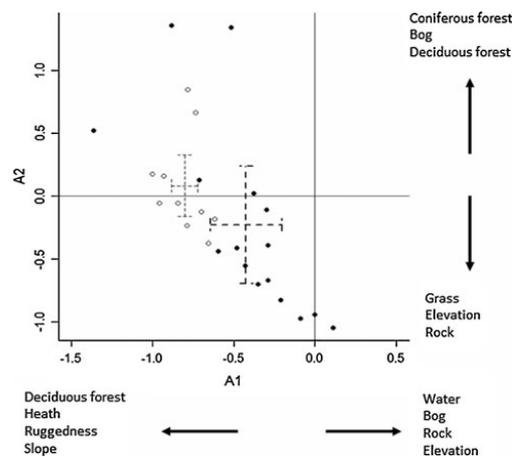
The first two columns describe combinations of habitat variables in the study area, and the last two within the individual home ranges. A1 and A2 are the first and second axis of the principal component analysis, respectively

the species (logistic regression, Wald's test  $z = 0.84$ ,  $P = 0.40$ ). Wolverines had a higher variability along both axes in home range habitat selection than lynx (A1,  $F_{\max} = 7.46$ ,  $P < 0.01$ ; A2,  $F_{\max} = 3.63$ ,  $P < 0.05$ ).

Selection strength tended to be related to home range size in lynx (linear regression,  $F_{1,8} = 4.95$ ,  $P = 0.057$ ), whereas selection strength was not significantly related to home range size in wolverine (linear regression,  $F_{1,14} = 0.36$ ,  $P = 0.55$ ). When testing for seasonal differences in selection for home ranges, the first principal component of the *K*-select represented 81 % of the mean selection and the second axis (A2) represented 17 %, and we chose to include both in the further tests. All individuals selected for slope, ruggedness, deciduous forest, and heath (A1), whereas the selection along A2 representing coniferous and deciduous forest was more diffuse. The selection along A1 was stronger during winter for both wolverines (one-sided Wilcoxon signed rank test,  $W = 3$ ,  $n = 7$ ,  $P = 0.039$ ) and lynx ( $W = 1$ ,  $n = 8$ ,  $P = 0.0078$ ). The selection along A2 did not differ between seasons for wolverines ( $W = 19$ ,  $n = 8$ ,  $P = 0.81$ ) or lynx ( $W = 17$ ,  $n = 8$ ,  $P = 0.47$ ).

### Habitat selection within individual home ranges

We here only present the *K*-select analysis performed on the original data set. The two first axes of the *K*-select analysis accounted for 50 and 12 % of the mean habitat selection (i.e. eigenvalues of 0.50 and 0.12 in the multivariate analysis) and were kept in the analysis. The vegetation classes of water, bog, rock, and elevation had positive loadings for the first axis (A1), whereas deciduous



**Fig. 2** Result of the *K*-select analysis of selection for home ranges (second-order selection) of lynx and wolverines in northern Sweden. The first axis (*A1*) represents selection along the first principal component, comprising 49 % of the mean habitat selection (marginality), whereas *A2* represents 24 %. The origin of space (0, 0) represents the mean available habitat in the study area, which is the

same for all individuals. *Dots* represent the end point of the marginality vector for each individual. The *length* of this vector represents selection strength, and the *direction* of the vector which habitats are selected. *Open dots* represent lynx individuals, and *filled dots* represent wolverine individuals. *Bars* represent 95 % confidence intervals (CI) of mean marginality for the two species

forest, heath, slope, and ruggedness had negative loadings (Table 2). The second axis (*A2*) had positive loadings for deciduous forest, water, and bogs, whereas slope, ruggedness, coniferous forest, and rock had negative loadings (Table 2).

Both lynx and wolverine individuals selected negatively along *A1* (Fig. 3) (i.e. selected for rugged and steep areas in deciduous forest and in heaths), whereas there was no significant selection along *A2*. Lynx selection was stronger (i.e. longer marginality vectors) for habitats within their home ranges than wolverines (Wilcoxon rank sum test,  $W = 147$ ,  $P < 0.001$ ). Selection along *A1* differed between the species (logistic regression, Wald's test  $z = 2.39$ ,  $P = 0.017$ ), but the selection along *A2* was not different between the species (logistic regression, Wald's test  $z = 1.23$ ,  $P = 0.22$ ). There was no significant difference in variability in habitat selection within home ranges between lynx and wolverine ( $F_{\max} = 2.11$ ,  $P > 0.05$  and  $F_{\max} = 0.44$ ,  $P > 0.05$  for *A1* and *A2*, respectively, Fig. 3).

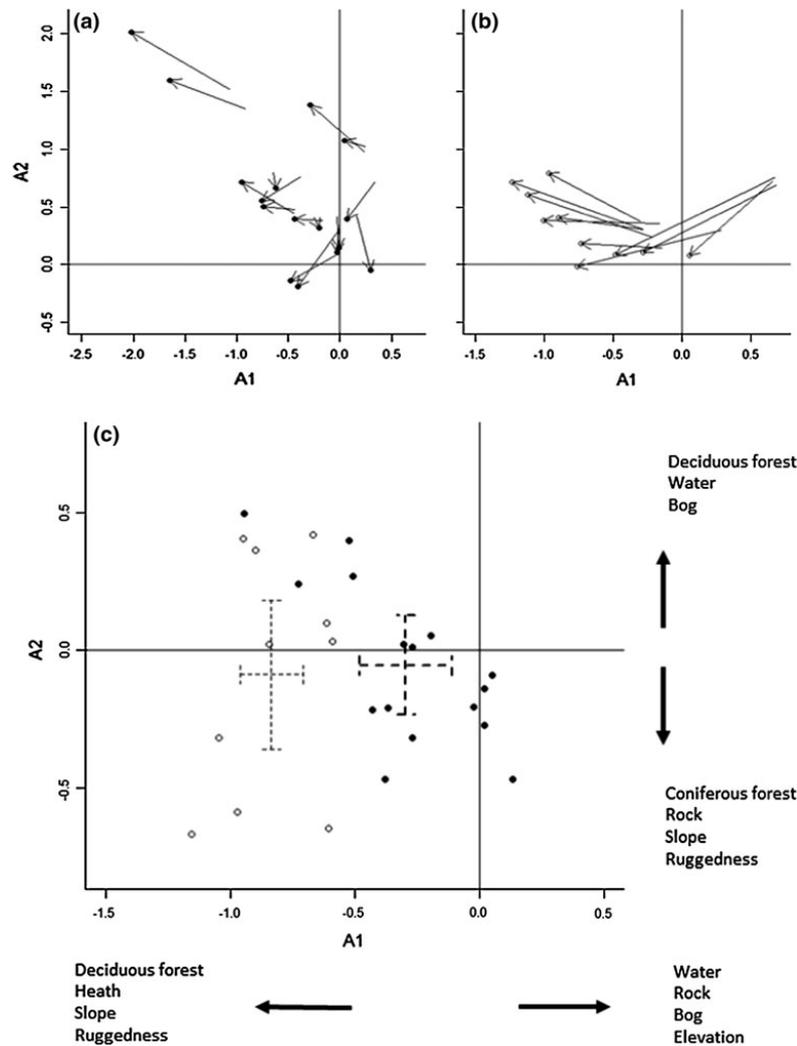
Selection strength along *A1* in lynx was not related to the corresponding habitat availabilities (linear regression,  $F_{1,8} = 1.54$ ,  $P = 0.25$ ), whereas selection along *A2* was negatively related to the corresponding availabilities (linear regression,  $F_{1,8} = 14.8$ ,  $P = 0.0049$ ). Selection strength in wolverine along both *A1* and *A2* was positively related to the corresponding availabilities (linear regression, *A1*,  $F_{1,14} = 5.48$ ,  $P = 0.035$ ; *A2*,  $F_{1,14} = 11.8$ ,  $P = 0.0040$ ).

When testing for seasonal differences in habitat selection within the home range, the first principal component of the *K*-select (axis *A1*; Fig. 4) represented 73 % of the variation in marginality and the second principal component represented 8 %, and we chose to only include *A1* in the further tests and the visual representation. All individuals selected negatively along *A1* (Fig. 4), which corresponds to selection for deciduous forest, heath, ruggedness, and slope. The selection was stronger during winter for wolverines (one-sided Wilcoxon signed rank test,  $W = 1$ ,  $n = 7$ ,  $P = 0.016$ ), and tended to be stronger for lynx ( $W = 6$ ,  $n = 8$ ,  $P = 0.055$ ). Selection strength was negatively related to home range size in lynx (linear regression,  $F_{1,8} = 17.14$ ,  $P < 0.001$ ; Fig. 5). For wolverines there was no relationship between selection strength and home range size (linear regression,  $F_{1,14} = 1.84$ ,  $P = 0.20$ ).

**Discussion**

This study revealed that both lynx and wolverines select for steep and rugged terrain in mountainous birch forest and heaths independent of scale and habitat availability (Figs. 2, 3). This is in accordance with our prediction that the two species, sharing causes of mortality and prey base, select for the same resources. In a landscape of risk associated with poaching (Andrén et al. 2006; Persson et al.

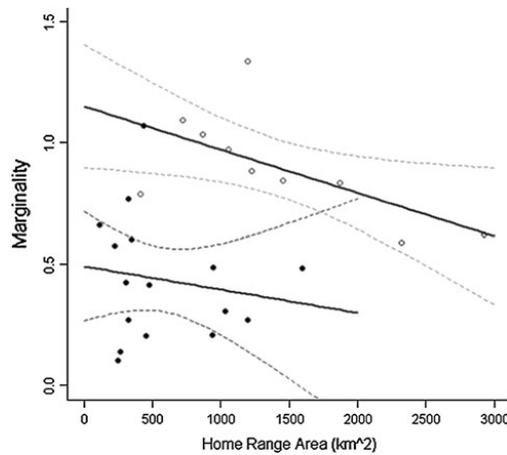
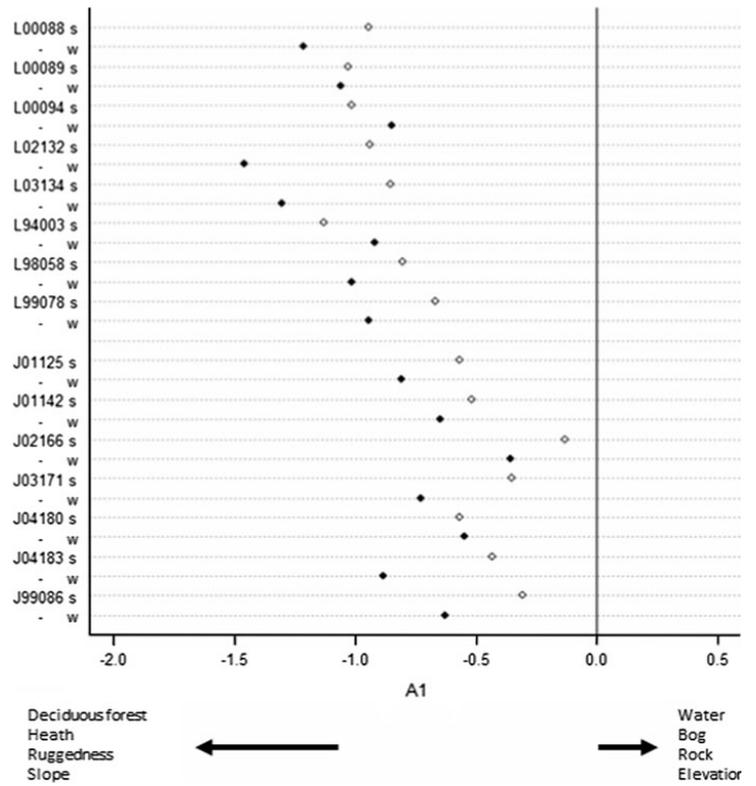
**Fig. 3** Results of the *K*-select analysis for habitat selection within home ranges (third-order selection) in **a** wolverines and **b** lynx in northern Sweden. The first axis (*A1*) represents selection along the first principal component, comprising 50 % of the mean habitat selection (marginality), whereas *A2* represents 11 %. Vectors represent individual habitat selection in terms of the marginality vector. The origins of the marginality vectors represent available habitat for each individual (i.e. available habitats within the home range). **c** Individual habitat-selection strength. *Dots* represent the end points of the individual marginality vectors in **a** and **b** when the starting points are centred to a common origin of space, i.e. (0, 0). *Open dots* represent lynx individuals, and *filled dots* represent wolverine individuals. *Bars* represent 95 % CI of mean marginality for the two species



2009) the selected habitats promote survival in terms of avoiding human disturbance (i.e. restricted accessibility both by snowmobile and on foot). The mean individual selection strength for these preferred habitats was stronger during winter when human disturbance and poaching are high. This strongly emphasizes the importance of low-risk habitats during the snow season. In addition, the selected habitats include the birch forest—low alpine ecotone, which is rich in several prey species (May et al. 2010 and references therein). The majority of lynx-killed reindeer in this area were observed in the low alpine tundra close to the tree line (Mattisson et al. 2011a). Both the density of reindeer and alternative small prey is substantially lower

during winter in the study area, and the distribution of reindeer and carrion during winter will influence winter habitat selection. These general results contradict the low overlap between suitable habitats for the two species in southern Norway (May et al. 2008). However, in southern Norway both sources of mortality (i.e. different human hunting techniques) and main prey differ between the species (May et al. 2008; Basille et al. 2009; Brøseth et al. 2010). Basille et al. (2009) found a trade-off in lynx habitat selection between roe deer (*Capreolus capreolus*) abundance and avoidance of human activity. Thus, human activity seems to be a strong factor affecting habitat selection in lynx.

**Fig. 4** Individual seasonal habitat selection (marginality) of the *K*-select analysis within annual home ranges of wolverines (ID numbers commencing with J) and lynx (ID numbers commencing with L) in northern Sweden. The axis A1 represents selection along the first principal component, comprising 73 % of the marginality. The vertical line represents the origin (i.e. habitat availability within the home ranges), and the distance from the origin represents selection strength. Each individual is represented by two separate lines [open dots represent summer season (s), filled dots represent winter season (w)]



**Fig. 5** Individual habitat-selection strength (marginality) of the *K*-select analysis for wolverines and lynx within individual home ranges in relation to home range size. Open dots represent lynx individuals, and filled dots represent wolverine individuals. Lines represent linear regressions, and dotted lines represent the corresponding 95 % CIs

Lynx selection for habitats was stronger than that of wolverines when forming their home ranges. Wolverine, however, displayed a higher individual variation than lynx when selecting home ranges. Wolverine home range compositions ranged from low elevations with large portions of coniferous forests to higher elevations with large portions of bare rock and glaciers. The wolverine is a generalist predator and scavenger (van Dijk et al. 2008; Mattisson et al. 2011a), and has a lower mean energy demand than the lynx (Andrén et al. 2011). As a food hoarder the wolverine is not depending on a constant supply of fresh kills, as it may utilise stored food items that can be used throughout the winter. Wolverines may therefore be able to retrieve the necessary food resources from more varying habitats, and also counteract seasonal variation in prey abundance. There is also a difference in the strategies wolverines use to avoid risk, with some implication for their vulnerability. Wolverines are as prone to poaching as lynx (Persson et al. 2009), but an important difference between the species is the ability of wolverines to seek shelter below-ground in e.g. deep snow and rocky formations like boulder fields. A mean wolverine home

range is smaller than for lynx and in our heterogeneous study area small home ranges enable more differentiated home range compositions. Finally, the higher variation displayed by wolverines in our study area when selecting for habitats may reflect a higher relative density of wolverines compared to the lynx, or rather a lack of high-quality territories to occupy. If this was the case, the proportion of preferred habitats within the study area was lower for wolverines, and the selection for home range habitats will to a lesser extent represent true habitat preference (Gaillard et al. 2010).

Lynx selection was stronger than that of wolverines for habitats within their home ranges. Selection strength in lynx was only weakly related to home range composition, but was reduced when individual home range sizes increased. This is explained by their strong selection when establishing home ranges, where the home ranges include the sufficient amount of preferred habitats, which were also unilaterally selected for. Larger home ranges were inhabited by males, which are expected to have a weaker association with their environment, e.g. they do not need to carefully select habitats for nursing offspring. Additionally, with increasing size the home ranges include larger patches of non-preferred habitats that must be traversed by inter-patch movements, also decreasing habitat-selection strength. Wolverine selected habitats within their home ranges according to home range composition, i.e. they displayed functional responses to habitat availability (Mysterud and Ims 1998), where they selected for rugged terrain and slope, presumably representing safety, both at high and low elevation.

Despite some differences in habitat-selection strength and the different selection mechanisms at the scales of this study, the overall picture is a very high degree of overlap in selected home ranges and habitat patches between the two species. In addition, lynx and wolverines show no evidence of intra-guild killing (Andrén et al. 2006; Persson et al. 2009), no temporal or spatial avoidance (Mattisson et al. 2011c), and only weak evidence of exploitation competition for reindeer carcasses (Mattisson et al. 2011a). The two species also have a similar circadian activity pattern (Mattisson et al. 2010) and highly overlapping diets (Mattisson et al. 2011a, b). On the contrary, lynx provide increased resources for the wolverine through increased scavenging opportunities in the form of lynx-killed reindeer (Mattisson et al. 2011a). Altogether this suggests that competition between the two species is unlikely to produce the observed patterns in habitat selection.

When studying habitat selection we often a priori assume that the observed patterns represent an optimum because species behaviour is shaped over generations by natural selection (Giraldeau 2008). Considering both species have relatively large home ranges (i.e. substantially

larger than mean habitat patch size) and both are long-distance dispersers (Vangen et al. 2001; Samelius et al. 2012), the observed individual differences are more likely a result of behavioural plasticity than genetically fixed alternatives. The observed patterns may represent the intrinsic remnant of an evolutionary past, e.g. intra-guild competition with wolves (*Canis lupus*) (Boles 1977; May et al. 2010) or human hunting techniques of former ages. However, the question of interest is rather how the observed behaviours affect the present fitness. From this perspective, both species select habitats that work functionally well to avoid human-caused mortality, as they select for habitats where human encounters are limited. Ultimately, hypotheses regarding mechanisms of home range placement and habitat selection should best be tested by the realised fitness of the individuals inhabiting the different home ranges.

**Acknowledgments** The study was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas), the World Wide Fund for Nature (Sweden), and the private foundations Olle och Signhild Engkvists Stiftelser and Marie-Claire Cronstedts Stiftelse. We thank Peter Segerström and Tom Wiklund for field assistance and Jon Arnemo for veterinary assistance. We thank Gustaf Samelius, Johan Månsson, Tomas Willebrand, and an anonymous reviewer for valuable comments on earlier drafts.

## References

- Anderson DP, Turner MG, Forrester JD, Zhu J, Boyce MS, Beyer H, Stowell L (2005) Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *J Wildl Manage* 69:298–310
- Andrén H, Linnell JDC, Liberg O, Andersen R, Danell A, Karlsson J, Odden J, Moa PF, Ahlqvist P, Kvam T, Franzén R, Segerström P (2006) Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biol Conserv* 131:23–32
- Andrén H, Persson J, Mattisson J, Danell AC (2011) Modelling the combined effect of an obligate predator and a facultative predator on a common prey—lynx and wolverine predation on reindeer. *Wildl Biol* 17:33–43
- Arnemo JM, Evans A, Fahlman Å (2011) Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. <http://www.rovviltportalen.no/content.ap?thisId=500039688>. Accessed 29 Jan 2011
- Basille M, Herfindal I, Santin-Janin H, Linnell JDC, Odden J, Andersen R, Hogda KA, Gaillard JM (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32:683–691
- Belant JL, Griffith B, Zhang Y, Follmann EH, Adams LG (2010) Population-level resource selection by sympatric brown and American black bears in Alaska. *Polar Biol* 33:31–40
- Beyer HL, Haydon DT, Morales JM, Frair JL, Hebblewhite M, Mitchell M, Matthiopoulos J (2010) The interpretation of habitat preference metrics under use-availability designs. *Philos Trans R Soc Lond B* 365:2245–2254
- Boles BK (1977) Predation by wolves on wolverine. *Can Field Nat* 91:68–69

- Boulinier T, Mariette M, Doligez B, Danchin É (2008) Choosing where to breed: breeding habitat choice. In: Danchin É, Giraldeau L-A, Cézilly F (eds) Behavioural ecology. Oxford University Press, New York, pp 285–321
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecol Model* 157:281–300
- Breitenmoser U, Breitenmoser-Würsten C, Capt S, Molinari-Jobin A, Molinari P, Zimmermann F (2007) Conservation of the lynx *Lynx lynx* in the Swiss Jura Mountains. *Wildl Biol* 13:340–355
- Breitenmoser-Würsten C, Zimmermann F, Stahl P, Vandel JM, Molinari-Jobin A, Molinari P, Capt S, Breitenmoser U (2007) Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. *Wildl Biol* 13:365–380
- Brøseth H, Flagstad Ø, Wardig C, Johansson M, Ellegren H (2010) Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. *Biol Conserv* 143:113–120
- Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- Calenge C, Dufour AB, Maillard D (2005) K-select analysis: a new method to analyse habitat selection in radio-tracking studies. *Ecol Model* 186:143–153
- Copeland JP, Peek JM, Groves CR, Melquist NE, McKelvey KS, McDaniel GW, Long DC, Harris CE (2007) Seasonal habitat associations of the wolverine in central Idaho. *J Wildl Manage* 71:2201–2212
- Danell AC, Andrén H, Segerström P, Franzen R (2006) Space use by Eurasian lynx in relation to reindeer migration. *Can J Zool* 84:546–555
- Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B (2010) Habitat-performance relationships: finding the right metric at a given spatial scale. *Philos Trans R Soc Lond B* 365:2255–2265
- Giraldeau L-A (2008) Solitary foraging strategies. In: Danchin É, Giraldeau L-A, Cézilly F (eds) Behavioural ecology. Oxford University Press, New York, pp 233–255
- Haglund B (1966) De stora rovdjurens vintervanor I. (Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow). *Viltrevy* 4:81–310
- Hall LS, Krausman PR, Morrison ML (1997) The habitat concept and a plea for standard terminology. *Wildl Soc Bull* 25:173–182
- Hebblewhite M, Merrill EH (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454
- Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83:2027–2036
- Hutchinson GE (1957) Population studies—animal ecology and demography—concluding remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71
- Kittle AM, Fryxell JM, Desy GE, Hamr J (2008) The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* 157:163–175
- Linnell JDC, Strand O (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Divers Distrib* 6:169–176
- Mattisson J, Andrén H, Persson J, Segerström P (2010) Effects of species behavior on global positioning system collar fix rates. *J Wildl Manage* 74:557–563
- Mattisson J, Andrén H, Persson J, Segerström P (2011a) Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *J Mammal* 92:1321–1330
- Mattisson J, Odden J, Nilsen EB, Linnell JDC, Persson J, Andrén H (2011b) Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system? *Biol Conserv* 144:3009–3017
- Mattisson J, Persson J, Andrén H, Segerström P (2011c) Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Can J Zool* 89:79–89
- May R, Landa A, van Dijk J, Linnell JDC, Andersen R (2006) Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. *Wildl Biol* 12:285–295
- May R, van Dijk J, Wabakken P, Swenson J, Linnell JDC, Zimmerman B, Odden J, Pedersen HC, Andersen R, Landa A (2008) Habitat differentiation within the large-carnivore community of Norway’s multiple-use landscapes. *J Appl Ecol* 45:1382–1391
- May R, van Dijk J, Landa A, Andersen R (2010) Spatio-temporal ranging behaviour and its relevance to foraging strategies in wide-ranging wolverines. *Ecol Model* 221:936–943
- McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL (2010) Considering ecological dynamics in resource selection functions. *J Anim Ecol* 79:4–12
- Mysterud A, Ims RA (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441
- Odden J, Linnell JDC, Andersen R (2006) Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *Eur J Wildl Res* 52:237–244
- Pedersen VA, Linnell JDC, Andersen R, Andrén H, Linden M, Segerström P (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildl Biol* 5:203–211
- Persson J, Ericsson G, Segerström P (2009) Human caused mortality in the endangered Scandinavian wolverine population. *Biol Conserv* 142:325–331
- Persson J, Wedholm P, Segerström P (2010) Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *Eur J Wildl Res* 56:49–57
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478
- Rodgers AR, Carr AP, Beyer HL, Smith L, Kie JG (2007) HRT: home range tools for ArcGIS. In: Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada
- Sokal RR, Rohlf FJ (1981) Biometry. The principles and practice of statistics in biological research, 2nd edn. Freeman, San Francisco
- Sæther BE, Engen S, Persson J, Brøseth H, Landa A, Willebrand T (2005) Management strategies for the wolverine in Scandinavia. *J Wildl Manage* 69:1001–1014
- Sæther BE, Engen S, Odden J, Linnell JDC, Grotan V, Andrén H (2010) Sustainable harvest strategies for age-structured Eurasian lynx populations: the use of reproductive value. *Biol Conserv* 143:1970–1979
- Samelius G, Alisauskas RT, Larivière S, Bergman C, Hendricson CJ, Phipps K, Wood C (2002) Foraging behaviours of wolverines at a large arctic goose colony. *Arctic* 55:148–150
- Samelius G, Andrén H, Liberg O, Linnell JDC, Odden J, Ahlqvist P, Segerström P, Sköld K (2012) Spatial and temporal variation in natal dispersal by Eurasian lynx in Scandinavia. *J Zool* 286:120–130

- Sappington JM, Longshore KM, Thompson DB (2007) Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J Wildl Manage* 71:1419–1426
- Skarin A, Danell O, Bergström R, Moen J (2008) Summer habitat preferences of GPS-collared reindeer *Rangifer tarandus tarandus*. *Wildl Biol* 14:1–15
- van Dijk J, Gustavsen L, Mysterud A, May R, Flagstad Ø, Brøseth H, Andersen R, Andersen R, Steen H, Landa A (2008) Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *J Anim Ecol* 77:1183–1190
- Vangen KM, Persson J, Landa A, Andersen R, Segerström P (2001) Characteristics of dispersal in wolverines. *Can J Zool* 79:1641–1649





II





# National Parks as refuges for illegal killing of large carnivores

Geir Rune Rauset<sup>1</sup>, Gustaf Samelius<sup>1</sup>, Peter Segerström<sup>1</sup>, Jon E. Swenson<sup>2,3</sup>, Henrik Andrén<sup>1</sup>, Jens Persson<sup>1</sup>

<sup>1</sup>*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden*

<sup>2</sup>*Norwegian University of Life Science, Department of Ecology and Natural Resource Management, N-1432 Ås, Norway*

<sup>3</sup>*Norwegian Institute of Nature Research, N-7485 Trondheim, Norway*

## Abstract

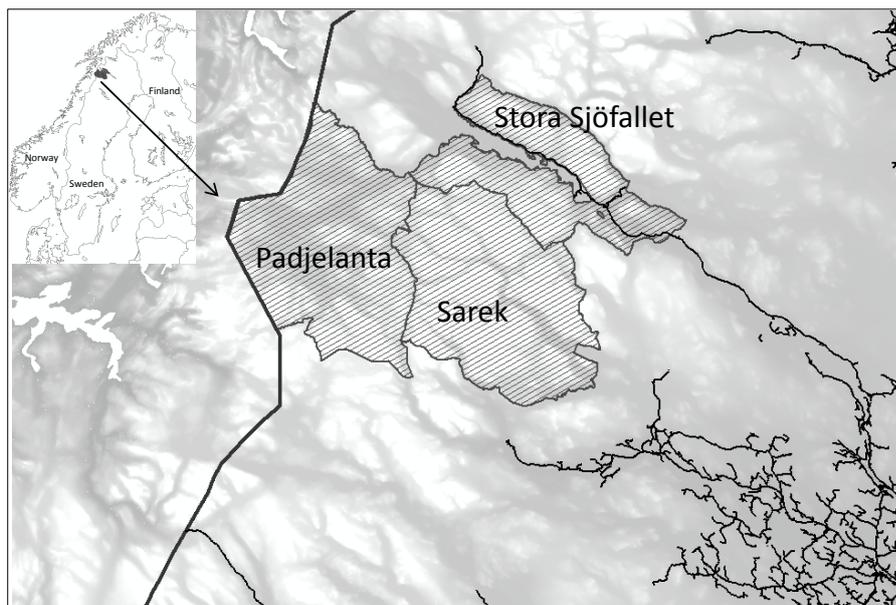
Large carnivores are characterized by high trophic levels, low population densities, and slow life histories; all which makes them especially sensitive to human activities. It has been argued that carnivore extinction risk is as much a question of availability of large protected areas as it is of population size itself. Consequently securing protected areas of sufficient size and reducing negative edge effects in these protected areas has received much attention in carnivore conservation. However, we show that carnivore (brown bear, lynx and wolverine) survival rates in northern Sweden's large national parks are lower than in surrounding unprotected areas due to illegal killing in the parks. These flagship reserves of Europe once played a critical role for preserving endangered carnivores. We suggest that this is the result of low enforcement and public attention in these remote parks which, in turn, result in a low probability for perpetrators to be caught when illegally killing large carnivores. We emphasize the importance of critically evaluating the conservation performance and ecological baseline of protected areas for effective and adaptive conservation.

## Main text

National Parks (NPs) originally preserved monuments and wonders of nature (Hansen & DeFries, 2007; Pressey, 1994), and have together with other forms of protected areas (PAs) become one of the most important tools in biodiversity conservation (Hoffmann *et al.*, 2010; Margules & Pressey, 2000). The recognition and success of PAs have spurred scientific effort into designing representative and persistent reserves (Margules & Pressey, 2000). Still, protection of grand scenery and wilderness often win political advantage as this usually include areas that are remote and rugged, with little human use, and thus are of lower economically value (Margules & Pressey, 2000; Soule & Sanjayan, 1998; Pressey, 1994). Large carnivores (LCs) are often favored by such PAs; because of world-wide persecution, high trophic levels, low population densities, and slow life histories they are especially sensitive to human activities (Cardillo *et al.*, 2005; Cardillo *et al.*, 2004; Purvis *et al.*, 2000; Woodroffe, 2000). Therefore, effective PAs are often perceived as the most important factor affecting carnivore population persistence (Woodroffe & Ginsberg, 1998). However, LCs require large reserves, and humans around reserves may cause strong edge effects (Loveridge *et al.*, 2007). Woodroffe and Ginsberg (1998) suggested that critical reserve size could predict local carnivore population extinctions. Consequently, one core question in carnivore conservation has been how to hinder the negative impact from people living at the edges of attractive PAs (Wittemyer *et al.*, 2008; Treves & Karanth, 2003). This paradigm has seldom been tested empirically, but some studies support the prediction of lower survival outside reserves, increased carnivore mortality at reserve edges, and carnivore densities declining from core to edges (Balme *et al.*, 2010; Johnson *et al.*, 2004). However, Linnell *et al.* (2001) noted that many carnivore populations in North America and Europe have been stable or increasing also outside PAs and despite high human population densities, and concluded that LC conservation is possible at high human densities when management is favorable. Sweden is a case in point. Following eradication programs, these LC populations were very low in numbers or regionally extinct during the 19<sup>th</sup> and 20<sup>th</sup> century. Today, after decades of more favorable management policies, the populations have recovered, and now mainly persist outside PAs in privately owned multi-use landscapes. Northern Sweden is a special situation of human-carnivore conflict, where the main large prey of LCs is semi-domestic reindeer *Rangifer tarandrus* (i.e. private property; Mattisson *et al.*, 2011; Swenson & Andrén, 2005), and the presence of LC negatively influences the harvest within the reindeer herding industry (Hobbs *et al.*, 2012). To ensure carnivore persistence despite this obvious negative influence on the rural economy, Sweden has implemented a conservation

payment system for LCs, combined with intensive monitoring and research (Dickman *et al.*, 2011; Zabel & Holm-Muller, 2008; Swenson & Andrén, 2005).

We assessed the effectiveness of LC conservation in northern Swedish national parks by studying the spatial variation in mortality (Materials and methods are available in the supplementary material), using long-term individual-based demographic and location data for the three species constituting the present large mammalian carnivore guild in the region: brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), and wolverine (*Gulo gulo*). The study took place in and adjacent to the largest national parks in Sweden; Sarek, Stora Sjöfallet and Padjelanta (Fig. 1). Sarek and Stora Sjöfallet were among the nine Swedish NPs founded in 1909 as the first in Europe. The large NPs of northern Sweden are the European equivalents to the large NPs of North America, chosen for their scenic and recreational value and situated on state land of low commercial value (Götmark & Nilsson, 1992). One of the additional rationales for forming these NPs was to protect the critically endangered Scandinavian brown bear population that only survived in the most remote mountains (Swenson *et al.*, 1994). This area also hosted most of the few Swedish wolverines that remained during a historical bottleneck in the mid-1900s (Haglund, 1965). Together with other PAs, the three national parks



*Figure 1.* Study area for large carnivore survival in northern Sweden. The national parks are marked in gray. The bold black line is the boarder to Norway; black lines are public and private roads.

form the 9 400 km<sup>2</sup> Laponia UNESCO world heritage site; one of the largest PA networks in Europe. The justification for UNESCO world heritage designation included its nature qualities and indigenous Sámi reindeer herding culture. The area constitutes important spring-to-fall grazing areas and spring calving grounds for semi-domestic reindeer both inside and outside the NPs. Human infrastructure and agriculture is very low, both inside and outside the NPs (0.0044% of the park area vs. 0.024% outside), and the road density is equally low (0.017 km road / km<sup>2</sup> inside the park, essentially one road on the perimeter of the parks, vs. 0.15 km road / km<sup>2</sup> outside). Snowmobile access and hunting inside the NPs is restricted to reindeer herders.

Poaching was an important source of mortality for sub-adults and adults of all three species (Table 1; Bischof *et al.*, 2009; Persson *et al.*, 2009; Andren *et al.*, 2006)). There was an increased mortality risk for all species during the late snow season (Fig. 2), due to an increased accessibility for humans on snowmobiles as the days are getting longer and the snow more suitable for snowmobiling (Persson *et al.*, 2009; Andren *et al.*, 2006). In addition, brown bears were poached in fall during the bear and moose hunting season.

Table 1. *Causes of mortality of individuals included in the survival analysis of large carnivores in northern Sweden (1984-2010).*

Mortality category	Brown bear	Lynx	Wolverine
Hunting	9	1	
Lethal control	3		6
Intraspecific killing	4	3	17
Natural		7	20
Unknown	12		2
Sum other mortality	28	11	45
Illegal killing	2	5	15
Likely illegal killing	18	20	20
Sum illegal killing	20	25	35
Sum total mortality	48	36	80

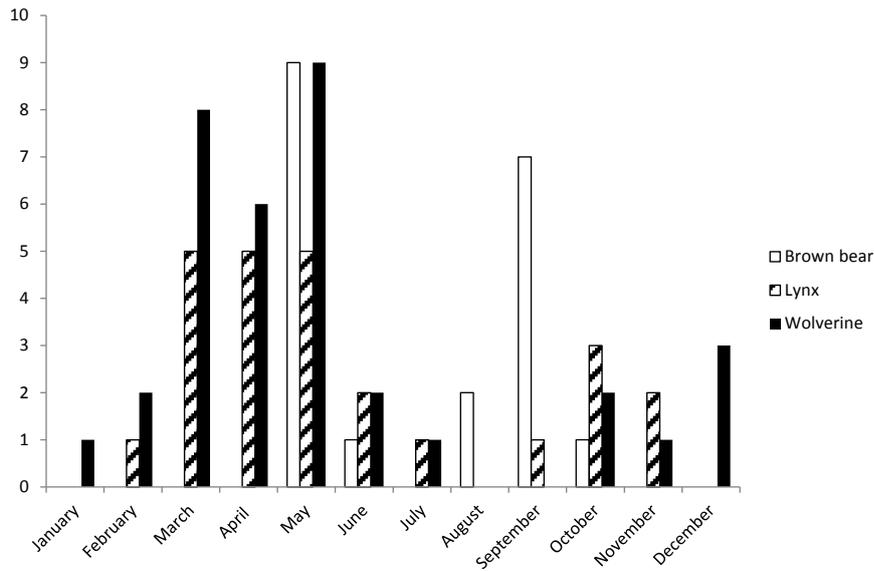


Figure 2. Monthly distribution of illegal killing of large carnivores in northern Sweden

Spatial variation in risk of mortality (Johnson *et al.*, 2004) was explained by both habitat and human land use. Both NPs and reindeer calving grounds represented an increased risk of being killed illegally, whereas forested and steep areas represented decreased risk (Table 2; Supplementary text). The increased risks of illegal killing inside the NPs were not compensated by reduced risk of mortality from other causes (Table 3). We suggest that the increased risk of mortality in large carnivores associated with these national parks results from 1) the large areas where reindeer herders have exclusive access on snowmobile lowers the risk for perpetrators to be caught when illegally killing large carnivores, due to lowered public attention and surveillance and 2) many important reindeer calving grounds are located inside these parks. The fact that human activity, represented by proximity to permanent human infrastructure or agriculture, had no explanatory power for carnivore mortality might be explained by how the carnivores are killed (i.e. mainly from snowmobiles capable of traversing throughout the parks) and by the very low level of human activity also in the areas outside the parks.

Table 2. Environmental variables influencing risk of mortality of large carnivores in northern Sweden. Parameter estimates (mean  $\beta \pm SE$ ) and the Variable Relative Importance (VRI) are AIC-weighted model averaged parameters of Andersen-Gill models with an AIC better than the null model and  $\Delta_{AIC} < 4$ . The set of candidate models included all possible combinations of the environmental variables; “national park” (NP), “reindeer calving ground” (Calf), “steep terrain” (Steep), and “Forest” and their two-way interactions. NP and Calf are binary variables, whereas Steep and Forest represent the area (range 0 to 28.3 km<sup>2</sup>) within a 3000 m buffer around the location. The effects of the different strata (Table 6) were corrected for and therefore always included.

Parameter	Brown bear		Lynx		Wolverine	
	$\beta \pm SE$	VRI	$\beta \pm SE$	VRI	$\beta \pm SE$	VRI
<i>The risk of illegal killing.</i>						
NP	2.3 $\pm$ 0.88	0.77	0.81 $\pm$ 0.68	0.56	1.7 $\pm$ 0.57	1.0
Calf	1.1 $\pm$ 0.47	0.76	-0.94 $\pm$ 1.1	0.37	0.56 $\pm$ 0.80	0.58
Steep	-0.024 $\pm$ 0.011	0.23	-0.088 $\pm$ 0.053	0.85	-0.14 $\pm$ 0.050	1.0
Forest	-0.0025 $\pm$ 0.061	1.0	-0.092 $\pm$ 0.045	1.0	-0.013 $\pm$ 0.037	0.46
NP*Calf	-0.40 $\pm$ 0.17	0.17	1.4 $\pm$ 0.89	0.07	-0.89 $\pm$ 0.83	0.15
NP*Steep	-	-	-0.0064 $\pm$ 0.086	0.07	0.027 $\pm$ 0.078	0.19
NP*Forest	-0.21 $\pm$ 0.073	0.77	-0.064 $\pm$ 0.047	0.16	-0.015 $\pm$ 0.051	0.06
Calf*Steep	-	-	-0.14 $\pm$ 0.092	0.11	0.068 $\pm$ 0.067	0.13
Calf*Forest	-0.086 $\pm$ 0.0051	0.07	-0.0054 $\pm$ 0.084	0.07	-0.062 $\pm$ 0.077	0.04
Forest*Steep	-	-	-0.0038 $\pm$ 0.0062	0.17	-0.0078 $\pm$ 0.0054	0.16
Null model <sup>a</sup>		0.01		0.00		0.00
<i>The risk of other mortality than illegal killing</i>						
NP	-0.76 $\pm$ 0.28	0.43	-	-	-0.15 $\pm$ 0.65	0.36
Calf	2.4 $\pm$ 1.5	0.89	-	-	1.3 $\pm$ 0.85	0.86
Steep	0.045 $\pm$ 0.022	0.37	0.11 $\pm$ 0.069	0.68	-0.055 $\pm$ 0.038	0.97
Forest	-0.008 $\pm$ 0.040	0.89	0.085 $\pm$ 0.080	0.33	-0.0043 $\pm$ 0.031	0.34
NP*Calf	-	-	-	-	-1.1 $\pm$ 0.77	0.11
NP*Steep	-	-	-	-	0.059 $\pm$ 0.060	0.07
NP*Forest	-	-	-	-	-0.078 $\pm$ 0.054	0.06
Calf*Steep	-0.16 $\pm$ 0.039	0.37	-	-	-0.093 $\pm$ 0.060	0.38
Calf*Forest	-0.25 $\pm$ 0.11	0.89	-	-	-0.064 $\pm$ 0.062	0.10
Forest*Steep	-	-	-	-	-0.00027 $\pm$ 0.0046	0.02
Null model <sup>a</sup>		0.11		0.32		0.03

Table 2 continue

Parameter	Brown bear		Lynx		Wolverine	
	$\beta \pm SE$	VRI	$\beta \pm SE$	VRI	$\beta \pm SE$	VRI
<i>The total risk of mortality</i>						
NP	0.55 $\pm$ 0.77	0.44	0.54 $\pm$ 0.50	0.33	0.65 $\pm$ 0.52	0.77
Calf	1.8 $\pm$ 1.1	0.77	-0.85 $\pm$ 1.1	0.20	0.98 $\pm$ 0.48	0.92
Steep	0.020 $\pm$ 0.046	0.39	-0.039 $\pm$ 0.043	0.22	-0.082 $\pm$ 0.030	1.0
Forest	-0.011 $\pm$ 0.030	1.0	-0.048 $\pm$ 0.029	0.84	-0.010 $\pm$ 0.024	0.45
NP*Calf	-	-	-	-	-0.89 $\pm$ 0.68	0.35
NP*Steep	-	-	-	-	0.025 $\pm$ 0.032	0.17
NP*Forest	-0.12 $\pm$ 0.083	0.27	-0.070 $\pm$ 0.056	0.11	-0.039 $\pm$ 0.033	0.12
Calf*Steep	-0.11 $\pm$ 0.061	0.23	0.13 $\pm$ 0.071	0.09	-0.037 $\pm$ 0.045	0.14
Calf*Forest	-0.17 $\pm$ 0.064	0.70	-	-	-0.061 $\pm$ 0.047	0.08
Forest*Steep	-	-	-	-	-0.0027 $\pm$ 0.0034	0.05
Null model <sup>a</sup>		0.03		0.07		0.00

<sup>a</sup> - The model weight for the null model is indicated in the VRI columns.

We conclude that the Laponia World Heritage Site presently has a negative effect on the persistence of Scandinavian large carnivores, contrary to expectations and the historical intention of the park to secure a refuge for the brown bear. That these NPs seem to provide refuges for those who illegally kill carnivores is, however, not an effect of the NPs *per se*, but rather the snowmobile restrictions that are intended to limit human disturbance on wildlife and reindeer inside the NPs. The ecological baseline represented by these PAs has thereby changed since their founding (Götmark & Nilsson, 1992), not through human development and habitat depletion (Liu *et al.*, 2001), but first of all as a result of technological innovations (i.e. snowmobiles) (Andren *et al.*, 2006). Thus, a critical reserve size based on historical data can be a poor predictor of carnivore persistence; the Laponia PA network is more than twice as large as the suggested critical reserve size for grizzly bears in North America (Woodroffe & Ginsberg, 1998). Similarly, common proxies of human disturbance (Cardillo *et al.*, 2004; Woodroffe, 2000) like distance to human infrastructure and permanent human activity, also failed to predict risk of mortality at the local scale

Efficient law enforcement is a necessity for all natural resource management (Keane *et al.*, 2008). It is beyond doubt that management measures against poaching must be a main conservation effort in many areas (Hilborn *et al.*, 2006), but this also leads to criticisms of PAs being creations of and for an elitist few in conflict with local community interests (Wittemyer *et al.*, 2008). A positive part of our results was that general public attention

seemed to reduce illegal killing of large carnivores in more accessible areas. Thus, measures promoting acceptance of carnivores from local people often are of crucial importance (Nawaz *et al.*, 2008). Managers thus must promote incentives to compensate local costs of carnivores, such as direct compensation of losses or conservation payment systems, depredation prevention measures, controlled legal harvest, and by promoting activities giving carnivores a direct value (Paper V). This is especially important in Lapland and similar areas having dual conservation goals; ensuring the conservation of native biodiversity and indigenous cultural heritage and livelihood.

Our results emphasize the importance of critically evaluating the conservation performance of PAs. We warn against passive PA management and public expectancies of positive carnivore conservation effects, even of large, remote NPs in a highly developed country. However, poaching is extremely challenging to study directly, because of its cryptic and illegal character (Liberg *et al.*, 2012). Expensive, individual-based, long-term telemetry studies of carnivore survival are not a likely option in many cases. Several alternative noninvasive techniques have been developed though, both for monitoring the presence and estimating densities of such species (Bellemain *et al.*, 2005; Karanth & Nichols, 1998). These can provide essential information to evaluate the conservation performance and should be implemented in effective and adaptive biodiversity conservation in PAs.

*Table 3. Parameter estimates ( $\beta \pm SE$ ) for the effect of national parks in Andersen-Gill models for the risk of being illegally killed, the risk of mortality from other sources, and the total mortality. The effects of the different strata (Table 6) were corrected for and always included. A positive parameter estimate represents an increased risk of mortality within the national park. The  $\Delta_{AIC}$  column represents the change in AIC when removing the effect of national parks from the model.*

Mortality source	$\beta \pm SE$	$\exp(\beta)$	$\Delta_{AIC}$
<i>Brown bear</i>			
Illegal	1.04 $\pm$ 0.46	2.8	2.9
Other	-0.46 $\pm$ 0.47	0.63	-0.96
Total mortality	0.23 $\pm$ 0.31	1.3	-1.3
<i>Lynx</i>			
Illegal	0.93 $\pm$ 0.46	2.5	2.3
Other	-0.31 $\pm$ 0.72	0.73	-1.8
Total mortality	0.55 $\pm$ 0.37	1.7	0.29
<i>Wolverine</i>			
Illegal	0.84 $\pm$ 0.36	2.3	3.5
Other	-0.084 $\pm$ 0.31	0.92	-1.9
Total mortality	0.38 $\pm$ 0.23	1.4	-0.26

## Acknowledgment

The study was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the World Wide Fund for Nature (Sweden), the Swedish University of Agricultural Sciences, EAZA (European Association of Zoos and Aquaria) the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas). We thank Jon Arnemo for veterinary assistance in the field.

## References

- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R. & Segerström, P. (2006). Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biological Conservation* 131(1), 23-32.
- Balme, G.A., Slotow, R. & Hunter, L.T.B. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation* 13(3), 315-323.
- Bellemain, E., Swenson, J.E., Tallmon, O., Brunberg, S. & Taberlet, P. (2005). Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears. *Conservation Biology* 19(1), 150-161.
- Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A. & Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78(3), 656-665.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science* 309(5738), 1239-1241.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004). Human population density and extinction risk in the world's carnivores. *Plos Biology* 2(7), 909-914.
- Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence (vol 108, pg 13937, 2011). *Proceedings of the National Academy of Sciences of the United States of America* 108(49), 19836-19836.
- Götmark, F. & Nilsson, C. (1992). Criteria Used for Protection of Natural Areas in Sweden 1909-1986. *Conservation Biology* 6(2), 220-231.
- Haglund, B. (1965). *Järv och varg*. Stockholm: P.A. Norstedt & Söners Förlag.
- Hansen, A.J. & DeFries, R. (2007). Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* 17(4), 974-988.
- Hilborn, R., Arcese, P., Borner, M., Hando, J., Hopcraft, G., Loibooki, M., Mduma, S. & Sinclair, A.R.E. (2006). Effective enforcement in a conservation area. *Science* 314(5803), 1266-1266.
- Hobbs, N.T., Andrén, H., Persson, J., Aronsson, M. & Chapron, G. (2012). Native predators reduce harvest of reindeer by Sami pastoralists. *Ecological Applications* 22(5), 1640-1654.

- Hoffmann, M., Hilton-Taylor, C., Angulo, A, et al. (2010). The Impact of Conservation on the Status of the World's Vertebrates. *Science* 330(6010), 1503-1509.
- Johnson, C.J., Boyce, M.S., Schwartz, C.C. & Haroldson, M.A. (2004). Modeling survival: Application of the Andersen-Gill model to Yellowstone Grizzly Bears. *Journal of Wildlife Management* 68(4), 966-978.
- Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79(8), 2852-2862.
- Keane, A., Jones, J.P.G., Edwards-Jones, G. & Milner-Gulland, E.J. (2008). The sleeping policeman: understanding issues of enforcement and compliance in conservation. *Animal Conservation* 11(2), 75-82.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B-Biological Sciences* 279(1730), 910-915.
- Linnell, J.D.C., Swenson, J.E. & Andersen, R. (2001). Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4, 345-349.
- Liu, J.G., Linderman, M., Ouyang, Z.Y., An, L., Yang, J. & Zhang, H.M. (2001). Ecological degradation in protected areas: The case of Wolong Nature Reserve for giant pandas. *Science* 292(5514), 98-101.
- Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* 134(4), 548-558.
- Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature* 405(6783), 243-253.
- Mattisson, J., Odden, J., Nilsen, E.B., Linnell, J.D.C., Persson, J. & Andrén, H. (2011). Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system? *Biological Conservation* 144, 3009-3017.
- Nawaz, M.A., Swenson, J.E. & Zakaria, V. (2008). Pragmatic management increases a flagship species, the Himalayan brown bears, in Pakistan's Deosai National Park. *Biological Conservation* 141(9), 2230-2241.
- Persson, J., Ericsson, G. & Segerström, P. (2009). Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142(2), 325-331.
- Pressey, R.L. (1994). Ad Hoc Reservations - Forward or Backward Steps in Developing Representative Reserve Systems. *Conservation Biology* 8(3), 662-668.
- Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B-Biological Sciences* 267(1456), 1947-1952.
- Soule, M.E. & Sanjayan, M.A. (1998). Ecology - Conservation targets: Do they help? *Science* 279(5359), 2060-2061.
- Swenson, J.E. & Andrén, H. (2005). A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. In: Woodroffe, R., et al. (Eds.) *People and*

- Wildlife: Conflict or coexistence?* pp. 323-339. New York: Cambridge University Press. (Conservation Biology; 9).
- Swenson, J.E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. & Franzén, R. (1994). Size, Trend, Distribution and Conservation of the Brown Bear *Ursus-Arctos* Population in Sweden. *Biological Conservation* 70(1), 9-17.
- Treves, A. & Karanth, K.U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17(6), 1491-1499.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O. & Brashares, J.S. (2008). Accelerated human population growth at protected area edges. *Science* 321(5885), 123-126.
- Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3, 165-173.
- Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* 280(5372), 2126-2128.
- Zabel, A. & Holm-Müller, K. (2008). Conservation performance payments for carnivore conservation in Sweden. *Conservation Biology* 22(2), 247-251.

## Supplemental Materials

### Materials and methods

The animals were immobilized by darting from helicopter or from the ground. We equipped individual brown bears, lynx and wolverines with radio transmitters, either Very High Frequency [VHF] collars, Global Positioning Satellite [GPS] collars, or intraperitoneally implanted VHF transmitters. The continuously updated capture and handling protocols (Arnemo *et al.*, 2011), were approved by the regional Ethical Committee on Animal Research in Umeå or Uppsala and fulfill the ethical requirements for research on wild animals in Sweden.

We located individual animals either by manually radio tracking VHF transmitters from fixed-wing airplane, helicopter, or from ground, or by automated GPS location sampling. The GPS locations were downloaded directly from the collars (e.g. from drop-off collars or collars retrieved at recapture), downloaded by VHF signals to a receiver, or automatically transferred by Global System for Mobile Communication [GSM] or Iridium™ satellite communication. Location data were analysed in ArcGIS 9.3™ (©1999-2004 ESRI Inc). We removed capture locations, repeated locations at bear dens, and when location accuracy was evaluated to exceed 2 000 m. We resampled the GPS records to include only one random location per individual per day.

### *Demographic data*

A high portion of the individuals were of known age, as they were captured as juveniles with their marked mother. Some wolverines and lynx were estimated to be adults at the time of first capture and classed as adults with unknown year of birth. A first premolar was extracted from brown bears of unknown age and sent to Matson's, Inc., Milltown, MT, USA for age determination using counts of cementum annuli layers (Matson *et al.*, 1993). We classified individuals into three age classes: juveniles, subadults, and adults. Brown bear cubs are born during winter hibernation, and separate from their mother at about 1.5 years of age (Dahle & Swenson, 2003a). We classed brown bears as subadults when  $\geq 1$  year (using 1 January as standardized birth date). Because we observed no mortality events in the winter dens, they were subadults when leaving the den as yearlings in May. The earliest record of primiparity in brown bears is 3 years (Zedrosser *et al.*, 2004), and in northern Scandinavia male brown bears reproduce successfully from 3 years of age (Zedrosser *et al.*, 2007). We classified brown bears as adults when  $\geq 3$  years. Lynx kittens in northern Scandinavia are typically born in June (Nilsen *et al.*, 2012), and follow their

mother until separation and later dispersal at about the age of 12 months (Samelius *et al.*, 2012). We classified lynx  $\geq 1$  year (using 1 June as standardized birth day) as subadults. First age of primiparity in lynx in northern Scandinavia is 2 years (Nilsen *et al.* 2012) and we classified lynx  $\geq 2$  years as adults. Wolverine cubs are born in Jan-March and rely on their mother's territory for survival until dispersal at a mean age of 13 months (Vangen *et al.*, 2001). We classified wolverines as subadults when  $\geq 1$  years (using 1 January as standardized birth day). The earliest observation of primiparity in Scandinavian wolverines is 2 years (Paper III), and we classified wolverines as adults when  $\geq 2$  years.

We removed locations of radio-marked juveniles with their radio-marked mothers from the dataset for all species, because they are tied location events. Similarly, we removed tied events of mortality in juveniles from the dataset for all species, when they died at the same time and same location as their mothers.

We attempted to determine the cause of death for all individuals that died while carrying a functional radio-transmitter. The animals we found dead were examined carefully in the field and sent to the Swedish National Veterinary Institute for necropsy. However, in some cases the cause of death could not be reliably determined and were classified as unknown. Studying illegal killing of carnivores is extremely challenging; there is a strong incentive to conceal it because it is illegal and those responsible risk jail sentences (Liberg *et al.*, 2012; Persson *et al.*, 2009; Andren *et al.*, 2006). We documented 22 cases when carnivores were definitively killed illegally; e.g. the body was found shot, animals with collars removed but with functioning radio implants or smashed or cut-off/out and attempted hidden radio-transmitters (Persson *et al.*, 2009; Andren *et al.*, 2006). In addition there were several occasions where we lost contact with an animal, and whose fate was difficult to determine. We know that people may remove or destroy radio-transmitters on animals they kill illegally, but telemetry units may also malfunction and young individuals may disperse from the study area (Samelius *et al.*, 2012; Vangen *et al.*, 2001; Swenson *et al.*, 1998). We therefore classified animals we lost contact with as "likely illegally killed" or of "unknown fate", based on several criteria (Persson *et al.*, 2009; Andren *et al.*, 2006). We classified an animal as being "likely illegal killed" if 1) it was a resident animal with an external and internal transmitter and both quit simultaneously, 2) it was a resident animal with a new transmitter that had not shown any signs of malfunction (abnormal or weak signals) and was in an area that we searched often and/or observed snowmobile or other human-made tracks in the same area at the time of disappearance, or 3) we received an anonymous call or message that a specific animal had been

killed, when we had not made the loss public. All other animals that we lost contact with were classified as “unknown fate” and they were censored as uncertain. We were restrictive in our judgment of cases of “likely illegal killing”, but we recognize that we could have included some individuals that actually were still alive. However, the results of an earlier study suggested that this probability was very low (Swenson & Sandegren, 1999). Similarly, when using data from the individual-based population monitoring system of the Scandinavian wolf population and hierarchical state-space models, Liberg *et al.* (2012) found a close correspondence between model-based estimates of illegal killing and estimates based on radio-tracking procedures similar to those described here. We classified sources of mortality into two main classes: 1) “illegal killing” (illegal killing and likely illegal killing) and 2) “others” (legal hunting, intraspecific killing, lethal control, natural death, and unknown cause of mortality; Table 1). When individuals were observed dead, the time of mortality was assigned to the date at 40 % of the time span between the last observation alive and the observation as dead (Johnson, 1979). Similarly, when we lost contact with an individual, we assigned the time of censoring or being likely killed illegally to the date 40% into the monitoring interval.

#### *Environmental data*

The study area (total 48 536 km<sup>2</sup>) contains a gradient from Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) forests starting at about 200 m a.s.l. via mountain birch (*Betula pubescens*) forests, heaths, and grass to mountain peaks and plateaus of bare rock and glaciers above 2 000 m a.s.l. The climate is continental and the ground is usually snow-covered from November until May. For the analysis of habitat-specific survival, we applied three continuous topographical raster maps: elevation, terrain ruggedness, and slope, one categorical vegetation raster, and two vector maps representing human land use: national parks (NP) and calving grounds of semi-domesticated reindeer (Table 4). Elevation was obtained from a 50 m x 50 m digital elevation map (Geographical Data Sweden [GSD], National Land Survey of Sweden). We calculated terrain ruggedness and slope from the elevation map using the tool “Vector Ruggedness Measure” (VRM; Sappington *et al.*, 2007) in ArcGIS 9.3™ (©1999-2004 ESRI Inc.). We set the VRM neighborhood size to 3, resulting in a local scale ruggedness index based on 9 neighboring cells. We defined slope and ruggedness values in the upper quantile as steep and rugged, and resampled these layers into binary grids (steep/rugged = 1). Vegetation was obtained from a 25 m x 25 m vegetation map (Swedish Land Cover [SMD], National Land Survey of Sweden), which was aggregated into a 50 m x 50 m raster to fit the cell size of the topographical layers. The 49

vegetation classes in our study area were reclassified into 6 classes (Table 4). The national parks data was obtained from a Nature Conservation Area vector map (Geographical Data Sweden 2008), and the reindeer calving grounds were based on a map from the county administrations in Sweden (GIS data Länsstyrelserna© 2000-2008, SWECO), modified by local knowledge to represent the use during the study.

We calculated the mean step length between succeeding relocations (Table 5) and buffered each location with both  $\sim 1/2$  step lengths (3 000 m) and one step length (6 000 m). We extracted environmental data both at each individual location and as the mean value of topographical layers, or area of each categorical layer within the two buffer distances, using Hawth's tool in ArcGIS 9.2.

Table 4. *Environmental variables used and different strata included and corrected for in the survival analysis of large carnivores of northern Sweden. SMD vegcode refers to the Swedish Land Cover vegetation map from the National Land Survey of Sweden. The structure describes how the variables were estimated; "area" represents the area within a buffer of either 3 000 m or 6 000 m around the location, "distance" represents the shortest distance between a location and the specific habitat, "binary" represents whether a location is within or outside the specific habitat or whether a buffer contains the specific habitat or not.*

Code	Description	SMD vegcode	Structure
Veg1	Coniferous forest	43-50, 54-56	Area/distance
Veg2	Deciduous forest	40-42	Area/distance
Veg3	Heath, grass	51-53, 63-64	Area/distance
Veg4	Bare rock, glaciers	59-60, 62	Area/distance
Veg5	Bogs, lakes	70-73, 80-82	Area/distance
Veg6	Human infrastructure	1-32	Area/distance
Forest <sup>a</sup>	Forest (Veg1 + Veg2)		Area <sup>a</sup> /distance
Steep <sup>a</sup>	Upper quantile of slope (1=upper quantile)		Binary/Area <sup>a</sup>
Rugged	Upper quantile of ruggedness index (1=upper quantile)		Binary/Area
Elev	Elevation		Mean
NP <sup>a</sup>	National Parks (1=within NP)		Binary <sup>a</sup> /Area
Calf <sup>a</sup>	Reindeer calving grounds (1=within Calf)		Binary <sup>a</sup> /Area
Strata	Description		Structure
Sex	Female, male		Binary (1=female)
Age	Juvenile, Sub-adult, Adult		Categorical
Season	Snow (Nov-May) or non-snow (June to Oct) season		Binary (1=non snow)
VHF	VHF or GSP data		Binary (1=VHF)

<sup>a</sup> - Variables and variable structure included in the final models (Table 2)

There were several rationales for evaluating environmental variables as means or portions within buffered locations were several: 1) The location error of many VHF locations was large compared to the patch size of several of the environmental variables, thus data sets including relatively few mortality events would be sensitive to observation error (i.e. misclassifications) in the environmental characteristics. This was especially the case for the fine-scaled vegetation categories and the topographical variables. NPs and calving grounds, however, represented large and continuous patches relative to the mean location error and would thus be less sensitive to such misclassification; 2) In several occasions the last location of an animal was likely not the actual location of death. This was the case for individuals classified as “likely illegally killed”, where we only had the environmental characteristics at the last location observed alive. This would also be the case when animals were killed and later removed and attempted hidden, with the environmental variables describing the place where it was moved; 3) The location of death might not always represent the true risk. This can be the case if an animal is chased for a distance, e.g. by snowmobile, and the animal finally is killed in an environment other than where it was first observed. These circumstances stress the need for evaluating risk at a landscape scale rather than at the exact locations. One approach is to provide each location with a buffer of sufficient size to adequately represent the risk associated with the radio-tracking intervals included in the survival modeling. On the other hand, such buffers must not be too large to “average out” true patterns of risk, nor introduce spatiotemporal autocorrelation between succeeding locations. Using a buffer size of ~ one step length (i.e. a buffer area of 113 km<sup>2</sup>) we would not be able to identify areas of different risks within the home ranges of many carnivore individuals (e.g. a mean home range size for an adult female wolverines is 99-195 km<sup>2</sup>, depending on home range estimator and reproductive status; Mattisson *et al.*, 2011c; Persson *et al.*, 2010), and would also introduce autocorrelation. An alternative approach to using buffers of each succeeding location is to use home range composition to describe the risk individual animals were exposed to, but arguments similar to those given above also apply for this method. In addition, we would then not be able to include individuals without a fixed home range, e.g. dispersing or floating individuals of all species, or brown bears expanding their ranges during the mating season (Dahle & Swenson, 2003b). Such individuals were predicted to have an increased mortality risk, and are thus important to include when modeling spatial variation in risk. Thus, from both a methodological and biological perspective, a buffer distance of ~½ step lengths (3 000 m) is preferred (i.e. a buffer area of 28 km<sup>2</sup>). Still we chose to extract environmental variables at all three scales and include them in

separate models to evaluate whether the choice of scale had implications for the results.

Several of the potential environmental variables were expected to be highly correlated. To prevent multicollinearity, we evaluated correlation between pairs of variables by Pearson's residuals, and also evaluated suits of potential variables by Variance Inflation Factor (Zuur *et al.*, 2010) in the R library *AED* (Zuur, 2010). We did not include variables with a correlation of  $R^2 \geq 0.70$  or VIF  $\geq 3$  in the same models.

### *Survival modeling*

To estimate the risk of mortality among individuals of the three species, we applied the Andersen-Gill (A-G) formulation of the Cox proportional hazards (CPH) model (Andersen & Gill, 1982). The hazard function  $h(t)$  represents the instantaneous probability of mortality, conditional upon the individual having survived to the beginning of the interval:

$$h(t) = \lim_{\Delta t \rightarrow 0} \frac{\Pr(t + \Delta t > T > t \mid T > t)}{\Delta t}$$

The multivariate CPH model with linear predictors is defined by:

$$h_i(t) = h_0(t) \exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik})$$

where  $h_0(t)$  represents the unspecified baseline hazard function,  $x_1$  to  $x_k$  represent explanatory variables, and  $\beta_1$  to  $\beta_k$  the corresponding parameter estimates (Murray, 2006). A-G is the counting process analogue of CPH; using robust standard errors clustered within units. A-G allows for left and right censoring of data, time-varying continuous and categorical variables, multiple events, and discontinuous intervals of risk (Johnson *et al.*, 2004). Each interval between sequential relocations was treated as a unique interval of risk, and was attributed to different strata and environmental variables (Table 4) belonging to the end point of the interval (Johnson *et al.*, 2004). Events were coded as 1 for mortality and 0 for right censoring. We truncated monitoring intervals  $>30$  days, considering these as discontinuous (Johnson *et al.*, 2004). We added the additional number of days equaling 40% of the mean monitoring interval to the end point before discontinuous intervals (Johnson 1979). We build A-G models in R library *Survival* (Therneau, 2011) separately for each of the three species. We separately built models using interval-specific environmental data, both from the exact location at the end of the step and at the landscape level, as the mean environmental composition within buffer distances corresponding to  $\sim 1/2$  step length (3 000 m) and one step length (6 000 m) from this location. As these environmental representations yielded practically the same best models,

we chose to use the models with a buffer distance of 3 000 m in our final analyses. We stratified all models by sex, age class, season, and location data quality (VHF vs. GPS data, Table 4), allowing for the calculation of separate baseline hazards for each stratum. For each species and environmental buffer distance, we built separate hazard models for “risk of being illegally killed”, “risk of mortality from other causes than illegal killing”, and “total risk of mortality”. We used the Efron approximation for tied failure times. For all the best models, we tested the model assumption of proportional hazards, and plotted both Schoenfeld residuals along with the smoothed hazard curve and Martingale residuals (Grambsch & Therneau, 1994; Therneau *et al.*, 1990). We performed model selection by AIC, and assessed relative model strength by AIC weights ( $w$ ; Burnham & Anderson, 2002). We performed model averaging and calculated variable relative important (VRI), choosing the variables most consistently reoccurring among top models of the three species (Grueber *et al.*, 2011; Burnham & Anderson, 2002).

Table 5. *Data used in the survival analysis of large carnivores in northern Sweden.*

	Brown bear	Lynx	Wolverine
Years	1984 - 2009	1993 - 2010	1993 - 2010
Individuals	147	96	212
Censored	99	60	132
Censored alive/uncertain	68	56	92
Censored, telemetry gap/tied events	31	4	40
Events	48	36	80
VHF locations	12 474	5 966	9 093
GPS locations	115 153	86 624	116 150
GPS days	2 496	9 702	8 340
Radio tracking intervals	9 100	12 351	12 480
Radio days	55 469	31 854	44 796
Average # days between VHF observation	8.0	8.1	8.8
Average # days between GPS observation	1	1	1
Average distance [m] between succeeding relocations	5 922	5 584	5 929

### Risk models interpretation

For all the three species (brown bear, Eurasian lynx, wolverine) there was an increased risk of being killed illegally within national parks (Table 2, Table 3). However, there were differences between the species in the other environmental factors influencing mortality, which can be attributed to both species biology and patterns of human-caused mortality. The risk of being killed illegally was higher for males and higher during November to May (snow season) for all three species (Table 6).

Table 6. The effects of different strata (Table 4.) in Andersen-Gill models for the risk of being illegally killed among large carnivores in northern Sweden. Parameter estimates ( $\beta \pm SE$ ), where  $\exp(\beta)$  represents the effect size, i.e. the difference in risk of group 1 relative to group 0 of Sex (males=0/females=1), Season (snow=0/non-snow=1), Age01 (juvenile=0/sub adult = 1, Age02 (juvenile=0/adult =1), Age12 (sub adult=0/adult =1), VHF (GPS data=0/VHF=1). The  $\Delta_{AIC}$  represents the change in AIC when removing the demographic variable from the full model including all variables

Strata	$\beta \pm SE$	$\exp(\beta)$	$\Delta_{AIC}$
<i>Brown bear</i>			
Sex	-0.28 ± 0.47	0.76	26
Season	-0.57 ± 0.45	0.57	31
Age01 <sup>a</sup>	-	-	14
Age02 <sup>a</sup>	-	-	14
Age12	1.9 ± 1.0	6.6	14
VHF <sup>a</sup>	-	-	3.1
<i>Lynx</i>			
Sex	-0.47 ± 0.40	0.63	34
Season	-0.61 ± 0.45	0.55	24
Age01 <sup>a</sup>	-	-	27
Age02	-0.047 ± 0.50	0.95	27
Age12 <sup>a</sup>	-	-	27
VHF	-2.42 ± 0.76	0.0891	15
<i>Wolverine</i>			
Sex	-0.95 ± 0.34	0.39	59
Season	-1.3 ± 0.45	0.28	34
Age01	1.9 ± 1.1	6.7	41
Age02	1.9 ± 1.0	6.7	41
Age12	-0.004 ± 0.49	1.0	41
VHF	-6.78 ± 0.93	0.00114	40

<sup>a</sup> Zero events (i.e. no individual being illegally killed) in one of the two group

Spatial variation in illegal killing of brown bears was best explained by the variable forest (Table 2), but also the variables national park (NP), calving ground (calf) and the interaction forest\*NP had substantial support. In terms of illegal human-caused killing, forest represents both decreased probability of detection and decreased accessibility on snowmobile. The parameter estimate of forest was, however, very close to 0, and the effect of forest was therefore observed in the interaction term forest\*NP; within the national parks the risk decreased with increasing amount of forest. The distribution of illegal killing throughout the year (Fig. 2) and the spatial variation in risk suggests two main sources of illegal killing of brown bears: 1) retaliatory killing at or close to, reindeer calving grounds and 2) opportunistic poaching during the regular moose and bear hunting season in the fall. Brown bears are omnivores, and able to utilize pulses of neonate ungulates in spring (Barber-Meyer *et al.*, 2008; Swenson *et al.*, 2007; Adams *et al.*, 1995). However, there are often large individual differences in their kill rates (Rauset *et al.*, 2012), and there is likely a great difference in the risk of being killed illegally between a brown bear on reindeer calving ground, killing reindeer calves and disturbing reindeer herds during the vulnerable calving season, and a brown bear in dense coniferous forest feeding on ants and carrion. The most common way of hunting brown bears in the fall is by spotting bears in high areas when they are foraging on berries, usually above or close to the tree line.

Mortality in brown bears from other sources than illegal killing was best explained by the variables calving ground, forest, and the interaction term calf\*forest (Table 2). The risk decreased with increasing amount of forest on the calving grounds. Reindeer calving grounds probably attract bears in spring during the calving season, and therefore represent areas of increased risk of both illegal and legal human-caused killing. The County Administration has occasionally shot brown bears at calving grounds, including several radio-collared individuals, as a preventive measure to reduce the loss of reindeer calves. An increased risk of mortality for adult males may have consequences for other bears, as Scandinavian brown bears show evidence of sexually selected infanticide (Swenson *et al.*, 1997). Calving grounds with no trees to climb and hide in are thus risky areas for vulnerable bear cubs.

Spatial variation in illegal killing of Eurasian lynx was best explained by the variables; forest, followed by steep terrain (steep) and national parks (Table 2). None of the interaction terms had substantial support. Forests probably represent reduced risk of detection, and both forests and steep terrain represent reduced accessibility for snowmobiles. National parks had a weaker influence on the risk of illegal killing for lynx than for brown bears and wolverines (Table 2). Notable was the absence of increased risk of illegal killing of lynx at

reindeer calving grounds, which was observed for both bears and wolverines. Contrary to brown bears and wolverines, the lynx is a skilled stalker and still hunter, able to kill reindeer of every category year round (Mattisson *et al.*, 2011b), and the lynx is thus not depending on neonate reindeer calves nor does it cause as much disturbance on calving grounds as coursing predators. Altogether, these characteristics make the lynx less prone to be killed illegally at reindeer calving grounds. There were no clear spatial patterns in mortality causes other than illegal killing observed in the lynx and the null model had some support (Table 2).

Spatial variation in illegal killing of wolverines was best explained by the variables national parks and steep terrain (Table 2). None of the interaction terms had substantial support. Contrary to brown bears and lynx the risk of being killed illegally was not related to forested areas, probably because wolverines find shelter in rugged terrain or below ground e.g. in snow, cavities, or boulder fields. In winter, wolverines usually give birth below in snow tunnel systems dug out in close to cliffs or boulders (May *et al.*, 2012; Magoun & Copeland, 1998). The wolverine is a generalist forager; both scavenger and opportunistic predator upon reindeer (Mattisson *et al.*, 2011a). Like the brown bear, wolverines utilize neonate reindeer calves (Gustine *et al.*, 2006; Bjärvall *et al.*, 1990) and also hoard food for later consumption (Inman *et al.*, 2012). No important spatial patterns in mortality causes other than illegal killing were observed in wolverines (Table 2). However, there was a tendency for an increased risk in mortality other than illegal killing in flat areas at or close to calving grounds. There is evidence of infanticide in wolverine cubs as well (Persson *et al.*, 2003). Because the wolverine is strictly territorial (Mattisson *et al.*, 2011c; Persson *et al.*, 2010) we do not expect an aggregation of wolverines at attractive reindeer calving grounds. However, a high turnover rate of resident males in flat areas at or close to calving grounds could influence the rate of infanticide in wolverine cubs (Persson *et al.*, 2009).

## References

- Adams, L.G., Singer, F.J. & Dale, B.W. (1995). Caribou calf mortality in Denali National Park, Alaska. *Journal of Wildlife Management* 59(3), 584-594.
- Andersen, P.K. & Gill, R.D. (1982). Cox's Regression Model for Counting Processes: A Large Sample Study. *The Annals of Statistics* 10(4), 1100-1120.
- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R. & Segerström, P. (2006). Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biological Conservation* 131(1), 23-32.

- Arnemo, J.M., Evans, A. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Available at: <http://www.rovviltportalen.no/content.ap?thisId=500039688>
- Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008). Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* (169), 1-30.
- Björvall, A., Franzén, R., Nordkvist, M. & Åhman, G. (1990). *Renar och rovdjur*: Naturvårdsvärkets Forlag, Solna Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*. 2nd. ed. New York: Springer-Verlag New York, Inc.
- Dahle, B. & Swenson, J.E. (2003a). Family breakup in bears: Are young forced to leave? *Journal of Mammalogy* 84(2), 536-540.
- Dahle, B. & Swenson, J.E. (2003b). Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology* 72(4), 660-667.
- Grambsch, P.M. & Therneau, T.M. (1994). Proportional Hazards Tests and Diagnostics Based on Weighted Residuals. *Biometrika* 81(3), 515-526.
- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24(4), 699-711.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* (165), 1-32.
- Johnson, C.J., Boyce, M.S., Schwartz, C.C. & Haroldson, M.A. (2004). Modeling survival: Application of the Andersen-Gill model to Yellowstone Grizzly Bears. *Journal of Wildlife Management* 68(4), 966-978.
- Johnson, D.H. (1979). Estimating Nest Success - Mayfield Method and an Alternative. *Auk* 96(4), 651-661.
- Inman, R.M., Magoun, A.J., Persson, J. & Mattisson, J. (2012). The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93(3), 634-644.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B-Biological Sciences* 279(1730), 910-915.
- Magoun, A.J. & Copeland, J.P. (1998). Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62(4), 1313-1320.
- Matson, G.M., Van Daele, L., Goodwin, E., Aumiller, A., Reynolds, H.V. & Hristenko, H. (1993). A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth. *Matson's Laboratory, Milltown, Montana, USA*
- Mattisson, J., Andrén, H., Persson, J. & Segerström, P. (2011a). Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *Journal of Mammalogy* 92(6), 1321-1330.
- Mattisson, J., Odden, J., Nilsen, E.B., Linnell, J.D.C., Persson, J. & Andrén, H. (2011b). Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system? *Biological Conservation* 144, 3009-3017.

- Mattisson, J., Persson, J., Andrén, H. & Segerström, P. (2011c). Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 89(2), 79-89.
- May, R., Gorini, L., van Dijk, J., Brøseth, H., Linnell, J.D.C. & Landa, A. (2012). Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. *Journal of Zoology* 287(3), 195-204.
- Murray, D.L. (2006). On improving telemetry-based survival estimation. *Journal of Wildlife Management* 70(6), 1530-1543.
- Nilsen, E.B., Linnell, J.D.C., Odden, J., Samelius, G. & Andrén, H. (2012). Patterns of variation in reproductive parameters in Eurasian lynx (*Lynx lynx*). *Acta Theriologica* 57(3), 217-223.
- Persson, J., Ericsson, G. & Segerström, P. (2009). Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142(2), 325-331.
- Persson, J., Wedholm, P. & Segerström, P. (2010). Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife Research* 56(1), 49-57.
- Persson, J., Willebrand, T., Landa, A., Andersen, R. & Segerström, P. (2003). The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. *Wildlife Biology* 9(1), 21-28.
- Rauset, G.R., Kindberg, J. & Swenson, J.E. (2012). Modeling female brown bear kill rates on moose calves using global positioning satellite data. *The Journal of Wildlife Management* 76(8), 1597-1606.
- Samelius, G., Andrén, H., Liberg, O., Linnell, J.D.C., Odden, J., Ahlqvist, P., Segerström, P. & Sköld, K. (2012). Spatial and temporal variation in natal dispersal by Eurasian lynx in Scandinavia. *Journal of Zoology* 286, 120-130.
- Sappington, J.M., Longshore, K.M. & Thompson, D.B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71(5), 1419-1426.
- Swenson, J.E., Dahle, B., Busk, H., Opseth, O., Johansen, T., Söderberg, A., Wallin, K. & Cederlund, G. (2007). Predation on moose calves by European brown bears. *Journal of Wildlife Management* 71(6), 1993-1997.
- Swenson, J.E. & Sandegren, F. (1999). Misstänkt illegal björnjakt i Sverige. Bilagor till sammanhållen rovdjurspolitik; Slutbetänkande av Rovdjursutredningen. *Statens offentliga Utredningar* 1999:146. Stockholm: Ministry of Environment.
- Swenson, J.E., Sandegren, F. & Söderberg, A. (1998). Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67(5), 819-826.
- Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. (1997). Infanticide caused by hunting of male bears. *Nature* 386(6624), 450-451.
- Therneau, T. (2011). Survival analysis, including penalised likelihood. *R package 'survival'*.
- Therneau, T.M., Grambsch, P.M. & Fleming, T.R. (1990). Martingale-Based Residuals for Survival Models. *Biometrika* 77(1), 147-160.

- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerström, P. (2001). Characteristics of dispersal in wolverines. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 79(9), 1641-1649.
- Zedrosser, A., Bellemain, E.V.A., Taberlet, P. & Swenson, J.E. (2007). Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. *Journal of Animal Ecology* 76(2), 368-375.
- Zedrosser, A., Rauer, G. & Kruckenhauser, L. (2004). Early primiparity in brown bears. *Acta Theriologica* 49(3), 427-432
- Zuur, A. (2010). AED: Data files used in Mixed effects models and extensions in ecology with R (in Zuur et al. 2009). *R package version 1.0*.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1(1), 3-14.



III





# Age-specific reproduction and reproductive costs in female wolverines

Geir Rune Rauset<sup>1</sup>, Matt Low<sup>2</sup>, Jens Persson<sup>1</sup>

<sup>1</sup>*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91, Riddarhyttan, Sweden*

<sup>2</sup>*Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07, Uppsala, Sweden*

## Abstract

Age-specific patterns of reproduction and reproductive costs are vital for understanding life-history evolution and population dynamics; however, such knowledge is scarce among large carnivores. Using 18 years of longitudinal data from 62 radio-tracked female wolverines (*Gulo gulo*), we analyzed age-specific reproductive patterns and related these to seasonal and territory-specific resource distribution. Wolverines produced up to six litters during their lifespan at a mean of 0.84 (range 0-3, n=249) cubs per potential reproductive event. Females showed strong age-specific reproduction, with a large increase occurring between 2 and 3-year-olds (most likely resulting from maturity effects), followed by a slow decline as a function of age (most likely reproductive senescence). The number of cubs produced per year was correlated with early winter (pre-breeding) resources (i.e. distribution of reindeer *Rangifer tarandus* carrion) and summer primary production (i.e. normalized difference vegetation index NDVI). Reproductive costs also showed an age-related pattern, with the probability of breeding in successive years peaking at 5-6 years of age and being strongly correlated with summer primary production. This study illustrates the potential and importance of using longitudinal data from known-age individuals with known home ranges to learn more about animals' life history under varying intrinsic and environmental conditions over a lifetime.

## Introduction

Life history theory predicts an optimal reproductive effort based on the residual reproductive value, i.e. an increase in current reproduction decreases future reproduction, either through reproduction or parent survival (Stearns, 1992; Williams, 1966). An individual's ability to acquire resources throughout its life will vary, and the allocation of these limited resources to competing biological functions like growth, maintenance, and reproduction will also vary, resulting in age-specific patterns of reproductive output (Stearns, 1992). Age-specific reproduction often shows increased reproductive output during the first years, usually explained in terms of maturation and increasing experience, or trade-offs between early and late reproductive effort (Forslund & Pärt, 1995). An early increase in reproduction may eventually be counteracted by reproductive senescence; i.e. a decline in reproductive output due to age-related physiological changes (Dugdale et al., 2011; Ericsson et al., 2001; Bérubé et al., 1999; Clutton-Brock et al., 1982).

In female mammals, reproduction involves energy expenditures both in embryo growth and subsequent maternal care. Extended maternal care (e.g. lactation, vigilance, and learning) leads to a fitness cost for the mother, involving trade-offs between current reproduction and other life-history traits (Hamel et al., 2010; Clutton-Brock, 1991). Among mammals, age specific reproductive costs have typically been documented in ungulate species (Hamel et al., 2010; Bérubé et al., 1999; Clutton-Brock et al., 1983). However, there is a scarcity of information on age-related variation in the cost of reproduction in predators (Proaktor et al., 2007). Among predators there is a tendency for short gestation, which results in the production of heavily dependent offspring that require extended and energetically-demanding parental care (Proaktor et al., 2007; Gittleman & Thompson, 1988; Millar, 1977). With such high reproductive effort, there are strong trade-offs between current and future reproduction manifested in long inter-birth intervals in many large carnivores (Zedrosser et al., 2009; Persson, 2005). However, carnivora is an extremely diverse order (Gittleman, 1985; Bekoff et al., 1984), and different classes of life history strategies are predicted to display different patterns of reproductive costs (Ferguson & Larivière, 2002). Competitor carnivores (*sensu* Ferguson & Larivière, 2002) invest heavily in their offspring during gestation, and show no signs of reproductive costs to future reproduction other than for primiparous individuals, but rather a cost to survival (e.g. Hadley et al., 2007). In contrast to this, bet-hedging carnivores are predicted to not risk its own survival on the cost of offspring survival, and thereby trade present reproduction against future reproduction (Ferguson & Larivière, 2002).

When environmental heterogeneity is high, home range composition and individual resource selection might influence the reproductive potential among individuals (McLoughlin *et al.*, 2007; McLoughlin *et al.*, 2006). Many species also face great temporal variation in resource availability and exhibit life histories adapted to such variation, and varying ability to deal with shifting environmental conditions might drive individual fitness differences (Harrison *et al.*, 2011; Norris, 2005). In many observational studies of age-specific reproductive cost, individual and environmental heterogeneity are considered solely as sources of confounding effects (e.g. Schwarzkopf, 1993; Reznick, 1992). In real-life, however, individuals make reproductive decision based on their physiological status and in the face of shifting environmental pressures. Instead of perceiving environmental and individual heterogeneity as confounding effects masking general patterns, analyzing age-specific reproduction within the same framework as environmental components should rather have the potential of adding substantial information regarding life-history evolution.

We studied age-specific reproduction in 62 female wolverines (*Gulo gulo*) from northern Sweden, using 18 years of individual-based demographic and radio telemetry data. Wolverine reproduction follows a bet-hedging strategy, adapted to environments characterized by low productivity and seasonal variation (Ferguson & Larivière, 2002), where virtually all mature female wolverines are pregnant every year, but resorption or early litter loss is common when conditions are poor (Inman *et al.*, 2012 and references therein). In northern Sweden, the mean annual proportion of adult female wolverines that were confirmed to reproduce ranged 0.29-0.82 (mean 0.58; Persson *et al.*, 2006), presumably depending on varying resource availability that influence female condition (Persson, 2005). This suggests that reproduction is costly for female wolverines and should follow patterns related to female condition and resource availability. Thus, reproductive costs should be a function of reproductive output, female quality and environmental resources. Based on earlier studies and wolverine life history (i.e. delayed implantation of embryos), relationships between reproductive success and resource distribution should be most important in the season prior to giving birth. Because our dataset contains multi-year longitudinal data from known-age individuals with known home ranges, this allows a unique study on the reproductive output and the cost of reproduction in the wolverine.

Specifically we wanted to answer the following four questions on the patterns and drivers of age-related reproductive patterns in female wolverines. First, do female wolverines show age-related changes in reproductive output? Second, if the pattern followed the general expectation of a rapid increase in

reproductive performance early in life and a gradual senescent decline later in life, is there evidence that different processes drive the initial increase and later decrease? Third, is there evidence that environmental characteristics are important drivers in determining reproductive success? Finally, is there evidence of a cost of reproduction from one year on the next, and is this influenced by female age and/or environmental factors?

## Materials and methods

### Study species

Wolverine reproduction is characterized by delayed implantation, short gestation length, reproductive denning behavior, and extended maternal care following weaning (Inman *et al.*, 2012). The timing of birth is earlier in wolverines than in other non-hibernating carnivores (Inman *et al.*, 2012), and the female cares for the cubs in dens during the snow season (May *et al.*, 2012; Magoun & Copeland, 1998), yielding weaned but not self-sustaining cubs at the onset of spring (Inman *et al.*, 2012). The cubs rely on maternal resources, including food and territory until age of dispersal (in average 11 months; Vangen *et al.*, 2001). The most important demographic parameter among bet-hedging carnivores is survival among adult females (Sæther *et al.*, 2005; Ferguson & Larivière, 2002, Paper 5). Wolverines display year-round intra-sexual exclusive territoriality (Mattisson *et al.*, 2011b; Persson *et al.*, 2010). During winter, ungulates in terms of both prey and carrion constitute the main food source (Inman *et al.*, 2012; Mattisson *et al.*, 2011a; van Dijk *et al.*, 2008; Haglund, 1966), and the presence of top predators might increase food availability in form of increased scavenging opportunities (Mattisson *et al.*, 2011a; van Dijk *et al.*, 2008). A vital adaptation in wolverines to cold and seasonal environments is extensive food hoarding (Inman *et al.*, 2012), and increased resources during the pre-breeding season in terms of ungulate carrion is reported to reduce wolverine reproductive costs (Persson 2005). There is limited information on wolverine summer food (Inman *et al.*, 2012), but lemming (*Lemmus lemmus*) abundance is reported to positively influence wolverine reproduction in Scandinavia (Landa 1997).

### Study area

The study was carried out in and around Sarek National Park in northern Sweden (67°N, 17°E). The area is characterized by large spatial and seasonal heterogeneity, and spans gently rolling hills and valleys at about 300 m a.s.l. to high mountainous plateaus and peaks up to 2 000 m a.s.l., encompassing distinct vegetation gradients within short distances. Vegetation at lower

elevations mainly consist of mixed conifer forest (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*) interspersed by numerous bogs and lakes, followed by mountain birch (*Betula pubescens*) forest which form the tree line at 600-700 m a.s.l. The alpine tundra above tree line is 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., 2012). The climate is continental with distinct seasons, and the ground is usually snow-covered from October until May. Mean onset of greenness in the area was ~ 1 June, and the primary production peaked (i.e. maximum normalized difference vegetation index NDVI; Pettoirelli et al., 2005) around 15 July (ORNL DAAC, 2012). Semi-domesticated reindeer (*Rangifer tarandus*) constituted the most important large prey for wolverines (Mattisson et al., 2011a), and the area included important spring to autumn grazing pastures for semi-domestic reindeer. During winter the reindeer herds were moved to coniferous forest closer to the coast (Danell et al., 2006), but some reindeer remained also during the winter season. The area is inhabited by Eurasian lynx (*Lynx lynx*), a main predator on reindeer which provide scavenging opportunities on reindeer carrion for wolverines and other scavengers (Mattisson et al., 2011a). Alternative small prey is mountain hare (*Lepus timidus*), willow and rock ptarmigan (*Lagopus* spp.), black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*), but it is unknown to which extent these play a role in the wolverine's diet. Rodents have been shown to represent a substantial part of wolverines diets in Scandinavia (Landa et al., 1997), and the densities of these fluctuate strongly among years. The main source of mortality in sub-adult and adult wolverines in the study area was poaching (Persson et al., 2009), with substantial spatial variation in mortality which could be attributed human land use and activity (Paper II). Annual adult mortality from natural (i.e. non-human) sources was low; the main mortality source in juvenile wolverines was intraspecific predation (Persson et al., 2009).

#### Wolverine data

Individual wolverines were immobilized (adults were darted from helicopter or from the ground and juveniles were captured by hand; Fahlman *et al.*, 2008) and equipped with radio transmitters, either Very High Frequency [VHF] collars, Global Positioning Satellite [GPS] collars, or intraperitoneally-implanted VHF transmitters. The continuously updated capture and handling protocols (Armeno *et al.*, 2011) were approved by the Animal Ethics Committees in Sweden and fulfill the ethical requirements for research on wild animals.

We located individual animals either by manually radio tracking VHF transmitters from fixed-wing airplane, helicopter, or from ground, or by automated GPS location sampling. The GPS locations were downloaded directly from the collars (e.g. from drop-off collars or collars retrieved at recapture), downloaded by VHF signals to a receiver, or automatically transferred by Global System for Mobile Communication [GSM]. Location data were analyzed in ArcGIS 9.3™ (©1999-2004 ESRI Inc). We removed locations belonging to capture events, and when location accuracy was evaluated to exceed 2000 m. We resampled the GPS records to only include one random location per individual per day.

During the denning period (Jan-May), we radio-located and monitored adult females intensively to evaluate whether they displayed denning behaviors that indicate a reproductive event. Because wolverines mostly have dens consisting of large tunnel systems in deep snow (Magoun & Copeland, 1998) we were not able to observe the number of cubs at parturition. After abandonment of dens (May-June), we located females and observed the number of cubs accompanying her. We also marked all the 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 was of known age. Because cementum analysis does not provide precise estimates of age in wolverines (Persson *et al.*, 2006), individuals captured as adults, and hence of unknown age, were removed from analyses of age-specific reproductive performance.

#### Spatial environmental heterogeneity represented by individual home range composition

To account for spatial environmental variation, we used a 25 m x 25 m vegetation map (Swedish Land Cover [SMD], National Land Survey of Sweden), and reclassified the 49 vegetation classes into 7 vegetation categories (see Rauset *et al.*, 2012 for details). Elevation was obtained from a 50 m x 50 m digital elevation map (Geographical Data Sweden [GSD]), which also was used to derive maps of terrain ruggedness and slope (VRM; Sappington *et al.*, 2007). However, our primary goal was to obtain a mechanistic understanding of the relationship between environmental and seasonal heterogeneity and individual reproductive performance in wolverines. Thus, we employed two different data sets: 1) spring pellet counts of prey species; (see details in Danell *et al.*, 2006) and 2) spatial distribution of reindeer carcasses; (see details in Mattisson *et al.*, 2011a) to derive five maps of seasonal resource distribution: winter/spring distribution of reindeer and winter/spring distribution of small game (all potential species pooled), and

three seasonal distributions of reindeer carcasses (winter/spring: Feb-May[rc25], summer: Jun-Sept[rc69], autumn/winter: Oct-Jan[rc101]). For the pellet count data we applied zero-inflated models in R package pscl (Zeileis et al., 2008) to account for excess number of zeros in the observations, and with negative binomial count processes to account for overdispersion in the count data (i.e. ZINB models). To correct for variation in number of sampling plots (10 m<sup>2</sup>) in each pellet count triangle (3×3 km), we weighted each location by number of sampling plots. We build a suite of competing models based on habitat and landscape features within a buffer distance of 2 000 m of the center of the triangle (corresponding to the spatial scale of the triangle), and assessed model performance by small sample corrected Akaike's Information Criterion (AICc; Burnham & Anderson, 2002). To avoid multicollinearity among many potentially correlated environmental variables, we evaluated suites of potential variables by Variance Inflation Factor (VIF; (Zuur et al., 2009) in the R package "AED" (Zuur, 2010). We did not include variables with a VIF  $\geq 3$  in the same models. Predictions of the best model were interpolated into density surfaces by kriging regression in ArcGIS. For the reindeer carrion data, we excluded carcasses belonging to multiple kills and other tied death events (e.g. avalanches killing several reindeer). Following a presence-only design we sampled 5 random locations conditional on the location of each carcass, within a buffer of 5 000 m. For the three seasons, we build separate suits of competing models with logistic discriminant functions (use-availability), using habitat and landscape explanatory variables. To avoid multicollinearity, we evaluated suites of potential variables by VIF. We assessed model performance by AICc, and interpolated the best models prediction in ArcGIS into distributions of relative probability of reindeer carrion occurrences.

Because wolverines are able to utilize the food pulse of neonate reindeer during spring (Mattisson *et al.*, 2011a; Gustine *et al.*, 2006), and reindeer calving grounds are also associated with increased risk of mortality (Paper II), we included a map of designated reindeer calving grounds (See details in Paper II). Alternative small prey is predicted to play an important role in wolverine energy acquisition during summer, but so far we do not know much about summer diet composition in wolverines (Inman *et al.*, 2012). We used the mean integrated normalized difference vegetation index (NDVI) through the green season (June-Sept) on a 250 x 250 m scale to represent spatial variation in primary production as a proxy for the distribution of alternative small prey (ORNL DAAC, 2012).

We estimated individual home ranges, using a 90 % kernel density estimator with a bivariate normal kernel function in the package AdehabitatHR (Calenge, 2011) in R (R Development Core Team 2012). A well-debated topic

when applying home range estimators is sample size limitations; for all kernel estimators, small sample size results in disproportionately large estimated home ranges, and a general recommendation is excluding samples containing < 30 relocations (Seaman *et al.*, 1999). However, Börger *et al.* (2006) achieved representative monthly roe deer (*Capreolus capreolus*) kernel density estimators with only 10 relocations. We excluded home ranges containing < 20 locations. We extracted environmental representations for each individual home range; both as the mean for each of all the continuous maps, and the proportional area of categorical vegetation classes.

#### Annual variation in resource availability and environmental conditions

To account for annual variation in spring primary production we used the day of onset of greenness (defined as the mean start of increase from the minimum NDVI throughout the study area). To account for annual variation in winter severity, we used the mean winter (Nov-March) values of the North Atlantic Oscillation Index (NAO). In our study area positive winter values of the NAO represent warm and moist climate with deep snow, which have negative impact on the winter condition of reindeer and possibly their vulnerability to predation from wolverines (Helle & Kojola, 2008), but which also influence spring snow cover. A rodent index was derived from the National Environmental Monitoring Programme in Sweden for the site Stora Sjöfallet (see e.g. Hörnfeldt, 2004). We pooled all the 8 different rodent species identified, and also pooled observations during spring and fall into one annual rodent index. The rodent index varied substantially between years (range 0.2 – 16.6, mean:  $4.1 \pm 1.1$  SE), and the index was dominated by the species *Clethrionomys rufocanus* (52 %), *Clethrionomys rutilus* (17%), *Microtus agrestis* (11%), and *Sorex araneus* (9%).

#### Reproductive output models

We estimated age of first reproduction in female wolverines (Persson *et al.*, 2006), mean number of cubs by age and reproductive lifespan, based on 62 wolverine individuals during 249 reproductive events. We analyzed age-related patterns of reproductive output (here defined as number of confirmed cubs) in female wolverines using zero-inflated Poisson (ZIP) models in R package *pscl* (Zeileis *et al.*, 2008). These models include a binomial process to model excess abundance of zeros, in addition to the count 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: (i) the ability of individual females to produce a litter (e.g. maturity; as a binomial process) and (ii) the number of cubs produced in a litter when a female is able

to reproduce. For each reproductive event, we included age of the female (as a linear or quadratic term), home range characteristics and year-specific variables; all models included wolverine identity as a random intercept. For the initial analysis of age-specific patterns only, we removed individuals of unknown age and reproduction events with unknown outcome from these analyses. Also, we removed data from four individuals when they were subject to a supplementary feeding experiment (Persson, 2005), leaving 53 individuals with 205 reproductive events ( $\geq 2$  yrs.). Later, when including environmental variables we removed individuals that lacked an estimated home range (floaters or with too few locations), leaving 41 individuals with 174 reproductive events. To avoid multicollinearity among many potentially correlated environmental variables, we tested for direct covariance between pairs of variables by Pearson's residuals and also evaluated suites of potential variables by Variance Inflation Factor (VIF; Zuur *et al.*, 2009) in the R package "AED" (Zuur, 2010). We did not include variables with a  $VIF \geq 3$  in the same models. The model development was performed in three stages: 1) we explored factors affecting the binomial part of the model, by using all combinations of variables; 2) we kept the best model parameters in the binomial part constant and explored which variables had the best support in the count part of the model; 3) we kept the best count variables and explored whether this affected which parameters had most support in the binomial part. We assessed model performance by small sample corrected Akaike's Information Criterion (AICc; Burnham & Anderson, 2002). 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 the corresponding ZINB models. To investigate the effect of individual heterogeneity for the ZIP model predictions, we reran the highest-ranked model using an MCMC sampler (JAGS: Just Another Gibbs Sampler; Plummer, 2003) called from R. For this we used 50 000 iterations with a 5 000 'burn in' and non-informative priors. Chains were checked for convergence using the Gelman and Rubin diagnostic in R 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 *et al.* 2006) to estimate the probability of breeding in year  $t + 1$  for animals that were either: (i) breeders, or (ii) non-breeders in year  $t$ . A multistate modelling framework was used because it allows the estimation of transition probabilities specific to the initial breeding state of each animal in each year (state transition ( $\psi$ ) i.e. non-breeder to breeder or breeder to breeder)

in addition to the survival ( $\Phi$ ) and resighting ( $p$ ) parameters, permitting a ‘cost of breeding’ analysis (see chapter 9 in White 2011). Survival and resighting parameters were separately estimated for breeders and non-breeders and had the same fixed structure for all analyses ( $\Phi$  (state)  $p$  (state)). Because we were interested in factors influencing the probability of breeding we fitted the following variables to the transition parameters of non-breeding to breeding ( $\psi_{\text{nonbreed-breed}}$ ) and breeding to breeding ( $\psi_{\text{breed-breed}}$ ): (1) wolverine age; this was initially fitted as a full age-varying, constant, linear and quadratic term. Based on AIC support, the highest-ranked age parameter (i.e. probability of reproduction was a quadratic function of age) was then used as the basis of fitting the other variables (see Low et al. 2010); (2) number of cubs raised in year  $t$ ; this was only fitted to the  $\psi_{\text{breed-breed}}$  parameter; (3) NDVI; (4-6) the three seasonal distributions of reindeer carrion rc25/rc69/rc101; (7) annual rodent density; (8) winter NAO. We used these factors as variables because they were expected to influence food availability and condition for breeding females. Because NDVI, rc25 and rc101 were highly correlated, they were not included in the same models. We fit them separately to the two transition parameters because we predicted that individual condition and habitat quality were more likely to show an effect in animals that had bred during the year before, than individuals who had not invested in breeding. 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 and for deriving model-averaged survival parameter estimates (Burnham & Anderson 2002).

## Results

We observed a total of 62 wolverine individuals during 249 potential reproductive events ( $\geq 2$  years). The earliest observation of primiparity was at the age of 2, and the last recorded litter was at 12 years of age. The mean age of primiparity was 3.4 years (SD = 0.79, range 2-5). Lifetime reproductive span ranged from 0 to 9 years and the number of weaned litters per lifespan ranged from 0 to 6. The mean number of cubs was 0.84, range 0-3 ( $n = 249$ ) for all individuals, and for individuals  $> 2$  year olds, the mean number of cubs was 0.90 ( $n = 229$ ).

### Age-specific reproductive output

Age was a strong factor influencing reproductive output in female wolverines (Table S1), with the best ZIP models including age terms in both the binomial process (quadratic) and count process (linear). Adding environmental variables

to the count process to explain the number of cubs produced each year improved the models substantially (Table S2). The variables “early winter reindeer carrion (rc101)”, “late winter reindeer carrion (rc25)” and NDVI all had substantial support, but were highly correlated and, thus, were not included together in the same models. The ratio residual deviance/df in the best model of Table S2 was 1.17, indicating no overdispersion in the count data, and that a Poisson distribution was adequate. When adding individual as a random effect in a hierarchical Bayesian model framework, the variation explained by the individual random intercept was of the same magnitude as the variation among the fixed effects (Table 1), revealing substantial individual heterogeneity that was not explained by age and home range composition alone. Plotting this model with its two components revealed that the binomial process only dealt with the probability of breeding at age 2, indicating that the low mean number of cubs at age 2 (i.e. the overwhelming majority of young females do not reproduce) derive from a process different from the number of cubs produced by older females (Fig. 1).

#### Age-specific reproductive costs

There was a ‘cost of breeding’ for female wolverines that was strongly age-dependent. Females that bred in one year were less likely to breed in the following year if they were young or old, with the probability of breeding in successive years peaking at around six years of age (Fig. 2). The two transition probabilities (i.e. from breed to breed versus from non-breed to breed) showed strong age-dependent differences, with the probability of non-breeders becoming breeders in the following year showing no age effects (Fig. 2; Table S3 & S4). For breeders, there was evidence that the probability of breeding in the following year was also strongly influenced by environmental variation (NDVI) between years, weakly influenced by the number of cubs weaned in the previous year, and little or no influence of the NAO or rodent density (Tables 2 & S3). This was in clear contrast to non-breeders, whose probability of breeding in the following year showed no evidence of being influenced by any environmental or age variables (Fig. 2, Table 2 & S4).

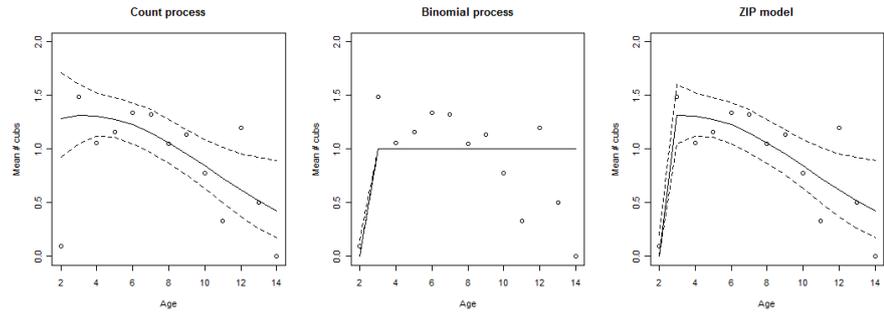


Figure 1. Zero-inflated Poisson (ZIP) mixed-effects model predicting annual reproductive output ( $n = 174$ ) in individual female wolverines ( $n = 41$ ), with its 95% credible intervals (dotted lines). The count process include age as a linear effect, the binomial include age as a quadratic term; with wolverine individuals as random intercept in both processes. Points represent the observed mean number of cubs by age.

Table 1. Zero-inflated Poisson (ZIP) mixed-effects model combining age and mean NDVI in individual home ranges to predict annual reproductive output ( $n = 174$ ) in individual female wolverines ( $n = 41$ ).

Model	Estimate ( $\beta$ )	SD ( $\beta$ )	95% CI ( $\beta$ )
<i>Binomial process</i>			
Random intercept		28.0	[4.8 – 1145]
intercept	-67.6	286.2	[-62.0 – 502.2]
age	-1114	625.8	[-2414 – -14.4]
age <sup>2</sup>	504	273.2	[55.2 – 1065]
<i>Count process</i>			
Random intercept		0.064	[0.008 – 0.227]
intercept	0.520	0.209	[0.095 – 0.897]
age	-0.078	0.032	[-0.138 – -0.015]
NDVI	0.127	0.070	[-0.025 – 0.249]

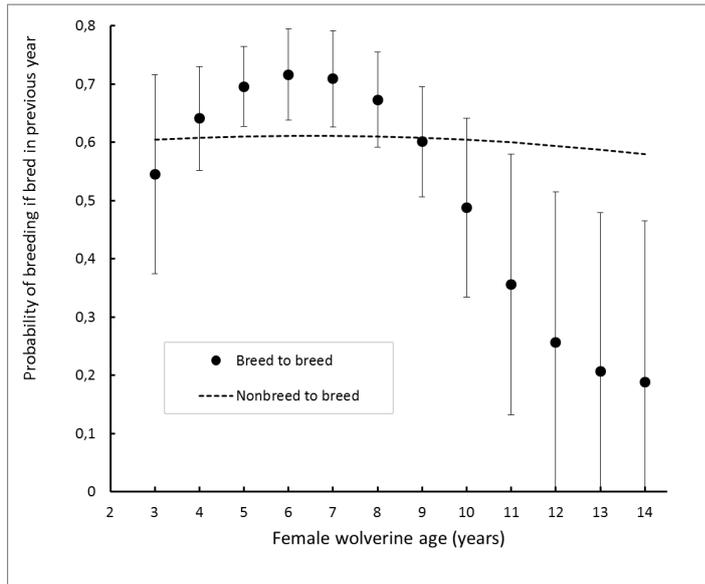


Figure 2. The probability to breed for female wolverines in relation to age for individuals that bred in previous year (point with 95 % CI) and for individual that not bred in previous year (dotted line).

Table 2. Factors influencing the probability of a female wolverine breeding in year  $t$  relative to her breeding status in year  $t - 1$ . Parameter estimates (means  $\pm$  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 multi-state mark-recapture models in Table S3 and S4. Parameters are in the following units: age (years), cubs (number of cubs raised in the previous year), mean home range NDVI (years 2001-2011, centralized and standardized by 2 SD, i.e. "z-scores"), annual winter NAO (z-scores), and annual rodent density (z-scores); with the probability of breeding calculated via a logit link.

Parameter	Breeder in previous year		Non-breeder in previous year	
	Estimate	VRI	Estimate	VRI
Intercept	0.39 $\pm$ 0.40	-	0.63 $\pm$ 1.6	-
Age	0.67 $\pm$ 0.52	1.0	0.011 $\pm$ 0.019	0.104
Age <sup>2</sup>	-0.095 $\pm$ 0.043	1.0	-0.0006 $\pm$ 0.0009	0.104
Cubs ( $t - 1$ )	-0.32 $\pm$ 0.20	0.56	-	-
NDVI	-0.67 $\pm$ 0.27	0.90	0.0002 $\pm$ 0.0005	0.257
NAO	-0.37 $\pm$ 0.26	0.42		
Rodent density	0.14 $\pm$ 0.19	0.29	-0.005 $\pm$ 0.03	0.245

## Discussion

Female wolverines displayed age-related patterns of reproductive output, where most individuals were incapable of reproducing before the age of three and after prime age showed a slow decline in reproduction with age, indicating reproductive senescence. Reproductive costs in wolverines were strongly age-dependent, where young and old females that bred in one year were less likely to breed the next, whereas the probability of non-breeders becoming a breeder was independent of age (Fig. 2). Both reproductive output and the cost of reproduction were strongly influenced by the available resources within the individual's home ranges, where reproductive output was best explained by summer primary production and early winter (pre-breeding) distribution of reindeer carrion (Table S2), and reproductive costs by summer primary production (Table S3).

### Age-related patterns of reproduction in wolverines

The ZIP modelling approach revealed that there were two different processes that influenced the age-specific reproductive output in female wolverines. The binomial process was only influenced by age; thus explaining the vast majority of 2 year-olds that were not able to reproduce. The lack of reproduction among the 2 year-olds was therefore not driven by a lack of territory or poor territory. Among individuals  $\geq 3$  years old, reproductive output depended on age, territorial and individual quality.

The increase from first potential reproduction to prime age is a relationship shown in numerous taxa and species. In group living species, such improvements are often related to dominance, reproductive repression, and exclusion from resources among young (Hamel *et al.*, 2010; Ordiz *et al.*, 2008; Bérubé *et al.*, 1999; Forslund & Pärt, 1995). In a strictly territorial species like the wolverine, with high territorial stability, the increasing reproductive success from young to prime-age probably relies on age-related phenotypic characteristics or other improvements of competence (e.g. breeding experience or foraging ability; Forslund & Pärt, 1995). Wolverines reach asymptotic growth at an earlier age than mean age of primiparity (Jens Persson unpublished data), hence we do not expect to see a strong trade-off between allocating resources for growth and reproduction (Zedrosser *et al.*, 2009). The slow decrease in reproductive output among older individuals is indicative of reproductive senescence in wolverines. This is in accordance with the bet-hedging life history of wolverines (Ferguson & Larivière, 2002), where survival of adult females is the most important demographic parameter (Sæther *et al.*, 2005, Paper V). A conservative reproductive strategy is thus favourable; wolverines do not trade current reproduction against their own survival.

The distribution of reindeer carcasses during early winter positively affected reproductive output. Increased abundance of resources in this season will potentially have a positive effect on body condition when entering the reproductive stage, and also contribute to vital food stores at the time of birth. Harrison *et al.* (2011) describe wolverines physiologically as income breeders but functionally as capital breeders because of this carry-over effect through hoarded food. Notable is also that the sympatric lynx presumably have a positive effect on wolverine reproduction, as lynx-killed reindeer provided a significant food resource in our study area (Mattisson *et al.*, 2011a).

During the most energy demanding period of the year, i.e. during lactation in late winter and spring, the wolverine diet relies heavily on reindeer in our study area (Mattisson *et al.*, 2011a; Haglund, 1966). However, reproductive success did not vary with the modelled carcass distribution for this season. Haglund (1966) suggested that March-April is the time of winter when availability of reindeer (prey and carrion) peaks in Scandinavia, due to increased hunting efficiency on reindeer (i.e. with beneficial spring snow conditions), winter deaths in ungulates and through accumulation of hoarded food throughout the winter season. It is possible that late winter and spring food is abundant, or at least quite predictable, in the study area. Starvation as the ultimate cause of wolverine mortality during late spring and summer is also rare (Persson *et al.*, 2009). This observation is strengthened by general considerations of wolverine life history. Because of short gestation length and low embryotic investment, embryonic resorption or early litter loss is not costly, whereas a loss of cubs late in the lactation period potentially implies a double loss in reproductive success; both this year and the following year as a result of reproductive costs. A frequent late litter loss is therefore maladaptive, implying that the “reproductive decisions” are taken before or soon after parturition, based on the current physiological and environmental conditions.

Summer primary production (NDVI) positively influenced reproductive output. Increased primary production is assumed to positively influence the abundance of various small prey, and the limited information on summer diet in wolverines indicates that small prey constitute the major summer food items (Inman *et al.*, 2012, and references therein). Summer reindeer carcass distribution was non-informative, supporting this conclusion.

We observed a large individual variation in reproductive success among the female wolverines. This is common in individual-based age-related reproductive studies, where many report that high-quality females always do better (e.g., Hamel *et al.*, 2010; Weladji *et al.*, 2008; Cam *et al.*, 2002; Bérubé *et al.*, 1999). In territorial species with a high degree of home range stability, it is hard to assess whether this quality difference stems from variation in

individual phenotypic quality, home range qualities not included in the models, or both (access to a high quality range might also depend on phenotypic quality). The process of selecting home range and balance reproduction to available resources is an important behavioural process, which lies in the core of understanding both life histories and population dynamics (McLoghlin *et al.*, 2007).

#### Age-related costs of reproduction in wolverines

Reproductive costs in female wolverines were strongly age-dependent. Young and old females that bred in one year were less likely to breed the next, whereas the probability of non-breeders becoming a breeder showed no age-effect. Interestingly, individuals at prime age that successfully reproduced also had a higher probability of weaning cubs the succeeding year than those that did not reproduce. Thus, the cost of reproduction was only expressed in young and old individuals. This result also implies that there is substantial individual heterogeneity in reproductive output among wolverines. After prime age, individual female wolverines have a longer recovery time following a successful reproduction; they experienced reproductive senescence.

Summer primary production in terms of NDVI modulated the reproductive costs in wolverines. Juvenile wolverines gain more absolute weight during the post-weaning period than from nidiation to weaning. Thus, although lactation may be the most energetically demanding period for a reproductive female, the period of post-weaning growth represents a greater energetic demand on the environment by the family group (Inman *et al.*, 2012). An increase in small prey availability with primary production provide both increased resources and possibly make the cubs independent from their mother at an earlier age, thus reducing maternal effort during summer; the longer the female continues to invest in the litter, the more she borrows significant physiological resources from the next potential litter to achieve success with the current litter (Persson 2005). Cost of locomotion is also potentially reduced at high prey density as the family group does not have to traverse long distances daily to search for food. Cubs rely on the resources within their mother's home ranges, and potentially also her food stores, until age of dispersal (Persson, 2005). This puts further stress on resource availability, and must be included in the extended maternal care (Persson, 2005).

We detected only weak effects of annual variation in resources. Annual abundance of rodents and winter climate slightly modulated the reproductive costs. These effects were substantially weaker than the spatial variation in home range composition. However, the proportion of lemmings in the index was very low, and we cannot exclude the possibility that extreme lemming

peaks might influence reproductive costs in high-elevation and poor environments.

### Summary

We demonstrated an age-related pattern in female wolverine reproduction, with increasing reproductive output to prime age, with a subsequent decline in reproduction with age. We also found that reproductive costs in wolverines are strongly age-dependent, as it was expressed only in young and old individuals. Both reproductive output and the effects of reproductive costs were strongly influenced by resource availability. We hypothesize that such patterns are more common among carnivores with similar life history, *bet-hedgers*, than what has previously been shown. Although survival of adult females is the most important parameter for population growth, reproduction can have large consequences for population dynamics if it is more variable (Charlesworth, 1994; Stearns, 1992). Therefore we suggest that the observed reproductive pattern should be considered when modelling populations of carnivores with a life history similar to that of wolverines.

To study demography and life history of large carnivores is challenging because they are generally ranging large areas, occur at low densities, are elusive and have long generation time. Thus, carnivore research is often limited by short study periods and low sample sizes, which make conclusions subject to chance events and vulnerable to individual and environmental heterogeneity. However, this study illustrates the potential and importance of using longitudinal data from known-age individuals with known home ranges to learn more about animals' life history under varying intrinsic and environmental conditions over a lifetime.

### Acknowledgment

The study was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the World Wide Fund for Nature (Sweden), the Swedish University of Agricultural Sciences, EAZA (European Association of Zoos and Aquaria). We thank Peter Segerström for capturing and monitoring wolverines, and Jon Arnemo for veterinary assistance. We thank Henrik Andrén for providing valuable comments on earlier drafts of the paper

## References

- Arnemo, J.M., Evans, A. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Available at:  
<http://www.rovviltportalen.no/content.ap?thisId=500039688>
- Bekoff, M., Daniels, T.J. & Gittleman, J.L. (1984). Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics* 15(1), 191-232.
- Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80(8), 2555-2565.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*. 2nd. ed. New York: Springer-Verlag New York, Inc.
- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T.I.M. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75(6), 1393-1405.
- Calenge, C. (2011). Home Range Estimation in R: the adehabitatHR Package. Accessed May 10, 2011.
- Cam, E., A. Link, W., G. Cooch, E., Jean-Yves Monnat & Etienne Danchin (2002). Individual Covariation in Life-History Traits: Seeing the Trees Despite the Forest. *The American Naturalist* 159(1), 96-105.
- Charlesworth, B. (1994). *Evolution in Age-Structured Populations*. New York, NY, USA: Cambridge University Press.
- Clutton-Brock, T.H. (1991). *The evolution of parental care*. Princeton, New Jersey, USA: Princeton University Press.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982). *Red deer: behavior and ecology of two sexes*. Chicago, Illinois, USA: University of Chicago Press.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1983). The cost of reproduction to red deer hinds. *Journal of Animal Ecology* 52, 367-383.
- Danell, A.C., Andrén, H., Segerström, P. & Franzén, R. (2006). Space use by Eurasian lynx in relation to reindeer migration. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 84(4), 546-555.
- Dugdale, H.L., Pope, L.C., Newman, C., Macdonald, D.W. & Burke, T. (2011). Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. *Molecular Ecology* 20(15), 3261-3274.
- Ericsson, G., Wallin, K., Ball, J.P. & Broberg, M. (2001). Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* 82, 1613-1620.
- Fahlman, Å., Arnemo, J.M., Persson, J., Segerström, P. & Nyman, G. (2008). Capture and Medetomidine-Ketamine anesthesia of free-ranging wolverines (*Gulo gulo*) *Journal of Wildlife Diseases* 44(1), 133-142.
- Ferguson, S.H. & Larivière, S. (2002). Can comparing life histories help conserve carnivores? *Animal Conservation* 5(1), 1-12.
- Forslund, P. & Pärt, T. (1995). Age and reproduction in birds — hypotheses and tests. *Trends in Ecology & Evolution* 10(9), 374-378.
- Gittleman, J.L. (1985). Carnivore Body Size: Ecological and Taxonomic Correlates. *Oecologia* 67(4), 540-554.

- Gittleman, J.L. & Thompson, S.D. (1988). Energy Allocation in Mammalian Reproduction. *American Zoologist* 28(3), 863-875.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* (165), 1-32.
- Hadley, G.L., Rotella, J.J. & Garrott, R.A. (2007). Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology* 76(3), 448-458.
- Haglund, B. (1966). De stora rovdjurens vintervanor I. (Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow). *Viltrevy* 4, 81-310.
- Hamel, S., Côté, S.D. & Festa-Bianchet, M. (2010). Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology* 91(7), 2034-2043.
- Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80(1), 4-18.
- Helle, T. & Kojola, I. (2008). Demographics in an alpine reindeer herd: effects of density and winter weather. *Ecography* 31(2), 221-230.
- Hörmfeldt, B. (2004). Long-Term Decline in Numbers of Cyclic Voles in Boreal Sweden: Analysis and Presentation of Hypotheses. *OIKOS* 107(2), 376-392.
- Inman, R.M., Magoun, A.J., Persson, J. & Mattisson, J. (2012). The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93(3), 634-644.
- Landa, A., Strand, O., Swenson, J.E. & Skogland, T. (1997). Wolverines and their prey in southern Norway. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 75(8), 1292-1299.
- Magoun, A.J. & Copeland, J.P. (1998). Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62(4), 1313-1320.
- Mattisson, J., Andrén, H., Persson, J. & Segerström, P. (2011a). Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *Journal of Mammalogy* 92(6), 1321-1330.
- Mattisson, J., Persson, J., Andrén, H. & Segerström, P. (2011b). Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology* 89(2), 79-89.
- May, R., Gorini, L., van Dijk, J., Brøseth, H., Linnell, J.D.C. & Landa, A. (2012). Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. *Journal of Zoology* 287(3), 195-204.
- McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B: Biological Sciences* 273(1593), 1449-1454.
- McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Moorter, B.V., Saïd, S. & Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* 88(12), 3192-3201.
- Millar, J.S. (1977). Adaptive Features of Mammalian Reproduction. *Evolution* 31(2), 370-386.
- Norris, D.R. (2005). Carry-over effects and habitat quality in migratory populations. *OIKOS* 109(1), 178-186.

- Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC). 2012. MODIS subsetting land products, Collection 5. Available on-line [<http://daac.ornl.gov/MODIS/modis.html>] from ORNL DAAC, Oak Ridge, Tennessee, U.S.A. Accessed Oct 8, 2012
- Ordiz, A., Støen, O.G., Swenson, J.E., Kojola, I. & Bischof, R. (2008). Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. *Ecology* 98(12), 3327-3335.
- ORNL DAAC. (2012). MODIS subsetting land products, Collection 5. Available on-line: [<http://daac.ornl.gov/MODIS/modis.html>] from ORNL DAAC, Oak Ridge, Tennessee, U.S.A. Accessed Oct 8, 2012
- Persson, J. (2005). Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83(11), 1453-1459.
- Persson, J., Ericsson, G. & Segerström, P. (2009). Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142(2), 325-331.
- Persson, J., Landa, A., Andersen, R. & Segerström, P. (2006). Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87(1), 75-79.
- Persson, J., Wedholm, P. & Segerström, P. (2010). Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife Research* 56(1), 49-57.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* 20(9), 503-510.
- Plummer, M. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. In: *Proceedings of Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna, Austria, March 20–22 2003.
- Proaktor, G., Milner-Gulland, E.J. & Coulson, T. (2007). Age-related shapes of the cost of reproduction in vertebrates. *Biology Letters* 3(6), 674-677.
- R Development Core Team (2012) R: A Language and Environment for Statistical Computing. In: R Foundation for Statistical Computing, Vienna, Austria (Accessed Feb 12, 2012)
- Rauset, G., Mattisson, J., Andrén, H., Chapron, G. & Persson, J. (2012). When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia* [early view].
- Reznick, D. (1992). Measuring reproductive costs - response to Partridge. *Trends in Ecology & Evolution* 7(4), 134-134.
- Sæther, B.E., Engen, S., Persson, J., Broseth, H., Landa, A. & Willebrand, T. (2005). Management strategies for the wolverine in Scandinavia. *Journal Of Wildlife Management* 69(3), 1001-1014.
- Sappington, J.M., Longshore, K.M. & Thompson, D.B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71(5), 1419-1426.
- Schwarzkopf, L. (1993). Cost of reproduction in water skinks. *Ecology* 74(1970-1981).
- Seaman, D.E., Millsbaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999). Effects of Sample Size on Kernel Home Range Estimates. *The Journal of Wildlife Management* 63(2), 739-747.

- Stearns, S.C. (1992). *The evolution of life histories*: Oxford University Press, Oxford.
- van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, O., Brøseth, H., Andersen, R., Steen, H. & Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology* 77(6), 1183-1190.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerstrom, P. (2001). Characteristics of dispersal in wolverines. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 79(9), 1641-1649.
- Weladji, R.B., Loison, A., Gaillard, J.-M., Holand, Ø., Mysterud, A., Yoccoz, N.G., Nieminen, M. & Stenseth, N.C. (2008). Heterogeneity in Individual Quality Overrides Costs of Reproduction in Female Reindeer. *Oecologia* 156(1), 237-247.
- Williams, G.C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. *The American Naturalist* 100(916), 687-690.
- Zedrosser, A., Dahle, B., Støen, O.G. & Swenson, J.E. (2009). The effects of primiparity on reproductive performance in the brown bear *Oecologia* 160, 847-854.
- Zeileis, A., Kleiber, C. & Jackman, S. (2008). Regression models for count data in R. *Journal of Statistical Software* 27, 1-25.
- Zuur, A. (2010). AED: Data files used in Mixed effects models and extensions in ecology with R (in Zuur et al. 2009). R package version 1.0.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*: Springer Science + Business Media, New York, USA..

## Supplemental Materials

Table S1. Candidate set of zero-inflated Poisson (ZIP) models using combinations of age (age = linear, age<sup>2</sup> = quadratic) to predict annual reproductive output (n = 205) in individual female wolverines (n = 53).  $\Delta AIC_c$  = difference in  $AIC_c$  relative to the best model;  $w_i$  =  $AIC_c$  weight of the model; df = number of parameters in the model.

Binomial process	Count process	df	$AIC_c$	$\Delta AIC_c$	$w_i$
age <sup>2</sup>	age	5	496.94	0.00	0.423
age	age	4	498.11	1.17	0.236
age <sup>2</sup>	age <sup>2</sup>	6	498.22	1.28	0.223
age <sup>2</sup>	intercept only	4	499.70	2.75	0.107
age	intercept only	3	504.09	7.15	0.012
intercept only	age <sup>2</sup>	4	513.91	16.96	0.000
intercept only	intercept only	2	522.02	25.08	0.000
intercept only	age	3	523.02	26.07	0.000

Table S2. Candidate set of zero-inflated Poisson (ZIP) models to predict annual reproductive output (n = 174) in individual female wolverines (n = 41). The explanatory variables include combinations of female age (age = linear, age<sup>2</sup> = quadratic) and home range composition: mean NDVI (NDVI), and three seasonal densities of reindeer carcasses (Feb-May: rc25; Jun-Sep: rc69; Oct-Jan: rc101).

Binomial process	Count process	df	$AIC_c$	$\Delta AIC_c$	$w_i$
age <sup>2</sup>	age + rc101	6	424.69	0.00	0.241
age <sup>2</sup>	age + NDVI	6	424.81	0.13	0.226
age <sup>2</sup>	NDVI	5	426.04	1.36	0.122
age	age + rc101	5	426.37	1.68	0.104
age	age + NDVI	5	426.49	1.80	0.098
age <sup>2</sup>	age + rc25	6	426.99	2.30	0.076
age <sup>2</sup>	age + rc69	6	427.62	2.93	0.056
age	age + rc25	5	428.56	3.87	0.035
age	age + rc69	5	428.97	4.29	0.028
age <sup>2</sup>	age	5	432.52	7.83	0.005
age <sup>2</sup>	intercept only	4	432.99	8.30	0.004
age <sup>2</sup>	age <sup>2</sup>	6	434.03	9.35	0.002
age	age	4	434.09	9.40	0.002
age	intercept only	3	437.54	12.85	0.000
intercept only	age <sup>2</sup>	4	444.15	19.46	0.000
intercept only	age + veg2	4	446.27	21.58	0.000
intercept only	intercept only	2	449.61	24.93	0.000
intercept only	age	3	450.80	26.11	0.000

Table S3. Candidate set of multistate mark-recapture models showing relative support for different variable structures for the transition ( $\psi$ ) parameter of breeding in year  $t$  to breeding in year  $t+1$ . The survival ( $\Phi$ ), resighting ( $p$ ) and other transition parameters were held constant while modelling various effects on  $\psi_{\text{breed-breed}}$ . These were female age (age = linear, age<sup>2</sup> = quadratic), normalized difference vegetation index (NDVI), the number of cubs weaned in year  $t$  (cubs), the north Atlantic oscillation index (NAO) and an index of rodent density (rodent).  $\Delta AIC_c$  = difference in  $AIC_c$  relative to the best model;  $w_i$  =  $AIC_c$  weight of the model;  $K$  = number of parameters in the model.

Breed-to-breed transition ( $\psi$ ) models	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
age <sup>2</sup> + NDVI + cubs + NAO	11	292.9	0	0.18
age <sup>2</sup> + NDVI + cubs	10	293.0	0.01	0.18
age <sup>2</sup> + NDVI	9	293.1	0.12	0.17
age <sup>2</sup> + NDVI + NAO	10	293.9	1.01	0.11
age <sup>2</sup> + NDVI + cubs + rodent	11	294.2	1.29	0.09
age <sup>2</sup> + NDVI + rodent	10	294.6	1.68	0.08
age <sup>2</sup> + NDVI + cubs + NAO + rodent	12	295.2	2.28	0.06
age <sup>2</sup> + NDVI + NAO + rodent	11	296.2	3.27	0.03
age <sup>2</sup>	8	297.2	4.29	0.02
age <sup>2</sup> + cubs	9	297.6	4.61	0.02
age <sup>2</sup> + cubs + NAO	10	297.7	4.78	0.02
age <sup>2</sup> + NAO	9	298.0	5.03	0.02
age <sup>2</sup> + rodent	9	298.7	5.71	0.01
age <sup>2</sup> + cubs + rodent	10	298.9	5.97	0.01
age <sup>2</sup> + cubs + NAO + rodent	11	300.0	7.08	0.00
age <sup>2</sup> + NAO + rodent	10	300.2	7.24	0.00
intercept only	6	302.1	9.14	0.00
age	7	302.9	9.98	0.00

Table S4. Candidate set of multistate mark-recapture models showing relative support for different variable structures for the transition ( $\psi$ ) parameter of not breeding in year  $t$  to breeding in year  $t+1$ . The survival ( $\Phi$ ), resighting ( $p$ ) and other transition parameters were held constant while modelling various effects on  $\psi_{\text{nonbreed-breed}}$ . These were female age (age; as a linear & quadratic term) and home range environmental variables added in a univariate way: mean elevation (elev), mean NDVI (NDVI), mean portion of mountainous birch forest (veg2), mean portion of alpine heaths (veg3), and three seasonal densities of reindeer carcasses (Feb-May: rc25; Jun-Sep: rc69; Oct-Jan: rc101).  $\Delta AIC_c$  = difference in  $AIC_c$  relative to the best model;  $w_i$  =  $AIC_c$  weight of the model;  $K$  = number of parameters in the model.

Nonbreed-to-breed transition ( $\psi$ ) models	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Intercept only	10	301.96	0	0.25
elev	11	303.19	1.24	0.13
NDVI	11	303.34	1.39	0.12
rc101	11	303.45	1.49	0.12
rc69	11	303.69	1.73	0.11
NAO	11	304.07	2.11	0.09
age	11	304.34	2.39	0.08
rodents	11	304.35	2.40	0.08
age <sup>2</sup>	12	306.20	4.25	0.02



IV





# Environmental predictors of the Scandinavian wolverine population

Geir Rune Rauset<sup>1</sup>, Henrik Andrén<sup>1</sup>, Jenny Mattisson<sup>2</sup>, Henrik Brøseth<sup>2</sup>, Jens Persson<sup>1</sup>

<sup>1</sup>*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden*

<sup>2</sup>*Norwegian Institute of Nature Research, N-7485 Trondheim, Norway*

## Abstract

Spatial distributions of reproductive events have the potential to yield information on environments promoting fitness, valuable for the conservation and management of species. Using data from a globally unique large carnivore monitoring systems active in Norway and Sweden, which aim to document all wolverine (*Gulo gulo*) reproductive events in the Scandinavian population, we analyzed environmental factors predicting range and frequency of reproductions during 2001-2011 (1 442 observations). Latitude and elevation set the natural range for the population, and within these areas wolverine occupancy was positively influenced by rugged terrain and productive areas, and negatively affected by human dominated habitat. Wolverine range overlapped with their primary winter prey, reindeer (*Rangifer tarandus*), and the frequency of reproductions was enhanced by the presence of a top predator, the Eurasian lynx (*Lynx lynx*). Management policies strongly affected reproductive success: in Sweden the frequency of reproductions were 2 times higher than in otherwise similar habitats in Norway, and in a “zero-tolerance” management zone in southwestern Norway the probability of reproduction was 25 times lower than outside, thus efficiently preventing permanent colonization of otherwise primary wolverine habitat. Models of annual probabilities of wolverine reproduction were influenced by distance to earlier reproductions, with an observed effect up to mean dispersal distance in wolverines. The Scandinavian wolverine population experienced a historical bottleneck in the mid 1900’s following human campaigns of persecution, where areas characterized by

remoteness and ruggedness were essential refuges for successful reproductions. The population later recovered, but its range is still mainly limited to wilderness-like areas with low human development. A persistent and even increasing conflict between wolverine conservation and traditional land use point toward a future need for continuous monitoring combined with preventive measures and compensation within an adaptive management framework.

## Introduction

Developing trustworthy conservation planning for large carnivores, and other conflict prone or endangered species, requires a deep understanding of spatial and temporal variation in size and distribution of their populations. These variations are increasingly affected by human activities, both indirectly through loss and fragmentation of habitat and directly through hunting or poaching (Ray *et al.*, 2005). Sound management of wildlife populations requires reliable estimates of population size, trends and distribution. Hence, population monitoring has become an important tool for management of populations. However, for science-based adaptive management to be fully implemented, understanding factors influencing the size and distribution at population level is crucial. This in turn requires knowledge about the spatial and temporal variation in demographic rates (Gaillard *et al.*, 2010; Franklin *et al.*, 2000; Garshelis, 2000).

Species distribution and habitat suitability models have become increasingly important tools in conservation biology (Guisan & Thuiller, 2005; Rushton *et al.*, 2004), whether based on presence-only, presence-absence, or abundance data (Pearce & Boyce, 2006; Guisan & Zimmermann, 2000). Habitat suitability mapping, i.e. the projection of species response curves into geographical space where environmental conditions are known but where the species distribution is unknown, is of particular significance (Hirzel & Le Lay, 2008; Guisan & Zimmermann, 2000). However, ecological theory about source-sink dynamics (Pulliam, 2000; Pulliam & Danielson, 1991), and inter-patch movements over unsuitable habitats (Hirzel *et al.*, 2004), suggest that species may be located outside the bounds of the species niche (Pulliam, 2000) and that information on species presence or densities often can be misleading of which areas are valuable for a species (VanHorne, 1983). It is therefore generally recommended to use species data that are directly linked to fitness (e.g. nest sites instead of sightings) to reduce the number of fallacious presences (Hirzel & Le Lay, 2008). Fitness-related parameters can also be included into presence-only models, facilitating more accurate models of the true niche of the species (Titeux *et al.*, 2007). In territorial species, with fixed ranges throughout the year, the spatial distribution of reproductions can serve

as a combined fitness proxy for both adult female survival and reproduction, with the potential to reveal which factors that play a vital role for population persistence.

In Scandinavia (here defined as Norway and Sweden), a globally unique large carnivore monitoring system is implemented, with the aim to document all reproductive events of the entire wolverine (*Gulo gulo*), wolf (*Canis lupus*), and lynx (*Lynx lynx*) populations (Andrén *et al.*, 2002; Wabakken *et al.*, 2001; Landa *et al.*, 1998). Following generations of human persecution these populations were driven to historical lows or were regionally extirpated during the 20th century (Linnell *et al.*, 2010; Flagstad *et al.*, 2004; Vilà *et al.*, 2003). After the species received protection, and more favorable management policies were implemented, the populations have partly recovered in both countries. To ensure knowledge-based adaptive management, surveys were introduced to warrant a close monitoring of the carnivore populations' range and size and to facilitate national and regional management policies. In addition, they also serve as the base for the conservation performance payment system in the Swedish reindeer husbandry area, which is based primarily on the number of reproductions (Paper V, Zabel & Holm-Müller, 2008; Swenson & Andrén, 2005). These nation-wide surveys provide an excellent opportunity to develop population-wide environmental predictors for the presence of reproductions in Scandinavian carnivore populations, and thereby identify demographic performance of specific areas and habitats. In addition, it provides an opportunity to assess the effect of current management practices on populations.

Wolverines inhabit a Holarctic range, defined by a bioclimatic envelope of spring snow and low summer temperatures (Copeland *et al.*, 2010). Their reproductive chronology and extensive food hoarding suggest that they are specifically adapted to exploit a cold, unproductive niche where resources are scarce and interspecific competition is limited (Inman *et al.*, 2012a; Inman *et al.*, 2012b). Wolverine females exhibit low reproductive rates (Paper III, Persson *et al.*, 2006), with strong patterns of age-specific reproductive output, modulated by summer and early winter foods (Paper III). In general, reindeer (*Rangifer tarandus*) is the most important prey (Mattisson *et al.*, 2011a; Haglund, 1966), while moose is regionally important at least in winter (Koskela *et al.*, 2012; van Dijk *et al.*, 2008). In the reindeer area, lynx and wolverines select for the same habitats (Rauset *et al.*, 2012), and wolverines presumably benefit from occurrence of lynx as it provides reindeer carcasses (Mattisson *et al.*, 2011a).

Wolverines in Scandinavia are exposed to different patterns of mortality as a result of different management policies. Norway allows a public hunt with a

generous quota, and conduct extensive lethal control of wolverines (Brøseth *et al.*, 2010). National population goals are distributed into regional management zones, and in southwestern Norway (Fig. 1) the present policy is a “zero-tolerance” regarding wolverine reproductions to minimize conflicts with sheep husbandry. In Sweden there is no public hunt, and only limited lethal control has been allowed (Paper V). Instead, poaching is the main source of human-caused mortality in Sweden (Paper II, Persson *et al.*, 2009). During the period of extensive persecution, ruggedness and remoteness were essential factors for wolverine survival (Haglund, 1965), and still today, the risk of mortality shows substantial spatial variation depending on human land use and terrain ruggedness (Paper II). Wolverines have also been shown to avoid human disturbance in terms of human development and roads (May *et al.*, 2012; May *et al.*, 2006).

In this study we aim to identify factors affecting the present distribution of the Scandinavian wolverine population, using data on all observed reproductive events during 2001-2011. Based on current understanding of wolverine distribution and ecology, as well as management policies we generate specific predictions for the models: We predict that latitude and elevation will define the coarse scale range. Presence of spring snow cover represents an alternative explanation for wolverine reproductive range. On a coarse scale, we also expect a strong influence of management policy, where the “zero-tolerance-zone” should limit wolverine range, and different national policies should influence the frequency of reproductions (i.e. higher in Sweden than in Norway). We further predict rugged terrain and absence of human activity and infrastructure to positively influence reproductions. We predict wolverine range to be affected by reindeer occurrence, and that reproductive frequency will be higher in the most productive areas and in the presence of lynx. Finally, we expect annual probability of reproductions to be strongly positively influenced by the distance to earlier reproductions.

## Methods and materials

### Wolverine and lynx surveys

We used official annual survey data on wolverine reproductions (2001-2011) and lynx family groups (2003-2011) from the Swedish Environmental Protection Agency and County Administration Boards in Sweden and the Norwegian Directorate for Nature Management and State Nature Inspectorate (SNO) in Norway.

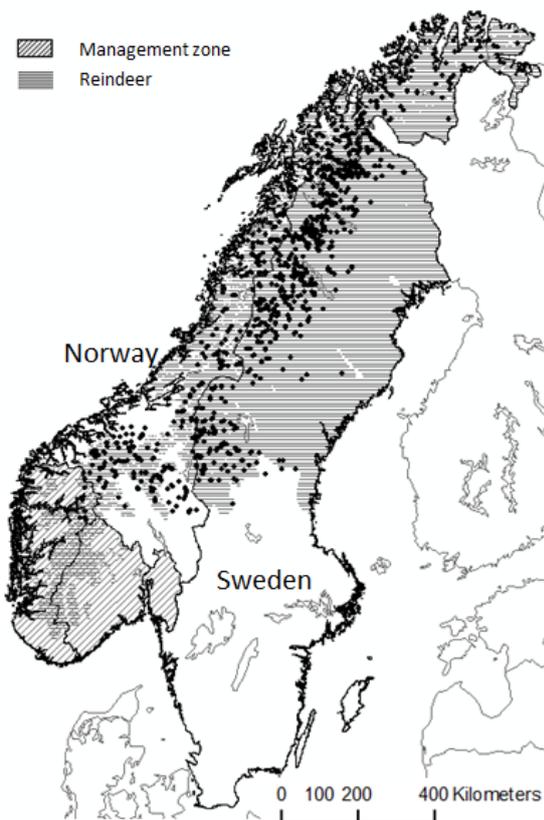


Figure 1. The study area (Sweden and Norway) with all documented wolverine reproductions (n=1442) during 2001-2011 (dots). The shaded part “reindeer” indicates designated reindeer areas (wild and semi-domesticated), and “management zone” in southwestern Norway indicates the area where wolverine reproductions are not tolerated according to the current large carnivore management strategy in Norway.

The wolverine survey is performed from March to June and registered reproductions are based on documentation of den sites, tracks of females with cubs or visual observations of cubs after den abandonment (c.f. Landa *et al.*, 1998). Documentation of a den site requires observations of concentrated activity of tracks for >3 weeks. Possible den sites with activity <3 weeks are revisited after snowmelt to document signs of a den (e.g. several beds, large amounts of scats, cub hair, prey remains; Brøseth & Andersen, 2009). The majority of reproductions are documented at or close to the den site. Thus, spatial coordinates of reproductions provide a strong indication of the activity center of wolverine females during the denning period. The number of wolverine reproductions is assumed to give a representation of all wolverines in the population (Landa *et al.*, 2001). Wolverines have been surveyed since

1996 in Scandinavia, but as the national monitoring system in Norway first started in 2001 we chose to include only reproductions from 2001-2011 in our analysis.

The lynx survey is performed during October to February by snow-tracking and documentation of family groups, i.e. adult females with 7-9 month old kittens. Tracks in the snow from two or more lynx traveling together until February are almost always indicative of a family group because kittens usually stay with the female until 10 months old (Samelius *et al.*, 2012), and mating does not occur until late March. Criteria based on observed home range sizes and movement rates (Linnell *et al.*, 2007) are used to separate between different family groups. These surveys provide a representation of the total number of lynx in an area (Andrén *et al.*, 2002).

#### Environmental variables

To analyze how different environmental factors influence the distribution and frequency of wolverine reproductions, we applied three continuous topographical raster maps (elevation, terrain ruggedness, and slope), one categorical vegetation raster, one raster representing a proxy for primary production (integrated normalized difference vegetation index, NDVI ; Pettorelli *et al.*, 2005) a spring snow cover index raster (Copeland *et al.*, 2010), one vector map of roads, and five binary maps representing human land use and management policies: country (Norway or Sweden), management zones (wolverine reproductions allowed or not), national parks, designated reindeer areas (semi-domesticated and wild reindeer), and calving grounds of semi-domesticated reindeer (Table S1)

Using a presence-absence modeling design (Brotons *et al.*, 2004), we divided the land area of Norway and Sweden into a 10 x 10 km grid, removing cells of water and islands with no natural land bridges. The spatial resolution of 10 x 10 km was chosen to increase the probability to only include one wolverine reproduction per year, while being large enough to represent the true environment associated to wolverine reproductions. Wolverines exhibit intra-sexual territoriality throughout the year, with a mean home range size of 195 km<sup>2</sup> ( $\pm 120$  km<sup>2</sup> st.dev.) for female wolverines (Mattisson *et al.*, 2011b). The minimum distance recorded between two den sites used by different radio-tracked female wolverines during the same year is 5.7 km (Aronsson 2009). Females can shift den sites several times during a reproductive season, and the maximum distance observed between den sites for the same radio-collared individual is 2.1 km (J. Persson unpublished data).

Within each cell, we counted the number of wolverine and lynx reproductions and calculated the environmental composition as the mean

values of the continuous raster maps, portions of the categorical habitat variables, and total road length (Table S2). For the binary human land use maps, we assigned cells as reindeer area, reindeer husbandry calving area, national park, or management zone not allowing wolverine reproductions, if such occurred within the cell. Thus, the assignment was independent on proportion in the cell. Cells shared by Norway and Sweden were assigned to the country having the largest portion. To simplify model interpretation, all variables except the binary were standardized by subtracting their means and dividing by two standard deviations (i.e. z-scores; Gelman & Hill, 2007).

To model annual presence of wolverine reproductions we calculated for each year (year  $t$ ) the distance to nearest wolverine reproduction the three preceding years (year  $t-1$  to  $t-3$ ), and to the nearest lynx reproduction the three latest years including the present year (year  $t$  to  $t-2$ ). This procedure reduced the years of study to 2005-2011. We estimated annual winter weather based on the integrated North Atlantic Oscillation index NAO (Helle & Kojola, 2008) from November until May ([http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao\\_index.html](http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html)). These variables were also standardized into z-scores.

#### Model development

To model the range and number of wolverine reproductions all years combined, we applied zero-inflated models (i.e. ZIP/ZINB; Zuur *et al.*, 2009) in the R package `pscl` (Zeileis *et al.*, 2008). These models consist of a binomial part (0 or 1; which contrary to a logistic regression gives the probability of zeroes) and a count part (0, 1, 2, etc.), which allow for the handling of excess number of zeroes and zeroes deriving from different processes (Zuur *et al.*, 2009). We interpreted the binomial part of these models to predict the range of the reproductive part of the Scandinavian wolverine population, and the count process to predict the frequency of reproductions within this range. This allowed us to include data from the entire Scandinavian land area in the models; we did not have to set an arbitrary geographical boundary for potential wolverine habitat to ensure the specificity of model predictions.

We developed a suit of competing zero-inflated models, using a three-step procedure starting with keeping the count process constant and finding the variables that performed best in the binomial process. Thereafter we added the variables best explaining the count process given the initial binomial process, and finally we assessed the best binomial process given the new count process. Several of the environmental variables were presumed to have a non-linear effect on the probability of reproductions. Therefore we included both a linear and a quadratic term of elevation, ruggedness, NDVI, and all the vegetation classes in the models. To avoid multicollinearity we evaluated correlation

between pairs of variables by Pearson's residuals, and evaluated suits of potential variables by Variance Inflation Factor (Zuur *et al.*, 2010) in the R library AED (Zuur, 2010). We did not include variables with a correlation of  $R^2 \geq 0.70$  or  $VIF \geq 3$  in the same models. Throughout this process, we assessed model performance by small sample corrected Akaike's Information Criterion (AICc; Burnham & Anderson, 2002). We tested for count data overdispersion (Ver Hoef & Boveng, 2007) by evaluating the dispersion parameter theta in the ZINB models, and by comparing AIC of the best ZINB and ZIP models. For model diagnostics we plotted model residuals vs. both observed values and the model variables. To allow for evaluation of the influence of each environmental variable on the final best model, we plotted model predictions over the range of each variable while keeping the other variable constant at their mean.

To model annual probability of wolverine reproduction we developed generalized linear mixed models (GLMM; Bolker *et al.*, 2009), with binomial error distributions and the logit link function (i.e. logistic regression), in the R library lme4. We included environmental variables and distance to earlier wolverine and lynx reproductions as fixed effects, and initially both individual cell-ID and year as random intercept effects. We applied restricted maximum likelihood (REML) estimation and a Laplace approximation of model parameters (Bolker *et al.*, 2009). We compared the variance explained by the random effects cell-ID and year. To address the influence of winter weather on the probability of wolverine reproductions, we replaced the random intercept year with NAO, both for the current year and for the preceding year (Paper III), as a fixed effect.

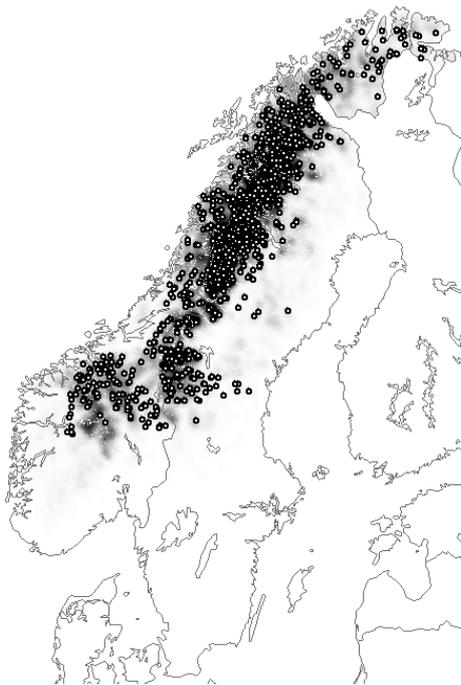
To visually present the modeled probabilities of reproduction, we exported the model predictions into ArcGIS 9.3 (©1999-2004 ESRI Inc). We interpolated the predictions, including 3 neighboring cells in each direction, into reproduction probability maps using kriging regression.

## Results

During the years 2001-2011 a total of 1 442 wolverine reproductions were documented in Scandinavia; 564 in Norway and 878 in Sweden. During 2003-2011 there were 2 526 lynx reproductions documented in Scandinavia; 560 in Norway and 1 966 in Sweden. We obtained a grid of 8 056 cells (10 x 10 km<sup>2</sup>) covering Norway and Sweden. The number of wolverine reproductions in each cell ranged from 0-12 (mean = 0.18). In 17 occasions two different wolverine reproductions were observed within the same cell the same year. The number of lynx reproductions in each cell ranged from 0-7 (mean = 0.31).

### Range and frequency of wolverine reproductions

The best zero-inflated negative binomial (ZINB) model predicting range and frequency of wolverine reproductions contained variables representing habitat and landscape features (latitude, elevation, ruggedness, NDVI, human-dominated habitats, and deciduous forest), presence of reindeer and lynx, and area specific management policies (country and management zones; Table 1, Fig. 2). The variables elevation, ruggedness, and NDVI influenced both the range and frequency of reproductions, and they were included as a linear and a quadratic term in one or both processes of the model (Table 1). The probability of wolverine range was 25 times higher outside the Norwegian management null-tolerance zone and 5.8 times higher within the reindeer area ( $\text{logit-1}(\beta)$  in Table 2). The frequency of reproductions was 2.0 times higher in Sweden than in Norway, given otherwise equal environments ( $1/\text{exp}(\beta)$  in Table 2). The number of lynx reproductions had a positive effect on the frequency of wolverine reproductions, with an effect size of 1.3. Elevation and latitude had the strongest influence on model prediction among the continuous habitat variables (Fig. 3).



*Figure 2.* The predicted wolverine distribution (shaded) based on the best ZINB model (Table 1) and all documented wolverine reproductions ( $n = 1\ 442$ ) during 2001-2011 (open dots).

Table 1. Candidate set of zero-inflated negative binomial (ZINB) models predicting wolverine reproductions during the years 2001-2011 (including 1 442 observed reproductions) within 10x10 km<sup>2</sup> cells covering the land area of Norway and Sweden (n = 8 055). The continuous environmental variables are z-scored values of latitude (lat), elevation (elev), integrated NDVI (NDVI), terrain ruggedness (rug), lynx reproductions (lynx), human dominated habitats (hum), deciduous forest (dfor), road density (road), spring snow cover (snow), and slope (slope); binomial variables are country (NS), management zone (zone), designated reindeer area (rdeer), national parks (NatPark), and reindeer calving grounds (rcalf).

Binomial model	Count process model	df	AIC	ΔAIC	w <sub>i</sub>
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup>	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 810.8	0	0.42
lat+elev <sup>2</sup> +rdeer+NDVI+rug <sup>2</sup>	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup> +zone	21	4 812.1	1.3	0.22
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +NatPark	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	22	4 812.7	1.9	0.16
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +rcalf	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	22	4 812.8	2.0	0.15
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +mb	NS+lynx+hum+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 816.3	5.5	0.03
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +lynx	NS+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 818.2	7.4	0.01
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +hum	NS+lynx+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 820.4	9.6	0.00
lat+elev <sup>2</sup> +zone+rdeer+NDVI+slope <sup>2</sup>	NS+lynx+hum+dfor+slope <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 825.1	14.3	0.00
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup>	NS+lynx+road+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 825.7	14.9	0.00
lat+elev <sup>2</sup> +zone+rdeer	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup>	16	4 827.0	16.2	0.00
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +NS	lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 829.6	18.8	0.00
lat+elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup> +road	NS+lynx+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup>	21	4 835.6	24.8	0.00
lat+elev <sup>2</sup> +zone+NDVI+rug <sup>2</sup>	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup> +rdeer	21	4 839.8	29.0	0.00
lat+snow <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup>	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +snow <sup>2</sup>	21	4 852.4	41.6	0.00
elev <sup>2</sup> +zone+rdeer+NDVI+rug <sup>2</sup>	NS+lynx+hum+dfor+rug <sup>2</sup> +NDVI <sup>2</sup> +elev <sup>2</sup> +lat	21	4 855.5	44.7	0.00
lat+elev <sup>2</sup> +zone+rdeer+hum+rug <sup>2</sup> +NDVI <sup>2</sup> +dfor <sup>2</sup>	Intercept only	15	4 924.5	113.7	0.00
Intercept only	Intercept only	3	6 579.3	1 768.5	0.00

Note: The second order variables include both a linear and a quadratic term.

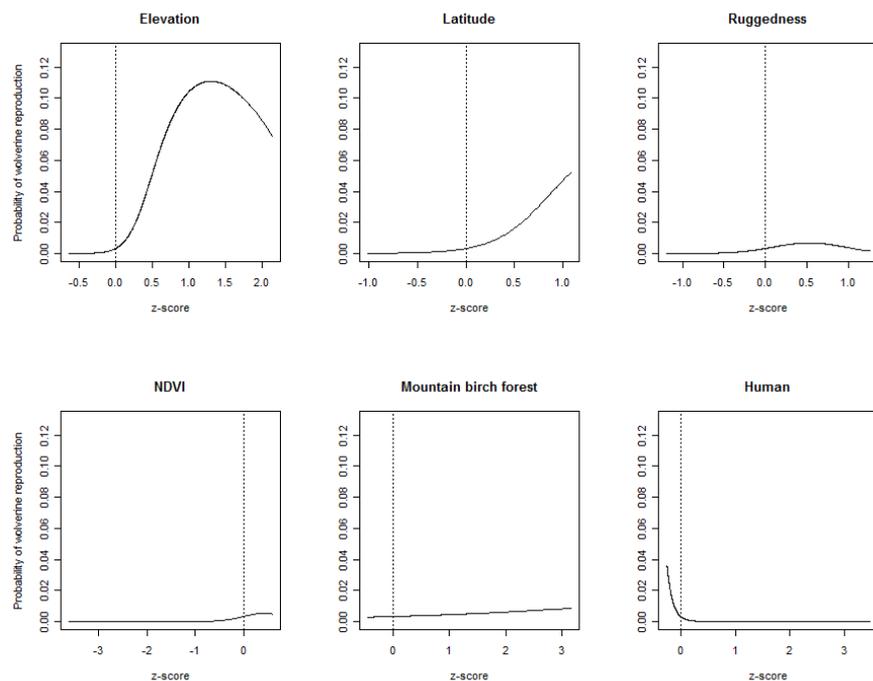
Table 2. Parameter estimates of the best model based on AIC weight predicting wolverine reproductions during the years 2001-2011 (including 1 442 observed reproductions) within 10x10 km<sup>2</sup> cells covering the land area of Norway and Sweden (n = 8 055). The continuous environmental variables are z-scored values of latitude (lat), elevation (elev), integrated NDVI (NDVI), terrain ruggedness (rug), lynx reproductions (lynx), human dominated habitats (hum), deciduous forest (dfor), binomial variables are country (NS), management zone (zone), designated reindeer area (rdeer).

Model part	Parameter estimate ( $\beta$ )	SE	z-value	p-value
<i>Binomial process</i>				
intercept	7.617	0.630	12	<0.001
lat	-3.633	0.622	-5.8	<0.001
elev	-273.9	31.8	-8.6	<0.001
elev <sup>2</sup>	65.07	13.03	5.0	<0.001
rug	-64.35	17.29	-3.7	<0.001
rug <sup>2</sup>	39.07	18.89	2.1	0.039
NDVI	-2.706	1.140	-2.6	0.018
zone	-3.167	0.517	-6.1	<0.001
rdeer	-1.576	0.364	-4.3	<0.001
<i>Count process</i>				
intercept	-3.357	0.469	-7.2	<0.001
NS	-0.6685	0.1162	-5.8	<0.001
lynx	0.2609	0.0923	2.6	0.006
hum	-9.713	1.660	-5.9	<0.001
dfor	0.3180	0.0856	3.7	<0.001
elev	29.05	11.68	2.5	0.013
elev <sup>2</sup>	-10.25	6.83	-1.5	0.13
rug	59.82	10.87	5.5	<0.001
rug <sup>2</sup>	-30.51	10.42	-3.0	0.003
NDVI	193.6	56.3	3.4	<0.001
NDVI <sup>2</sup>	-171.3	66.5	-2.6	0.010

Note: A *negative* parameter value in the binomial process positively influences the modeled probability of reproduction, whereas a *positive* parameter value in the count process positively influences the model.

The model presented above represents the best combination of the variables, ranked by AIC. The  $\Delta$ AIC to the null model was 1 768.5 and model weight 0.42 among the listed models, indicating that substantial variation in the data was explained by this model. The first step of our model development procedure, i.e. adding parameters to only the binomial part, resulted in a  $\Delta$ AIC to the null model of 1 654.8. Among the alternative models presented in Table 1, several show a distinct increase in model AIC when single variables

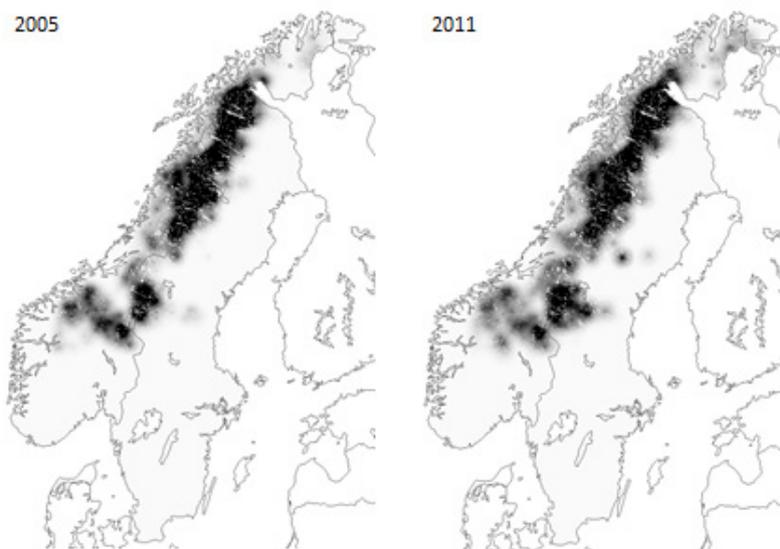
were moved from one of the processes to the other, which demonstrates that several of the variables performed substantially better in either predicting range or frequency of wolverine reproductions, e.g. reindeer area had substantial support as a predictor of wolverine range, but had almost no influence on the frequency of reproductions. The variables reindeer calving grounds and national parks were uninformative, and increased the AIC of about 2 when added to the best model (i.e. penalization for adding an uninformative variable). Replacement of variables in the best model with highly correlated alternatives did not improve model performance, e.g. road density performed substantially worse than human dominated habitats ( $\Delta AIC = 14.9$ ) and the snow index explained less than the strongly correlated elevation ( $\Delta AIC = 41.6$ ). A comparison between the best models using ZIP and ZINB suggested substantial overdispersion in the count data ( $\Delta AIC = 233.3$  in favor for the ZINB model).



*Figure 3.* The predicted probabilities for wolverine reproductions based on the best ZINB model (Table 1). The independent variables were standardized (z-scores), i.e. 0 represent the mean value (Table S2). In the prediction for each independent variable all the other variables are at their mean values (i.e. 0).

### Annual probability of wolverine reproductions

The best logistic regression models prediction annual probability of reproductions included most of the variables in the best ZINB model, but in addition “distance to wolverine reproduction” was introduced as the most influential variable (Table 3). The other year-specific variable, “distance to lynx reproduction” also had some support. The variable “reindeer area” was not informative in this model though, probably because almost all wolverine reproductions were located within the reindeer area, and the effect of this variable disappeared when introducing “distance to wolverine reproductions”. When comparing the variation explained by the two random intercept models, the random effect of “cell-ID” explained 565 times the variance as “year” did. Still, when adding annual NAO we found a year-effect explained by the integral winter NAO in the current year; cold and dry winters gave higher probability of observing reproductions. When mapping the annual probabilities of reproductions, we observe substantial dynamics in the annual model predictions (Fig. 4), mainly driven by the distance to earlier wolverine reproductions (Fig. 5).



*Figure 4.* The predicted annual probability of wolverine reproductions in 2005 and 2011, based on the best logistic regression model (Table 4).

Table 3. Candidate set of logistic regression models predicting annual wolverine reproductions during the years 2005-2011 (including 1 263 observed reproductions) within 10x10 km<sup>2</sup> grid cells covering the land area of Norway and Sweden (n = 8 055). The continuous environmental variables are z-scored values of distance to nearest wolverine reproduction the three preceding years (wdist), latitude (lat), elevation (elev), integrated NDVI (NDVI), terrain ruggedness (rug), distance to nearest lynx reproductions the last three years (lynxdist), human dominated habitats (hum), deciduous forest (dfor), road density (road), spring snow cover (snow), North Atlantic Oscillation (NAO) and slope (slope); the binomial variables are country (NS), management zone (zone), designated reindeer area (rdeer), national parks (NatPark) and reindeer calving grounds (rcalf).

Logistic regression model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist+NAO	15	7 337.6	0	0.34
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+NAO	14	7 338.7	1.1	0.19
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist+NAO+NatPark	16	7 338.8	1.2	0.18
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist+NAO+rdeer	16	7 339.6	2.0	0.12
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist+NAO+rcalf	16	7 339.6	2.0	0.12
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+lynxdist+NAO	14	7 343.3	5.7	0.02
wdist+lat+snow <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist	14	7 343.4	5.8	0.02
wdist+lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI+road+dfor+NS+zone+lynxdist+NAO	15	7 349.7	12.1	0.00
wdist+lat+elev <sup>2</sup> +slope <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist+NAO	15	7 352.5	14.9	0.00
wdist+lat+snow <sup>2</sup> +rug <sup>2</sup> +NDVI+hum+dfor+NS+zone+lynxdist+NAO	15	7 386.3	48.7	0.00
lat+elev <sup>2</sup> +rug <sup>2</sup> +NDVI <sup>2</sup> +hum+dfor <sup>2</sup> +NS+zone+lynxdist+rdeer	16	7 507.7	170.1	0.00
Intercept only	2	8 009.7	672.1	0.00

Note: The second order variables include both a linear and a quadratic term.

Table 4. Parameter estimates of the best model, based on AIC weight (Table 3) predicting annual wolverine reproductions during the years 2005-2011 (including 1 263 observed reproductions) within 10x10 km<sup>2</sup> grid cells covering the land area of Norway and Sweden (n = 8 055). The continuous environmental variables are z-scored values of distance to nearest wolverine reproduction the three preceding years (wdist), latitude (lat), elevation (elev), integrated NDVI (NDVI), terrain ruggedness (rug), distance to nearest lynx reproductions the last three years (lynxdist), human dominated habitats (hum), deciduous forest (dfor), and North Atlantic Oscillation (NAO); the binomial variables are country (NS), and management zone (zone).

Model part	Parameter estimate ( $\beta$ )	SE	z-value	p-value
intercept	-15.35	1.026	-15	<0.001
wdist	-14.78	1.442	-10	<0.001
lat	1.241	0.3292	3.8	0.002
elev	285.9	41.85	6.8	<0.001
elev <sup>2</sup>	-85.28	22.46	-3.8	<0.001
rug	267.4	37.86	7.1	<0.001
rug <sup>2</sup>	-196.6	47.17	-4.2	<0.001
NDVI	2.513	0.6033	4.2	<0.001
hum	-11.96	2.537	-4.7	<0.001
dfor	0.4020	0.1157	3.5	<0.001
NS	-0.7628	0.1625	-4.7	<0.001
zone	1.303	0.6798	1.9	0.055
lynxdist	-0.3612	0.2364	-1.5	0.12
NAO	-0.1781	0.0672	-2.7	0.008

## Discussion

Wolverine reproductions in Scandinavia generally occurred in the predicted habitats and landscapes; they also coincided with the occurrence of main winter prey (reindeer) and were positively influenced by the presence of a top predator (lynx), and responded to management policies along with our predictions. Latitude and elevation defined the current range of wolverine reproductions in Scandinavia, where latitude sets the southern limit and elevation confines the wolverine reproductions to mainly occur in alpine areas of the Scandinavian Peninsula. This is in accordance with the global scale definitions of the wolverine range (Inman *et al.*, 2012b; Copeland *et al.*, 2010; Pasitschniak-Arts & Larivière, 1995), and it agrees with the environmental settings of low productivity and high seasonality associated with a bet-hedging life history (Ferguson & Larivière, 2002), and constitutes environments where wolverine reproductive chronology will be beneficial (Inman *et al.*, 2012a).

The quadratic term of elevation in the model predicts a maximum probability of reproductions at mean altitudes of 1 100-1 200 m a.s.l. This is higher than the mean tree line ecotone in Scandinavia (tree line at 600-800 m a.s.l.), which wolverines often select for and perform well in (Paper III, Rauset *et al.*, 2012, May *et al.*, 2010). However, within these higher altitudes areas, wolverine reproductions are linked to areas of relatively high primary production, and with higher portions of mountain birch forests (Paper III). Another important environmental predictor, both for range and frequency of reproductions, was terrain ruggedness. Wolverines are reported to select for rugged terrain (Rauset *et al.*, 2012, May *et al.*, 2012), which also promote wolverine survival (Paper II). However, this relationship also had a quadratic form, where extremely rugged areas had fewer wolverine reproductions. Presumably, the increased cost of locomotion in such habitats lead to reduced abundance, potentially also through reduced abundance of the main large prey species. Human dominated habitats (human settlement, buildings and agriculture) had, as expected, a strong influence on reproductions; among the large carnivores of Scandinavia, wolverines are thought to be most sensitive to human disturbance (Krebs *et al.*, 2007; May *et al.*, 2006) and wolverine den sites are reported to be located away from roads (May *et al.*, 2012). Worth noticing is, however, that human dominated habitats influenced the frequency of reproductions more than their range. Human dominated habitats also performed better than road density to predict wolverine reproductions. This indicates that human settlement and their associated activities may negatively influence fitness parameters rather than inducing absolute avoidance from wolverines. In a sparsely populated area of northern Sweden, the spatial variation in mortality risk could not be explained by any measures of permanent human settlement or road density; instead the risk of being killed illegally was positively affected by national parks and reindeer calving grounds (Paper II). These variables were uninformative on the population level, suggesting that these effects were probably due to local dynamics.

This study confirms the vital importance of reindeer for the Scandinavian wolverine population. At the global scale and from a historical and evolutionary perspective these species are tightly linked; both species have a Holarctic distribution in seasonal and low productivity environments, and in Scandinavia they have coexisted since the last ice age. Today, reindeer have been domesticated within most of the wolverine range in Scandinavia, but this link is still essential. Reindeer provide winter food for the wolverine throughout most of its range in Scandinavia (van Dijk *et al.* 2008, Mattisson *et al.* 2011a); although reindeer migrate between winter and summer ranges, often 100-200 km apart, causing large seasonal variation in local abundance

(Jorner *et al.*, 1999; Bjärvall *et al.*, 1990). Notable is the positive effect of lynx reproductions on the frequency of wolverine reproductions, an effect that presumably have two explanations. First, there are no sign of competition between lynx and wolverines (Rauset *et al.*, 2012, Mattisson *et al.* 2011b); instead the lynx provide increased scavenging opportunities for the wolverine (Mattisson *et al.* 2011a). Second, the areas where lynx reproduce are probably of high quality also for the wolverine regarding both survival and food (Rauset *et al.*, 2012, Paper II). A similar positive relationship might occur between wolverines and wolves in the southern part of Scandinavia, although the presence of wolves might include a stronger trade-off between increased scavenging opportunities and interference competition (Koskela *et al.*, 2013; Inman *et al.*, 2012b; May, 2007). The observed positive effect of lynx diverges from the results of (May *et al.*, 2008), who found a very low overlap in suitable habitats between lynx and wolverines. Lynx reproductions in the southern part of Scandinavia are usually located in lower altitude boreal forests and productive human-modified habitats where its main prey is roe deer (Basille *et al.*, 2009; Bunnefeld *et al.*, 2006). However, within most of the reproductive range of the wolverine, the main large prey for lynx is reindeer (Mattisson *et al.*, 2011a), and in these areas where wolverines and lynx share prey base and main sources of mortality, the species generally select for similar habitats (Rauset *et al.*, 2012).

In addition to the varying availability of resources and constrains imposed by the natural environments, the wolverine population in Scandinavia is subject to varying national and regional management policies. Throughout the study period, Norway and Sweden had strikingly different harvest policies on wolverines, resulting in a two times higher frequency of reproductions in Sweden compared to otherwise similar habitats in Norway. Inside the management zone of southwestern Norway (Fig. 1) with a policy and practice to not tolerate a single wolverine reproduction, we had 25 times lower probability of observing reproductions than in otherwise similar habitats outside the zone. However, parts of this zone is so close to the more permanent wolverine range, and encompass such primary wolverine habitat, that they get constantly populated by dispersing wolverines. These areas represent permanent conflict zones and function as classical attractive sinks (Delibes *et al.* 2001). In this study we chose to handle reproductions that were removed through lethal control in the same manner as other reproductions. This choice has obvious implications for our models and maps as such lethal control in the study period was predominantly practiced in Norway (also outside the zero-tolerance zone), the country-effect would have been even larger if we had chosen differently. Contrary to this, illegal killing is the main source of

mortality in subadult and adult wolverines in Sweden (Persson *et al.* 2009, Paper II), but due to increased patrolling activity at and around den sites during monitoring activities, reproducing females are less vulnerable for poaching during this time (Paper V).

The models of annual probability of wolverine reproductions reveal that the probabilities of reproductions are influenced by the distance to earlier reproductions. There are several potential explanations to this. First of all, as wolverines display consistent inter-annual territorial stability (Aronsson, 2009) reproductions in the same area might belong to the same female from several years. Second, there is a high possibility that areas neighboring a successful reproduction also include environments suited for reproductions. Third, young females often settle close to their natal territory (Aronsson, 2009). Finally, the behavioral process of individual wolverines selecting range probably includes both components of innate preference and leaning; both will positively influence a selection for similar environments as where an individual is born (McLoughlin *et al.*, 2007). Thus, the realized niche of the Scandinavian wolverine population might at present also be limited by dispersal dynamics (Svenning & Skov, 2004). The influence from earlier reproductions had an effect up to about the mean dispersal distance for female wolverines (Fig. 5, Vangen *et al.*, 2001), suggesting that the model captured substantial dispersal dynamics in the wolverine range expansion. We see an expansion of the wolverine range throughout the study period (Fig. 4). Remarkable is the expansion into the, from a Scandinavian perspective, new wolverine habitats of low-altitude boreal forest (Aronsson & Persson, 2012; May, 2007). Historically, the Scandinavian wolverine range included such habitats (Persson & Brøseth, 2011), and throughout parts of the wolverine's global range, wolverine habitats are characterized by boreal forests (Copeland *et al.*, 2010). The methods presented in this study are not specifically designed to yield precise predictions for expansion into new habitats. To analyze and predict expansion processes it is preferred to focus on the expansion zones alone, using habitat suitability modeling tools designed for dynamic populations (e.g. MADIFA; Calenge *et al.*, 2008). Nevertheless, according to the mapped probabilities of reproduction (Fig. 2 & 4), there are still several areas with a potential to host wolverine reproductions that yet have no documented reproductions, especially in the boreal forest.

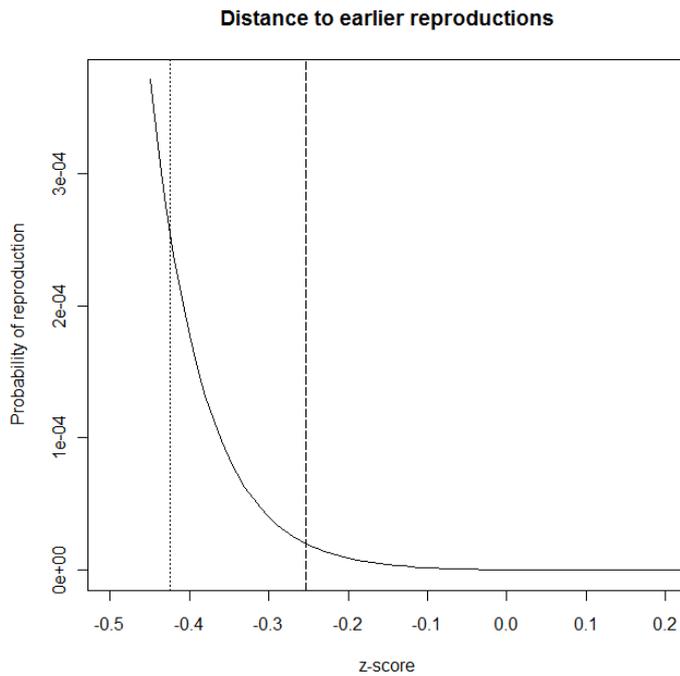


Figure 5. The influence of distance to nearest wolverine reproduction during the three preceding years (i.e. the parameter “wdist”) in the best model predicting annual probability of reproduction (Table 4), when each of the other variables were fixed at their mean value. The vertical dotted line represents the spatial resolution of the grid (10 km) and the vertical dashed line represents the mean dispersal distance for female wolverines (60 km; Vangen *et al.* 2001).

We observed an annual variation in the probability of reproduction, which could be explained by winter climate, measured as NAO, where cold and dry winters positively influenced the probability of observing reproductions. We consider this year-effect to primarily stem from annual variation in detection probability, which depends on weather and snow condition during the monitoring period, but did not quantify this effect. We have not included any procedures to handle the effect of the individual observer on detection probability; e.g. performing the analysis in a hierarchical Bayesian framework would have allowed separating sources of error deriving from different processes. Alternative hypotheses for annual variation in reproductions are resource fluctuations (e.g. rodents; Landa *et al.* 1997) or demographic processes (cohort effects, harvest rate, cost of reproduction; Paper III, Persson, 2005). For the future we see a need for analyses that specifically target annual variations in wolverine reproductions.

Altogether the environmental predictions of wolverine reproductions fit well with studies of habitat selection and spatial patterns of fitness in individual radio-tracked Scandinavian wolverines (Paper I-III, May *et al.*, 2012, 2010, 2006). Considering the entire population, there are scale-dependent factors that do not have general applicability, e.g. variation in mortality that is very site-specific (Paper II). Still, this exemplifies that single site studies might have inference also at population level when its environmental settings are representative for a large part of the population's range, and when treated with caution. However, the variation explained by the random intercept effect in our dynamic model was comparable to the variation in the environmental variables, and 565 times larger than the year effect. This reveals that there still are site-specific qualities within the Scandinavian wolverine range which we have not directly addressed by our explanatory variables; there is indeed a large variation between sites regarding the wolverine reproduction frequencies, where some areas seemingly produce wolverine reproductions year after year.

The Scandinavian wolverine population has recovered from its bottleneck in the mid-1900s. The traditional hunting of wolverines was often targeting family groups in connection to their den sites. Especially throughout the bounty-hunting period in Scandinavia, it was profitable to take out an entire family group as bounties were paid per dead wolverine. Thus, areas characterized by inaccessibility through remoteness and ruggedness have been vital for wolverine reproductions (Haglund 1965). This selection pressure may still have a strong impact on both the present range and the expansion process. Today, the Scandinavian wolverine population is mostly restricted to wilderness-like areas with relatively low human infrastructure and use. However, landscapes of Scandinavia are not wilderness, and the wolverine has a large impact on traditional rural economies and the cultures of reindeer and sheep herding (Hobbs *et al.*, 2012; Swenson & Andrén, 2005; Landa *et al.*, 1999). The future management challenge is to balance viable populations and minimize conflicts. Therefore, we see a need for continued monitoring, combined with preventive measures and compensation, within an adaptive management framework also for the future.

## Acknowledgement

The study was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, and the Swedish University of Agricultural Sciences. We thank J.P. and C.L. Copland for providing the spatial data layer of spring snow cover.

## References

- Andrén, H., Linnell, J.D.C., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., Franzén, R., Kvam, T., Odden, J. & Segerström, P. (2002). Estimating total lynx population size from censuses of family groups. *Wildlife Biology* 8(4), 299-306.
- Aronsson, M. (2009). Territorial dynamics of female wolverines. Msc Thesis, Swedish University of Agricultural Sciences.
- Aronsson, M. & Persson, J. (2012). Järv i skogslandet, Technical Report, Swedish University of Agricultural Sciences.
- Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Hogda, K.A. & Gaillard, J.M. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32(4), 683-691.
- Björvall, A., Franzén, R., Nordkvist, M. & Åhman, G. (1990). *Renar och rovdjur (Reindeer and predators, [In Swedish])*. Solna, Sweden: Naturvårdsverket förlag.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24(3), 127-135.
- Brotons, L., Thuiller, W., Araujo, M.B. & Hirzel, A.H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27(4), 437-448.
- Brøseth, H. & Andersen, R. (2009). Vurderinger knyttet til overvåking av ynglelokaliteter hos jerv i Sverige og Norge. (Evaluation of the monitoring of active wolverine dens in Sweden and Norway), NINA Rapport 437. Norwegian Institute for Nature Research, Trondheim, Norway
- Brøseth, H., Flagstad, O., Wardig, C., Johansson, M. & Ellegren, H. (2010). Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. *Biological Conservation* 143(1), 113-120.
- Bunnfeld, N., Linnell, J.D.C., Odden, J., van Duijn, M.A.J. & Andersen, R. (2006). Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. *Journal of Zoology* 270(1), 31-39.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*. 2nd. ed. New York: Springer-Verlag New York, Inc.
- Calenge, C., Darmon, G., Basille, M., Loison, A. & Jullien, J.M. (2008). The factorial decomposition of the Mahalanobis distances in habitat selection studies. *Ecology* 89(2), 555-566.
- Copeland, J.P., McKelvey, K.S., Aubry, K.B., Landa, A., Persson, J., Inman, R.M., Krebs, J., Lofroth, E., Golden, H., Squires, J.R., Magoun, A., Schwartz, M.K., Wilmot, J., Copeland, C.L., Yates, R.E., Kojola, I. & May, R. (2010). The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88(3), 233-246.
- Ferguson, S.H. & Larivière, S. (2002). Can comparing life histories help conserve carnivores? *Animal Conservation* 5(1), 1-12.
- Flagstad, O., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P. & Ellegren, H. (2004). Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18(3), 676-688.

- Franklin, A.B., Anderson, D.R., Gutierrez, R.J. & Burnham, K.P. (2000). Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70(4), 539-590.
- Gaillard, J.M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010). Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365(1550), 2255-2265.
- Garshelis, D.L. (2000). Delusion in habitat evaluation: measuring use, selection, and importance. In: Boitani, L., et al. (Eds.) *Research Techniques in Animal Ecology: Controversies and Consequences*. pp. 111–164. New York, USA: Columbia University Press.
- Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. New York, NY, USA: Cambridge University Press.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8(9), 993-1009.
- Guisan, A. & Zimmermann, N.E. (2000). Predicative habitat distribution models in ecology. *Ecological Modelling* 135, 147-186.
- Haglund, B. (1965). *Järv och varg*. Stockholm: P.A. Norstedt & Söners Förlag.
- Haglund, B. (1966). De stora rovdjurens vintervanor I. (Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow). *Viltrevy* 4, 81-310.
- Helle, T. & Kojola, I. (2008). Demographics in an alpine reindeer herd: effects of density and winter weather. *Ecography* 31(2), 221-230.
- Hirzel, A.H. & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45(5), 1372-1381.
- Hirzel, A.H., Posse, B., Oggier, P.-A., Crettenand, Y., Glenz, C. & Arlettaz, R. (2004). Ecological requirements of a reintroduced species, with implications for release policy: the bearded vulture recolonizing the Alps. *Journal of Applied Ecology* 41, 1103-1116.
- Hobbs, N.T., Andrén, H., Persson, J., Aronsson, M. & Chapron, G. (2012). Native predators reduce harvest of reindeer by Sami pastoralists. *Ecological Applications* 22(5), 1640-1654.
- Inman, R.M., Magoun, A.J., Persson, J. & Mattisson, J. (2012a). The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93(3), 634-644.
- Inman, R.M., Packila, M.L., Inman, K.H., McCue, A.J., White, G.C., Persson, J., Aber, B.C., Orme, M.L., Alt, K.L., Cain, S.L., Fredrick, J.A., Oakleaf, B.J. & Sartorius, S.S. (2012b). Spatial ecology of wolverines at the southern periphery of distribution. *Journal Of Wildlife Management* 76(4), 778-792.
- Jorner, U., Baer, E. & Danell, Ö. (1999). *Reindeer husbandry in Sweden*. Statistics Sweden. . (Technical report).
- Koskela, A., Kojola, I., Aspi, J. & Hyvärinen, M. (2012). The diet of breeding female wolverines (*Gulo gulo*) in two areas of Finland. *Acta Theriologica*, 1-6.
- Koskela, A., Kojola, I., Aspi, J. & Hyvärinen, M. (2013). Effect of reproductive status on the diet composition of wolverines (*Gulo gulo*) in boreal forests of eastern Finland. *Annales Zoologici Fennici* 50, 100-106.
- Krebs, J., Lofroth, E.C. & Parfitt, I. (2007). Multiscale habitat use by wolverines in British Columbia, Canada. *Journal Of Wildlife Management* 71(7), 2180-2192.

- Landa, A., Gudvangen, K., Swenson, J.E. & Røskoft, E. (1999). Factors associated with wolverine *Gulo gulo* predation on domestic sheep. *Journal of Applied Ecology* 36(6), 963-973.
- Landa, A., Tufto, J., Andersen, R. & Persson, J. (2001). Aktive ynglehi hos jerv som bestandsestimator basert på nye data om alder for første yngling. [In Norwegian]. NINA-notat, Norwegian Institute for Nature Research, Trondheim, Norway.
- Landa, A., Tufto, J., Franzen, R., Bo, T., Linden, M. & Swenson, J.E. (1998). Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia. *Wildlife Biology* 4(3), 159-168.
- Linnell, J.D.C., Brøseth, H., Odden, J. & Nilsen, E.B. (2010). Sustainably Harvesting a Large Carnivore? Development of Eurasian Lynx Populations in Norway During 160 Years of Shifting Policy. *Environmental Management* 45(5), 1142-1154.
- Linnell, J.D.C., Odden, J., Andrén, H., Liberg, O., Andersen, R., Moa, P., Kvam, T., Brøseth, H., Segerström, P., Ahlqvist, P., Schmidt, K., Jedrzejewski, W. & Okarma, H. (2007). Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. *Wildlife Biology* 13(4), 447-455.
- Mattisson, J., Andrén, H., Persson, J. & Segerström, P. (2011a). Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *Journal of Mammalogy* 92(6), 1321-1330.
- Mattisson, J., Persson, J., Andrén, H. & Segerström, P. (2011b). Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology* 89(2), 79-89.
- May, R. (2007). *Spatial Ecology of Wolverines in Scandinavia*. Diss. Trondheim:Norwegian University of Sciences and Technology.
- May, R., Gorini, L., van Dijk, J., Brøseth, H., Linnell, J.D.C. & Landa, A. (2012). Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. *Journal of Zoology* 287(3), 195-204.
- May, R., Landa, A., van Dijk, J., Linnell, J.D.C. & Andersen, R. (2006). Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. *Wildlife Biology* 12(3), 285-295.
- May, R., van Dijk, J., Landa, A. & Andersen, R. (2010). Spatio-temporal ranging behaviour and its relevance to foraging strategies in wide-ranging wolverines. *Ecological Modelling* 221(6), 936-943.
- May, R., van Dijk, J., Wabakken, P., Swenson, J.E., Linnell, J.D.C., Zimmermann, B., Odden, J., Pedersen, H.C., Andersen, R. & Landa, A. (2008). Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. *Journal of Applied Ecology* 45(5), 1382-1391.
- McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Moorter, B.V., Saïd, S. & Klein, F. (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* 88(12), 3192-3201.
- Pasitschniak-Arts, M. & Larivière, S. (1995). *Gulo gulo*. *Mammalian Species* 499, 1-10.
- Pearce, J.L. & Boyce, M.S. (2006). Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* 43(3), 405-412.

- Persson, J. (2005). Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83(11), 1453-1459.
- Persson, J. & Brøseth, H. (2011). *Järv i Skandinavien – status och utbredning 1996-2010*. (NINA Rapport).
- Persson, J., Ericsson, G. & Segerström, P. (2009). Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142(2), 325-331.
- Persson, J., Landa, A., Andersen, R. & Segerström, P. (2006). Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87(1), 75-79.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* 20(9), 503-510.
- Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecology Letters* 3(4), 349-361.
- Pulliam, H.R. & Danielson, B.J. (1991). Sources, sinks, and habitat selection - a landscape perspective on population-dynamics. *American Naturalist* 137, S50-S66.
- Rauset, G., Mattisson, J., Andrén, H., Chapron, G. & Persson, J. (2012). When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia* (early view).
- Ray, J., Redford, K.H., Steneck, R. & Berger, J. (2005). *Large Carnivores and the Conservation of Biodiversity*. Washington, D.C. , USA: Island Press..
- Rushton, S.P., Ormerod, S.J. & Kerby, G. (2004). New paradigms for modelling species distributions? *Journal of Applied Ecology* 41(2), 193-200.
- Samelius, G., Andrén, H., Liberg, O., Linnell, J.D.C., Odden, J., Ahlqvist, P., Segerström, P. & Sköld, K. (2012). Spatial and temporal variation in natal dispersal by Eurasian lynx in Scandinavia. *Journal of Zoology* 286, 120-130.
- Svenning, J.C. & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecology Letters* 7(7), 565-573.
- Swenson, J.E. & Andrén, H. (2005). A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. In: Woodroffe, R., *et al.* (Eds.) *People and Wildlife: Conflict or coexistence?* pp. 323-339. New York: Cambridge University Press. (Conservation Biology; 9).
- Titeux, N., Dufrene, M., Radoux, J., Hirzel, A.H. & Defourny, P. (2007). Fitness-related parameters improve presence-only distribution modelling for conservation practice: The case of the red-backed shrike. *Biological Conservation* 138(1-2), 207-223.
- Wabakken, P., Sand, H., Liberg, O. & Bjärvall, A. (2001). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology* 79(4), 710-725.
- van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, O., Brøseth, H., Andersen, R., Steen, H. & Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology* 77(6), 1183-1190.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerström, P. (2001). Characteristics of dispersal in wolverines. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 79(9), 1641-1649.

- VanHorne, B. (1983). Density as a Misleading Indicator of Habitat Quality. *The Journal of Wildlife Management* 47(4), 893-901.
- Ver Hoef, J.M. & Boveng, P.L. (2007). Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology* 88(11), 2766-2772.
- Vilà, C., Sundqvist, A.K., Flagstad, Ø., Seddon, Björnerfeldt, S.B., Kojola, I., Casulli, A., Sand, H., Wabakken, P. & Ellegren, H. (2003). Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270(1510), 91-97.
- Zabel, A. & Holm-Müller, K. (2008). Conservation performance payments for carnivore conservation in Sweden. *Conservation Biology* 22(2), 247-251.
- Zeileis, A., Kleiber, C. & Jackman, S. (2008). Regression models for count data in R. *Journal of Statistical Software* 27, 1-25.
- Zuur, A. (2010). AED: Data files used in Mixed effects models and extensions in ecology with R (in Zuur et al. 2009). *R package version 1.0*.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1(1), 3-14.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*: Springer Science + Business Media, New York, USA

## Supplemental Materials

Table S1. *Spatial variables used in models to predict distribution and frequency of reproduction of wolverines in Scandinavia*

Variables	Map	Source	Modifications / Comments
<i>Environmental</i>			
Elevation	GSD <sup>1</sup> 50×50m	National Land Survey of Sweden	
	ND <sup>2</sup> 50×50m	Norwegian Mapping Authority	
Terrain Ruggedness	50×50m	Calculated from DEM using “Vector Ruggedness Measure” (VRM) in ArcGIS 9.3™ ©1999-2004 ESRI Inc.	VRM neighbourhood size = 3: local scale ruggedness index based on 9 neighbouring cells
Slope	50×50m		
Vegetation	SMD <sup>3</sup> 25×25m	National Land Survey of Sweden(90 classes)	Merged to 25×25m raster. Swedish data kept when overlapping. Reclassified into 8 classes (Table S2)
	NORUT 30×30m	Northern Research Institute (25 classes)	
NDVI	NDVI 4×4 km	MOD13Q1 satellites images NASA’s MODIS TERRA <sup>4</sup>	Mean integrative NDVI from May to Oct
Snow cover	500×500m	MODIS satellite images (Copeland et al. 2010)	Years in which snow cover persisted through 15 May, in 2000-2006
Roads	1:100 000	Road map, National Land Survey of Sweden	Merged with N250. N250 data kept when overlapping Suitable for scale 1:100 000 - 1:300 000
	N250	MapData, Norwegian Mapping Authority	
<i>Human land use and Management policies</i>			
National Parks	NCA	Geographical Data Sweden 2008, Norwegian Mapping Authority	Nature Conservation Areas
Reindeer	Reindeer husbandry	GIS data Länsstyrelserna© 2000-2008, SWECO, Sweden	
	Wild reindeer	Reindeer husbandry administration of Norway The Norwegian Directorate for Nature Management <a href="http://www.dirnat.no/kart/villreinbase">http://www.dirnat.no/kart/villreinbase</a>	
Calving areas	Calving grounds	GIS data Länsstyrelserna© 2000-2008,SWECO	Sweden only
	Grazing areas	Reindeer husbandry administration of Norway ( <a href="http://www.reindriftno">http://www.reindriftno</a> )	Spring/early summer areas used as calving grounds
Carnivore	Large carnivore management zones	St.meld. nr. 15 (2003-2004) Rovvilt i norsk natur, Innst. S. nr. 174 (2003-2004) <sup>5</sup>	Zones in Norway were carnivores are allowed to reproduce

<sup>1</sup>Geographical Data Sweden, <sup>2</sup>Norwegian Digital, <sup>3</sup>Swedish Land Cover, <sup>4</sup>processed at Clark Labs (<http://edit.csic.es/GISdownloads.html>), <sup>5</sup>Available at <http://www.regjeringen.no>

Table S2. Variables used in models to predict distribution and frequency of reproduction of wolverines in Scandinavia. All measurements are estimated within 10\*10 km cells

Continuous environmental variable	Abbr.	Type <sup>1</sup>	Mean ( $\pm$ st.dev.)	Range
Latitude ( $^{\circ}$ N)	lat	R <sub>co</sub>	63.0 ( $\pm$ 3.83)	55.3-71.1
Elevation (m)	elev	R <sub>co</sub>	405 ( $\pm$ 321)	0-1781
Terrain ruggedness index	rug	R <sub>co</sub>	0.0018 ( $\pm$ 0.0022)	0-0.019
Slope ( $^{\circ}$ )	slope	R <sub>co</sub>	6.4 ( $\pm$ 5.2)	0-30
<u>Vegetation: 8 classes (proportions):</u>				
Coniferous forest	cfor	R <sub>ca</sub>	0.40 ( $\pm$ 0.31)	0-0.97
Deciduous forest	dfor	R <sub>ca</sub>	0.11 ( $\pm$ 0.12)	0-0.88
Heath and thickets	ht	R <sub>ca</sub>	0.15 ( $\pm$ 0.21)	0-1
Grasslands and meadows	gm	R <sub>ca</sub>	0.078 ( $\pm$ 0.17)	0-0.99
Bare rock and glaciers	rg	R <sub>ca</sub>	0.073 ( $\pm$ 0.091)	0-0.82
Bogs and marches	bm	R <sub>ca</sub>	0.13 ( $\pm$ 0.19)	0-1
Human dominated habitats (agricultural land and human infrastructure)	hum	R <sub>ca</sub>	0.067 ( $\pm$ 0.13)	0-1
Lakes and open water <sup>2</sup>	-	R <sub>ca</sub>	-	-
Mean integrative NDVI <sup>3</sup>	NDVI	R <sub>co</sub>	175 ( $\pm$ 24)	1-203
Spring snow cover index	snow	R <sub>co</sub>	2.1 ( $\pm$ 2.5)	0-7
Road density (km)	road	V <sub>co</sub>	913 ( $\pm$ 816)	0-6 517
Number of lynx reproductions	lynx	R <sub>co</sub>	0.31 ( $\pm$ 0.73)	0-7
<hr/>				
Annual measurements <sup>4</sup>	Abbr.	Type <sup>1</sup>	Mean ( $\pm$ st.dev.)	Range
Distance to nearest wolverine reproduction (km)	wdist	R <sub>co</sub>	135 ( $\pm$ 150)	0-687
Distance to nearest lynx reproduction (km)	lynxdist	R <sub>co</sub>	32 ( $\pm$ 32)	0-219
North Atlantic Oscillation <sup>5</sup>	NAO	-	-0.13 ( $\pm$ 0.42)	-1.15-0.27
<hr/>				
Binomial variables	Abbr.	Type <sup>1</sup>	Coding	
Country	NS	V <sub>bi</sub>	Sweden = 0, Norway = 1	
National park	NatPark	V <sub>bi</sub>	Within national park = 1	
Reindeer	rdeer	V <sub>bi</sub>	Within reindeer area = 1	
Calving areas	rcalf	V <sub>bi</sub>	Within calving areas = 1	
Carnivore management zone	zone	V <sub>bi</sub>	Wolverine reproduction allowed = 1	

<sup>1</sup>Raster continuous (R<sub>co</sub>) or categorical (R<sub>ca</sub>), Vector continuous (V<sub>co</sub>) or binary (V<sub>bi</sub>).

<sup>2</sup>This class was excluded when calculating vegetation composition within cells and in statistical analyses.

<sup>3</sup>Original NDVI real values (from -1 to +1) were rescaled by source to a range from 1 to 255 (byte format).

<sup>4</sup>Only 2003-2011

<sup>5</sup>One value for all observations in a given year





V





# Paying for coexistence: Assessing the performance of a large carnivore conservation performance payment system

Jens Persson, Geir Rune Rauset and Guillaume Chapron

*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden*

## Abstract

The conflict between conserving carnivores and their negative effects on local people raises an imminent need for tools to promote human-carnivore co-existence. Generally carnivore conservation has relied on (1) law enforcement to fight illegal activities such as poaching and (2) compensation and insurance schemes offered to those affected negatively by carnivore presence. Alternative approaches such as conservation performance payments, which are linked specifically to the production of a desired environmental output, have recently received an increasing attention but their effectiveness remains undocumented. In this paper, we evaluate the effectiveness of a large-scale conservation performance program for carnivores in Sweden. We use long-term individual data and a population model to analyse the interaction between the conservation performance payment scheme and human caused mortality in the Swedish wolverine population. We find that this scheme has likely been instrumental in the demonstrated increase and expansion of the population since it was introduced. While this scheme did not put an end to poaching, it leads to adult female wolverines – the demographic segment used as the performance indicator – having a significantly lower illegal mortality than adult males. Our evaluation illustrates that conservation performance payment schemes should be carefully designed and monitored to work. The fact that this scheme could still be successful where a predator feeds mainly on livestock reveals a promising potential for future implementations in other cases, especially where livestock is not the main prey.

## Introduction

Protection of species, such as large carnivores, that are highly valued at a global scale but have low or even negative value at a local scale is one of the most challenging tasks for contemporary biodiversity conservation (Dickman et al. 2011). With increasing human populations, the conflict between carnivore conservation and negative effects of carnivores on local people raises an imminent need for tools to mitigate conflicts and to promote human-carnivore co-existence. In carnivore conservation, two main approaches have been implemented. First, law enforcement is widely used to prevent poaching of carnivores or habitat destruction (Trouwborst 2010). Second, financial incentives to those affected negatively by carnivore presence are a common strategy for encouraging such coexistence (Dickman et al. 2011). These incentives can include compensation and insurance schemes (MacLennan et al. 2009; Nyhus et al. 2003), or giving carnivores a direct value through ecotourism, trophy hunting and conservation payment (Lindsey et al. 2012). In their essence, compensation and payment schemes are designed to remedy the imbalance between their value at a global scale and their costs at a local scale (Dickman 2011). The most common financial incentive for mitigation of carnivore-livestock conflicts is compensation (MacLennan et al. 2009, Schwerdtner & Gruber 2007, Naughton Treves et al. 2003, Wagner et al. 1997). However, due to problems with this method, e.g. moral hazards (Nyhus et al. 2003; Bulte & Rondeau 2005), there has been an increasing interest in alternatives financial incentives to promote carnivore-human coexistence (Nelson 2009; Dickman et a. 2011). One such alternative is conservation performance payments, which are linked specifically to the production of a desired environmental output, e.g., maintenance of carnivores (Zabel & Roe 2009).

The conservation and management of natural resources requires an understanding of mechanisms affecting human behavior. In general, policies are considered successful when they contribute to increase the frequency of desirable human behaviors and/or to decrease the frequency of less desirable ones. Behavioral theory has historically proposed 4 broad ways to influence behavior: positive or negative punishment and positive or negative reinforcement (Skinner 1938, Chase 2006) even if this classification has been questioned (Michael 1975, Baron & Galizio 2006). In this context, positive is understood as adding a stimulus while negative is understood as removing a stimulus. Punishment is defined as creating a situation that people dislike, while reinforcement is defined as creating a situation that people like. In practice, positive punishment consists in adding an aversive stimulus to decrease a certain behavior, e.g. jail time for poachers. Positive reinforcement

consists in adding an appetitive stimulus to increase a certain behavior, e.g. payment for conservation outcomes. Negative punishment consists in removing an appetitive stimulus to decrease a certain behavior, e.g. cutting agricultural subsidies to farmers convicted of poaching. Negative reinforcement consists in removing an aversive stimulus to increase a certain behavior and does not appear to be part of the usual conservation policy toolbox.

In fact, the vast majority of conservation and management policies rely nowadays on positive punishment (Trouwborst 2010). Both in civil and common law jurisdictional systems, penalties have been set that one faces when destroying protected species or habitat. In carnivore conservation, the wrong behavior is often illegal killing of protected species and the punishments are fines or jail time penalties faced by poachers (Eliason 2012; Keane et al 2008; Liu et al. 2011; Martin et al. 2009). A vast amount of research has been produced to elaborate on the pros and cons of such an approach and how to make it more efficient, e.g. whether the most cost-efficient way of curbing poaching was to increase the likelihood of poachers to be caught or to increase the penalties faced by poachers (Jachmann & Billiow 1997, Leader-Williams & Milner-Gulland 1993), or how to best patrol areas to deter poachers (Jachmann 2008; Jenks et al. 2012). However, this approach can only be successful on the long-term if the rules of the positive punishment are deemed as legitimate by a majority of people. Such rules can be elaborated at multiple geographic scales, can involve institutions at different levels, and can be imposed from an external authority or developed locally within communities (Keane et al. 2008). The outcome of positive punishment policies is further dependent on compliance with rules on how resources are managed. Therefore, enforcement (monitoring of rule adherence and punishment of infractions) is essential for the success of such policies (Gibson et al. 2005; Jachmann 2008; Keane et al. 2008; Rowcliffe et al. 2004).

Policies relying on a positive reinforcement approach have historically been less favored by policy makers but have recently benefited from an increased interest. In wildlife conservation, this alternative policy option is called "conservation performance payments" where a particular group is rewarded if they have contributed to the recovery of a particular species (Ferraro 2001; Ferraro & Kiss 2002; Engel et al. 2008; Nelson 2009; Zabel & Engel 2010; Dickman et al. 2011), which can somewhat be interpreted as a particular type of payment for ecosystem services (Zabel & Engel 2010; Dickman et al. 2011). It is worth noting however that conservation performance payments are schemes designed to pay for results that have been achieved and differ from general subsidies – often unlinked to achievements, or compensation schemes – linked to level of damages (Zabel & Roe 2009). No proper evaluation of the

few existing policies based on conservation performance payments has been made in a rigorous setting (Zabel & Engel 2010; Nelson 2009), which prevents policy makers to learn from experience (Nelson 2009) and hinders a more widespread adoption of such schemes. This is especially true for conservation performance payment approaches to mitigate predator–livestock conflicts, which typically have major livelihood impacts in rural environments (Zabel & Engel 2010).

One of the most well established examples of a large-scale, publicly funded conservation performance program for large carnivores was implemented in northern Sweden 17 years ago. In this scheme, indigenous Sámi reindeer herders are paid for presence of carnivores within an area, instead of documented losses of reindeer. In this paper, we evaluate the efficiency of this scheme, which targets wolverine (*Gulo gulo*) and other carnivores within the reindeer husbandry area (Zabel & Holm-Müller, 2008). We use long-term individual based data on wolverine survival to examine the reciprocal interaction between the conservation performance payment system and human caused mortality in a wolverine population, and its consequences on conservation performance.

## The context

### Wolverines and semi-domestic reindeer in Northern Sweden

Wolverines and semi-domestic reindeer (*Rangifer tarandus*) in Sweden represent an extreme case of predator-livestock coexistence, and a unique conservation challenge. In Sweden, the wolverine is red-listed (*vulnerable*; Gärdenfors 2010), and largely dependent on semi-domestic reindeer, with few alternative food sources regularly available (Persson 2005; Mattisson et al. 2011). Semi-domestic reindeer are private property owned by indigenous Sámi people, and depredation by wolverines and other predators on reindeer creates conflicts between carnivore conservation and sustainability of an important part of an indigenous culture (Hobbs et al. 2012). A consequence of this conflict is that poaching is the most important source of adult mortality in wolverines (Persson et al. 2009).

### Population history

The Swedish wolverine population decreased during the 20<sup>th</sup> century due to intense persecution encouraged by a bounty system (Persson 2003). When the bounty system was implemented, denning females with offspring were especially exposed to harvest, because bounties were paid per individual, and animals in den sites were easier to find and kill (Haglund 1965). Increased

accessibility following the introduction of snowmobiles accentuated the decline in the 1960s when the population size was at its lowest (Haglund 1965). Despite the introduction of total legal protection and penalties against poaching in 1969, the recovery of the population was very slow (Björvall & Ullström 1985). When large scale monitoring was first established in 1996 the population estimate was 265 individuals (Landa et al. 1998). Subsequently, the number of registered reproductions has increased with 3.8 % per year and the estimated population size was 552-790 individuals in 2010 (Persson & Brøseth 2011) with the population expanding into previously unoccupied areas (Aronsson & Persson 2012).

#### Current management policy and performance payment

Successfully conserving wolverines without increasing conflicts with reindeer herders is challenging because reindeer graze freely over extensive areas making it impossible to implement efficient preventive measures against depredation (Mattisson et al. 2007). The former approach for managing the conflict and reaching policy goals relied on financial schemes for compensating depredation losses. In 1996, the system abandoned an ex-post compensation system to instead adopt a system of conservation performance payment to offset for depredation losses caused by wolverines and other carnivores, but also to create incentives for conservation of wolverines. The Swedish authorities make payments to reindeer herding districts contingent on the number of recorded wolverine reproductions and occurrence of wolverines within each district and irrespective of actual predation levels (Zabel & Holm-Muller 2008). Current payments are set at 200,000 SEK (1 SEK  $\approx$  € 0.12) per documented wolverine reproduction. The payment is intended to cover depredation and disturbance of herds caused by the wolverine family group and other individuals in the population and the reproducing females is considered as an index for the entire population. This system was designed to not distort incentives to apply optimal livestock protection and consequently to not give rise to moral hazard (Zabel & Holm-Muller 2008). On the contrary, it is intended to stimulate herders to take actions that decrease losses.

A key aspect of the current system used in Sweden is that annual intensive population monitoring is an essential to its proper functioning. The wolverine population is monitored by annual registration of reproductions (i.e. documentation of natal dens and/or tracks or observations of cubs; [cf. Landa et al. 1998]) performed by the County Administration in collaboration with the reindeer herding districts. Most of the monitoring is conducted in late winter and spring until snow conditions become unfavorable for snow tracking. The main part of the monitoring includes search for tracks of concentrated activity

to document den sites or observations of cubs or their tracks. Thus monitoring personnel concentrate their activity in and around denning habitat during February-May.

There is no public hunting for wolverines allowed in Sweden. However, lethal control has been allowed in special cases as a final conflict-mitigating measure and is presumably of limited importance on a population-level (Persson et al. 2009). Wolverines exhibit a polygamous mating system, where one male overlap and mate with several females each year (Hedmark et al. 2007), thus sex-specific harvest levels presumably affect population growth.

## Material and methods

To assess the efficiency of the conservation performance payment we investigate whether reproductive females are less likely to be poached than males. We further estimate how the poaching rate for females influence population growth rate. Our data consist of 95 radio-marked adult (> 2 yrs. old) wolverines (33 males; 62 females) monitored during 356 radio-years. For details on protocol for capture and immobilization see Arnemo et al. (2011). The study was approved by the Animal Ethics Committee for northern Sweden, Umeå. For monitoring of marked wolverines and determination of mortality causes, see Persson et al. (2009).

We estimated cause-specific mortality rates for adult males and females as described by Heisey & Fuller (1996) in R (R Development Core Team 2012). We used the `wildl` package in R rather than the most commonly used `cmprsk` (Gray 2012) package because the former handles properly left truncation while the latter one does not (Pintille 2006).

We developed a 2-sex stochastic individual based model specific to wolverine. In this model, the population is structured into several stages: resident sexually mature adult individuals (>2 year old), subadults/floaters (1-2 year old), and juveniles (<1 year old). Resident sexually mature individuals are females holding a territory and having the possibility to reproduce each year. Floaters and juveniles are both non-resident and non-reproducing individuals. We made the assumption that the wolverine population in Sweden is well below its carrying capacity and that density-dependent effects can be neglected compared to other factors affecting mortality and reproduction. We parameterized our model for adult survival with rates estimated above, for juvenile and floater survival we used data from 95 radio-marked wolverines of these classes. We considered that reproduction takes place from age 2 to age 13, with average number of female cubs per 2-year old female  $f_2 = 0.05$  and per year, and average number of female cubs per sexually mature female and

per year  $f = 0.38 \pm 0.04$ . The model was written in C and used the GNU Scientific Library for random and statistic functions (Galassi et al. 2009). We run Monte Carlo simulations (10,000 runs per parameter set) to investigate how different levels of poaching on males and females would affect population growth rate.

We used data on wolverine harvest data from Norway (November 1995 to September 2012) to estimate sex ratio of animals killed during different kinds of harvest. We separated harvest methods into trapping (box-traps), license hunt (most animals shot with rifle at bait sites or during hunting for other game), and lethal control. Data was downloaded from the national database Rovbase 3.0 ([www.rovbase.no](http://www.rovbase.no)) September 30, 2012.

## Results

### Cause specific mortality risk

For adult males, the average annual natural mortality risk was  $0.026 \pm 0.026$  (mean  $\pm$  SE) and the average poaching risk was  $0.201 \pm 0.056$ . For adult females, the average natural mortality risk was  $0.070 \pm 0.021$  and the average poaching risk was  $0.082 \pm 0.021$ . Natural mortality risk was not significantly different between males and females ( $\chi^2 = 1.27$ ,  $df = 1$ ,  $p = 0.26$ ), but poaching risk was significantly higher in males than in females ( $\chi^2 = 4.71$ ,  $df = 1$ ,  $p = 0.03$ ).

### Effect of poaching on growth rate

Stochastic simulations run with the wolverine specific individual based model reveal that variations in female poaching rate have a much stronger impact on population growth than variations in male poaching rate (Figure 1). For example, consider a population with female and male poaching rates both equal to 10%. Its growth rate would be 1.027. Doubling the female poaching rate would lower the growth rate to 0.94, while doubling the male poaching rate would still keep the population slightly growing (growth rate of 1.01). The actual female (0.082) and male (0.201) poaching rates allow the Swedish wolverine population to grow (growth rate = 1.035; Figure 1).

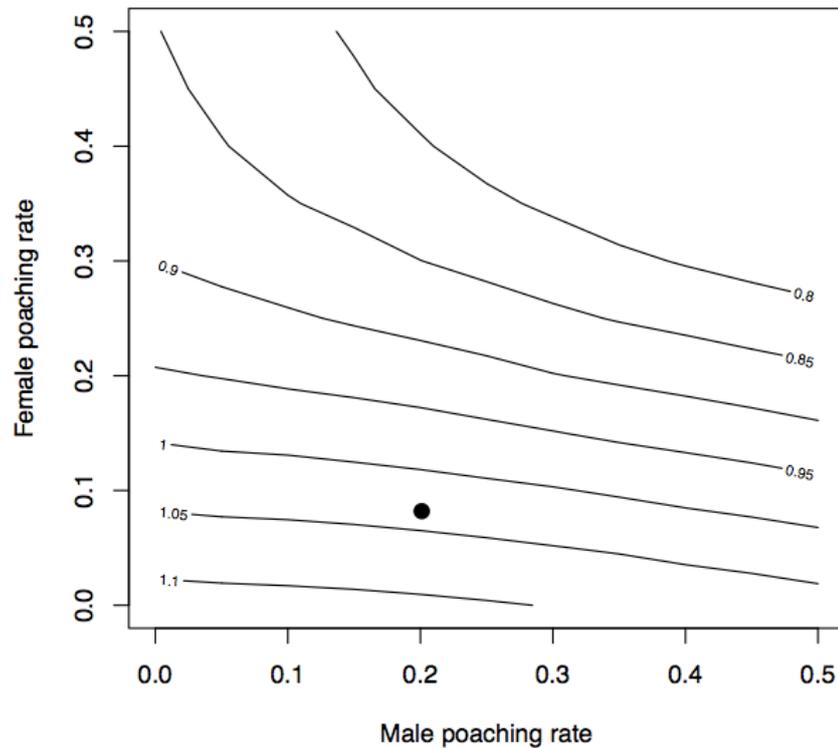


Figure 1. Iso-growth rate contour curves as a function of male and female poaching rates. Black dot indicates the values for the actual Swedish wolverine population

#### Sex ratio of harvested wolverines in Norway

Proportion of males in harvest separated on harvest type was 0.44, 0.49 and 0.51, respectively for trapping (n = 34), license hunting (n = 373) and lethal control (n = 302). The proportion of males with all harvest types pooled was 0.5. Thus, we could not find any sex-bias in the Norwegian wolverine harvest.

#### Discussion

This case study is the only well established large-scale conservation performance payment scheme implemented in carnivore conservation (Zabel et al. 2011). The analysis shows that this scheme did not put an end to poaching of wolverines. However, it leads to the demographic segment of the population used as the indicator in the scheme, adult female wolverines, having a significantly lower illegal mortality than adult males. In other words, Swedish authorities get what they have paid for. We suggest that this lower poaching

rate presumably explains the demonstrated increase (3.8 % per year) and expansion of the population since the scheme was introduced.

We can outline several mechanisms through which the conservation performance payment scheme is able to provide protection and thereby higher survival in adult females. First, because reproducing females are the indicator of the scheme, they de facto have a monetary value and are thus expected to constitute a segment of the population that poachers will deliberately avoid. Second, reproducing females are the indicator of the scheme, monitoring activity is concentrated around denning habitat and potential den sites during the denning period. These areas therefore act as habitat that poachers are expected to avoid to decrease both the risk of killing reproducing females and the likelihood of being caught when poaching. Furthermore, poaching in general is most prevalent in March-May when it is presumably most facilitated by beneficial snow and light conditions north of the Arctic Circle (Persson et al. 2009). This scheme therefore generates a disproportionate effect on illegal mortality risk exposure because poaching is more difficult to carry out outside the denning season. In addition, because County Administration personnel conduct the monitoring in collaboration with reindeer herders, the overall acceptance for both wolverines and the management may be increased, as regular communication and interaction between representatives of “the buyer and the seller” (cf. Zabel & Engel 2010) takes place and in turn improves trust and understanding.

We do not believe that more extensive movements and area use by males would make them indirectly more exposed to human mortality than females. In fact, data from different types of harvest in Norway suggest that male and female wolverines are equally vulnerable to human killing. Similarly, Krebs et al. (2004) did not find any difference in male and female survival in trapped wolverine populations in North America. We believe that the monetary value of reproducing females and the indirect protection from monitoring activity in denning habitat act in concert to provide females with more protection from poaching than males. We suggest that the actual mechanism is that poachers avoid poaching in the neighborhood of known denning habitat/sites. Hence, we have moved from legal harvest with bounties, where females presumably were legally harvested at higher rates than males (until 1969), to a system where females are illegally harvested at lower rates than males (from 1996).

The fact that adult males, a part of the population untargeted by the payment, does not benefit from this scheme highlights the importance of choosing the most efficient indicator when a conservation performance payment system is implemented. In our case, the scheme has an effect on the wolverine recovery because the payment indicator appears to be the

demographic segment (reproductive females) to which population growth is the most sensitive. The design was chosen for the same reason, that reproductive females have high conservation value, and that reproductions indicate regular occurrence (Naturvårdsverket 1991). The key part of the success is that there is no mismatch between what is rewarded and what is desired, so that no perverse incentives – analogous to people farming snakes when being paid a bounty for every dead snake, known as the “cobra effect” (Siebert 2001) – are created. In addition, since the compensation is made regardless of actual losses, efficient herding (to decrease losses) is economically beneficial and not penalized by lower compensation.

The price paid for each wolverine reproduction (200 000 SEK; 1 SEK  $\approx$  €0.12) was not decided based on a behavioral economic analysis but rather from expert judgment by authorities (Naturvårdsverket 1991). Attributing a too small value may not lead to lower female poaching rate, while attributing a too high value may be counterproductive by creating a cultural disruption when the economy is based more on carnivore compensation than on reindeer herding. In average circa 18 million SEK have been paid annually for wolverine reproductions in the Swedish reindeer husbandry area during the past 10 years. One may consider that this amount of money would have been better spent on direct poaching control. However, controlling poaching is very expensive and very few persons have been prosecuted for poaching in Sweden (Pyka et al. 2008), and such system would not compensate herders for losses. Worth noticing is that although the scheme entails high transaction costs through the extensive monitoring, the monitoring is not only a cost as it includes poaching deterrence as well. However, our analysis did not allow us to disentangle the combined effect of indirect protection from monitoring vs. the direct effect of monetary value. As such, it still remains unclear how the scheme would perform if monitoring would not require an extensive field presence around den sites.

While the scheme appears to have been successful since its implementation, its long-term efficiency requires further investigation. First, behavior theory predicts that when reinforcement is presented on a fixed schedule (a defined payment is made every time something happens), it loses its effectiveness on the long term and the frequency of the desired behavior would decrease (Kohn 1999). This is analogous to people doing lower quality work when they are motivated with money or grades rather than with more emotion or value-based incentives. Second and because the scheme does not increase acceptance enough to eliminate poaching (neither on males nor on females), we cannot rule out the emergence of a perverse mechanism where poachers would actively search for males in order to decrease the wolverine population without

immediately affecting the scheme indicator. Our model shows that a wolverine population can be quite resilient to relatively high rate of male poaching before declining, but highly skewed sex ratio of the adult populations could trigger unexpected dynamics that we did not incorporate.

This case study illustrates that conservation performance payment schemes have to be carefully designed and monitored to work. Important factors that will influence the success of a conservation performance payment scheme is the overall policy goal, who is the buyer and the seller of “the goods”, the policy context, indicators that are used and how they are monitored, the amount, timing and vehicle of payment (Zabel & Engel 2010). However, because our scheme focuses on an extreme system where carnivores feed mainly on livestock and can still be successful, it indicates a promising potential for future implementation of other systems, especially where livestock is not the main prey.

## Acknowledgment

The study was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the World Wide Fund for Nature (Sweden), the Swedish University of Agricultural Sciences, EAZA (European Association of Zoos and Aquaria), and the private foundation “Marie-Claire Cronstedt’s Stiftelse”. We thank Peter Segerström for capturing and collaring wolverines. We thank Malin Aronsson and Henrik Andrén for providing valuable comments on earlier drafts of the paper.

## References

- Arnemo, J.M., Evans, A., & Fahlman, Å., (2011). Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx.  
<<http://www.rovviltportalen.no/content.ap?thisId=500039688>>.
- Aronsson, M. & Persson, J. (2012). Järv i skogslandet [Wolverines in the forest landscape].  
*Report to WWF* [in Swedish]
- Baron, A. & Galizio, M. (2006). The Distinction Between Positive and Negative Reinforcement: Use With Care. *The Behavior Analyst* 29(1): 141–151.
- Björvall, A. & Ullström, S. (1985). *Däggdjur: Alla Europas arter*. W & W, p. 163. ISBN 91-46-14896-5
- Bulte, E. H. & Rondeau, D. (2005). Why compensating wildlife damages may be bad for conservation. *Journal of Wildlife Management* 69(1): 14-19.
- Chase P.N. (2006). Teaching the distinction between positive and negative reinforcement. *The Behavior Analyst*. 29: 113–115.

- Dickman, A. J., Macdonald, E. A. & Macdonald, D. W. (2011). A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences* 108: 13937–13944.
- Eliason, S. L. (2012). Trophy Poaching: A Routine Activities Perspective. *Deviant Behavior* 33: 72–87.
- Engel, S., Pagiola, S. & Wunder, S. (2008). Designing payments for environmental services in theory and practice: An overview of the issues. *Ecological Economics* 65: 663–674.
- Ferraro, P.J. (2001). Global habitat protection: Limitations of development interventions and a role for conservation performance payments. *Conservation Biology* 15(4): 990-100
- Ferraro, P.J. & Kiss A. (2002). Direct Payments to Conserve Biodiversity. *Science* 298 (5599): 1718-1719.
- Galassi, M. Davies, J., Theiler, J., Gough, B., Jungman, G., Alken, P., Booth, M., & Rossi, F. (2009). *GNU Scientific Library Reference Manual* (3rd Ed.), ISBN 0954612078. <http://www.gnu.org/software/gsl/>
- Gibson, C.C., Williams, J.T. & Ostrom, E. (2005). Local enforcement and better forests. *World Development* 33: 273–284.
- Gray, B. (2012). Cmprsk: Subdistribution Analysis of Competing Risks. *R package version 2.2-3*.
- Gärdenfors, U. 2010. The 2010 Red list of Swedish species. Swedish Species Information Centre, Swedish University of Agricultural Sciences
- Haglund, B. (1965). *Järv och varg*. Norstedt & Söners Förlag, Stockholm [in Swedish].
- Hedmark, E., Persson, J., Segerström, P., Landa, A. & Ellegren, H. (2007). Paternity and mating system in wolverines *Gulo gulo*. *Wildlife Biology* 13 (Suppl. 2): 13–30.
- Hobbs, T., Andrén, H., Persson, J., Aronsson, M. & Chapron, G. 2012. Native predators reduce harvest of reindeer by Sámi pastoralists. *Ecological Applications* 22 (5): 1640-1654.
- Jachmann, H. (2008a). Illegal wildlife use and protected area management in Ghana. *Biological Conservation*: 141: 1906–1918.
- Jachmann, H. (2008b). Monitoring law-enforcement performance in nine protected areas in Ghana. *Biological Conservation* 141: 89–99.
- Jachmann, H. & Billiouw, M. (1997). Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *Journal of Applied Ecology* 34: 233–244.
- Jenks, K. E., Howard, J. & Leimgruber, P. (2012). Do Ranger Stations Deter Poaching Activity in National Parks in Thailand? *Biotropica* 44(6): 826-833.
- Keane, A., Jones, J. P. G., Edwards-Jones, G. & Milner-Gulland, E. J. (2008). The sleeping policeman: Understanding issues of enforcement and compliance in conservation. *Animal Conservation* 11: 75–82.
- Kohn, A. (1999). *Punished by Rewards – The Trouble with Gold Stars, Incentive Plans, A's, Praise, and Other Bribes*. Boston: Houghton Mifflin.
- Krebs, J., Lofroth, E., Copeland, J., Banci, V., Cooley, D., Golden, H., Magoun, A., Mulders, R. & Shults, B. (2004). Synthesis of survival rates and causes of mortality in North American wolverines. *Journal Of Wildlife Management* 68: 493–502.
- Landa, A., Tufto, J., Franzen, R., Bø, T. & Linden, M. (1998). Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia. *Wildlife Biology* 4: 159-168

- Leader-Williams, N. & Milner-Gulland, E. J. (1993). Policies for the enforcement of wildlife laws: the balance between detection and penalties in Luangwa Valley, Zambia. *Conservation Biology* 7: 611–617.
- Lindsey, P.A., Balme, G.A., Booth, V.R., & Midlane, N. (2012). The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. *PLoS ONE* 7(1) Article number e29332
- Liu, F., McShea, W. J., Garshelis, D. L., Zhu, X., Wang, D. & Shao, L. (2011). Human-wildlife conflicts influence attitudes but not necessarily behaviors: Factors driving the poaching of bears in China. *Biological Conservation* 144: 538–547.
- Macdonald DW (2001) Postscript - carnivore conservation: science, compromise and tough choices. in *Carnivore Conservation*, eds Gittleman J, Funk S, Macdonald D, Wayne R (Cambridge Univ Press, Cambridge, UK), pp 524–538.
- MacLennan, S.D., Groom, R.J., Macdonald, D.W. & Frank, L.G. (2009) Evaluating a compensation scheme to bring about pastoralist tolerance of lions. *Biol Conserv* 142: 2419–2427.
- Martin, E., Talukdar, B. K. & Vigne, L. (2009). Rhino poaching in Assam: Challenges and opportunities. *Pachyderm* 46: 25–34.
- Mattisson, J., Odden, J., Nilsen, E.B., Linnell, J.D.C., Persson, J. & Andrén, H. (2011). Factors affecting Eurasian lynx kill rates and semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system? *Biological Conservation* 144: 3009-3017.
- Mattisson, J., Persson, J., Karlsson, J. & Andrén, H. (2007). Erfarenheter från försök att minska predation på ren [*Experiences from actions to decrease depredation on reindeer*]. Rapport till Rovdjursutredningen [in Swedish]
- Michael, J. (1975). Positive and negative reinforcement: A distinction that is no longer necessary; or a better way to talk about bad things. *Behaviorism* 3:33–44.
- Naughton-Treves, L., Treves, A. & Grossberg, R. (2003). Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation. *Conservation Biology* 17: 1500-1511.
- Naturvårdsverket. (1991). *Nytt ersättningssystem för rovdjursdödade renar*. Naturvårdsverket Rapport 3899. Naturvårdsverket, Stockholm [in Swedish]. ISBN: 91-620-3899-2
- Nelson, F. (2009). Developing Payments for Ecosystem Services Approaches to Carnivore Conservation. *Human Dimensions of Wildlife* 14: 381–392.
- Nyhus, P., Fischer, F., Madden, F., & Osofsky, S. (2003). Taking the bite out of wildlife damage: The challenge of wildlife compensation schemes. *Conservation in Practice* 4:37–40.
- Persson, J., Ericsson, G. & Segerström, P. (2009). Human caused mortality in an endangered wolverine population. *Biological Conservation* 142: 325-331.
- Persson, J. (2005). Wolverine female reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83: 1453-1459.
- Persson, J. & Brøseth, H. (2011). Järv i Skandinavien - status och utbredning 1996-2010. *MINA Rapport 732* [in Swedish with English summary].
- Pintilie, M. (2006). Competing Risks: A Practical Perspective. *Statistics in Practice*, vol. 58. John Wiley & Sons

- Pyka, M., Nyqvist, A., Monstad, T., Hagstedt, J. & Korsell, L. (2008). Poaching for large predators – conflict in a lawless land? . English summary of Brå report No 2007:22. Brottsförebyggande rådet: 1–28
- R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Rowcliffe, J. M., De Merode, E. & Cowlshaw, G. (2004). Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings Of The Royal Society B-Biological Sciences* 271: 2631–2636.
- Sargeant, G. A. (2011). wild1: R tools for wildlife research and management. R package version 1.09. U.S. Geological Survey Northern Prairie Wildlife Research Center, Jamestown, ND, USA.
- Schwerdtner, K. & Gruber, B. (2007). A conceptual framework for damage compensation schemes. *Biological Conservation* 134: 354-360.
- Siebert, H. (2001). *Der Kobra-Effekt. Wie man Irrwege der Wirtschaftspolitik vermeidet*. Munich: Deutsche Verlags-Anstalt. ISBN 3-421-05562-9 [In German]
- Skinner, B.F. (1938). *The behavior of organisms*. New York: Appleton-Century-Crofts.
- Trouwborst, A. (2010). Managing the Carnivore Comeback: International and EU Species Protection Law and the Return of Lynx, Wolf and Bear to Western Europe. *Journal of Environmental Law* 22(3): 347-372
- Wagner, K.K.; Schmidt, R.H.; Conover, M.R. (1997). Compensation programs for wildlife damage in North America. *Wildlife Society Bulletin* 25: 312-319.
- Wunder, S. (2005). Payments for environmental services: some nuts and bolts.
- Zabel, A. & Engel, S. (2010). Performance payments: A new strategy to conserve large carnivores in the tropics? *Ecological Economics* 70: 405–412.
- Zabel, A. & Holm-Müller, K. (2008). Conservation performance payments for carnivore conservation in Sweden. *Conservation Biology* 22: 247–251.
- Zabel, A. & Roe, B. (2009). Performance payments for environmental services: Lessons from economic theory on the strength of incentives in the presence of performance risk and performance measurement distortion. *Institute for Environmental Decisions (IED) Working Paper*, 7,
- Zabel, A., Pittel, K., Bostedt, G. & Engel, S. (2011). Comparing Conventional and New Policy Approaches for Carnivore Conservation: Theoretical Results and Application to Tiger Conservation. *Environmental and Resource Economics* 48: 287–301.



