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

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

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 & Lariviere, 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 adaption 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 20th 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 (Bjärvall & 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).

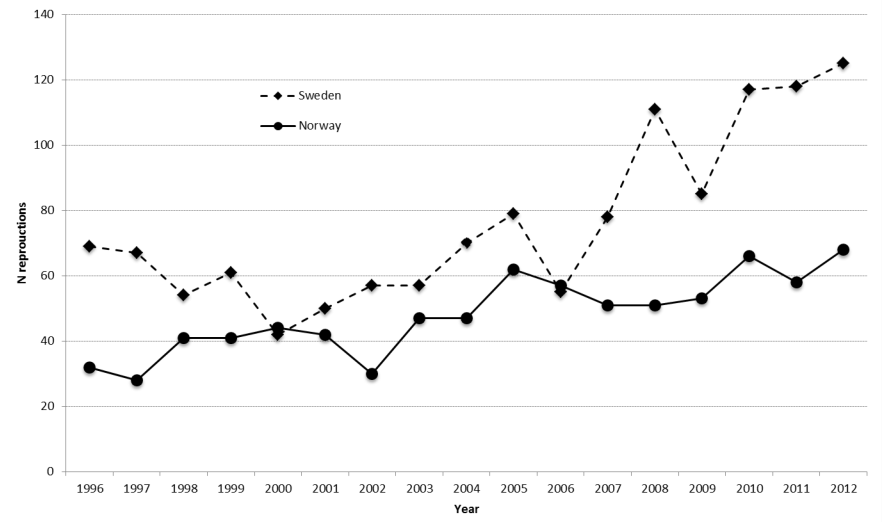

Figure 1. Number of wolverine reproductions in Norway and Sweden during 1996-2012.

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).

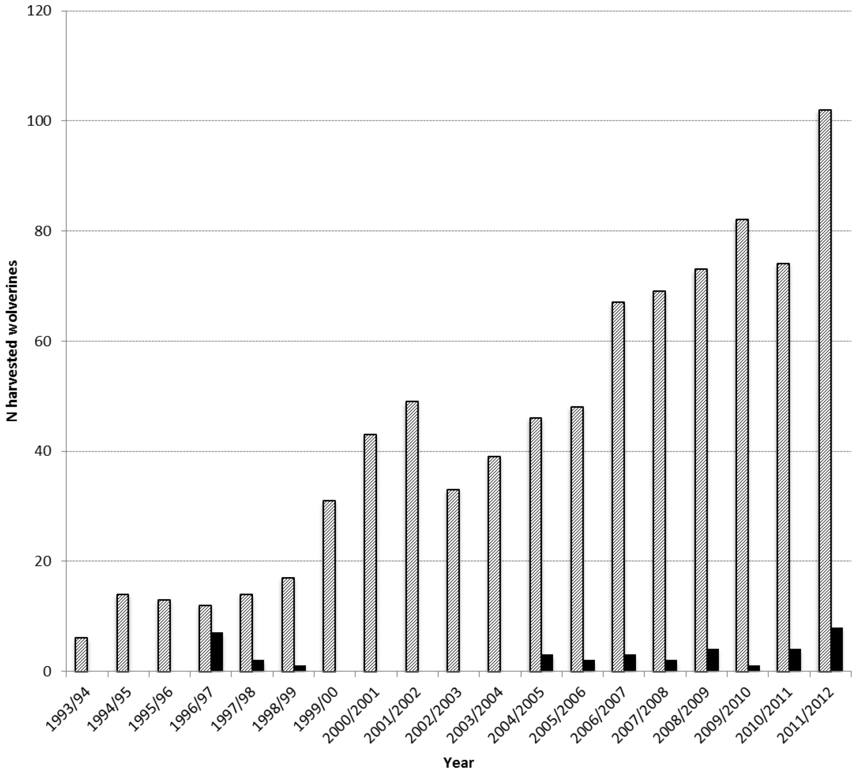

Figure 2. Annual harvest of wolverines in Norway (dashed bars) and Sweden (black bars).

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).

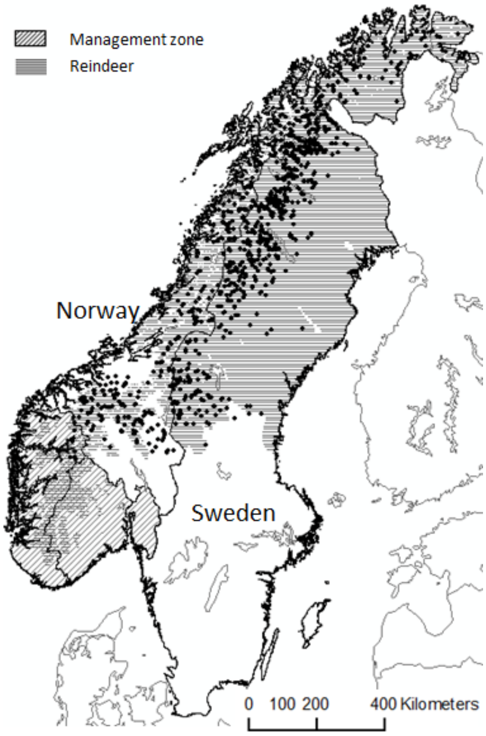

Figure 3. Norway and Sweden with all documented wolverine reproductions (n=1442) during 2001-2011 (dots).

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; *67ºN, 17ºE*). 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 ~ 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^2 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).

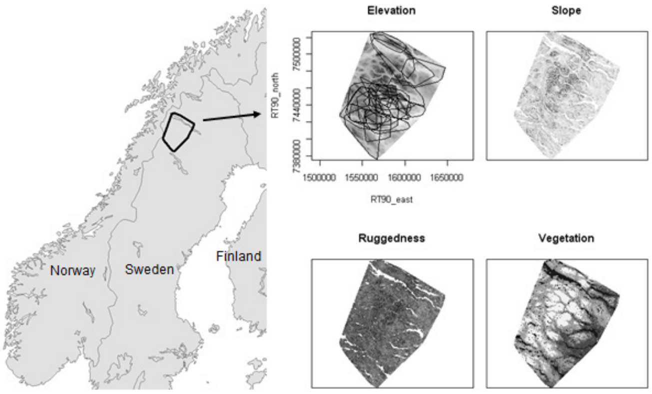

Figure 4. Map of the study area in northern Sweden with environmental variables. The elevation layer plot includes coordinate axis in the RT90 25gonV datum and the 100 % minimum convex polygon home ranges of 10 lynx individuals and 16 wolverine individuals.

To avoid multicollinarity 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 ≥ 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 *wild1* 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 (ψ) i.e. non-breeder to breeder or breeder to breeder) in addition to the survival (Φ) 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 (Φ (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.

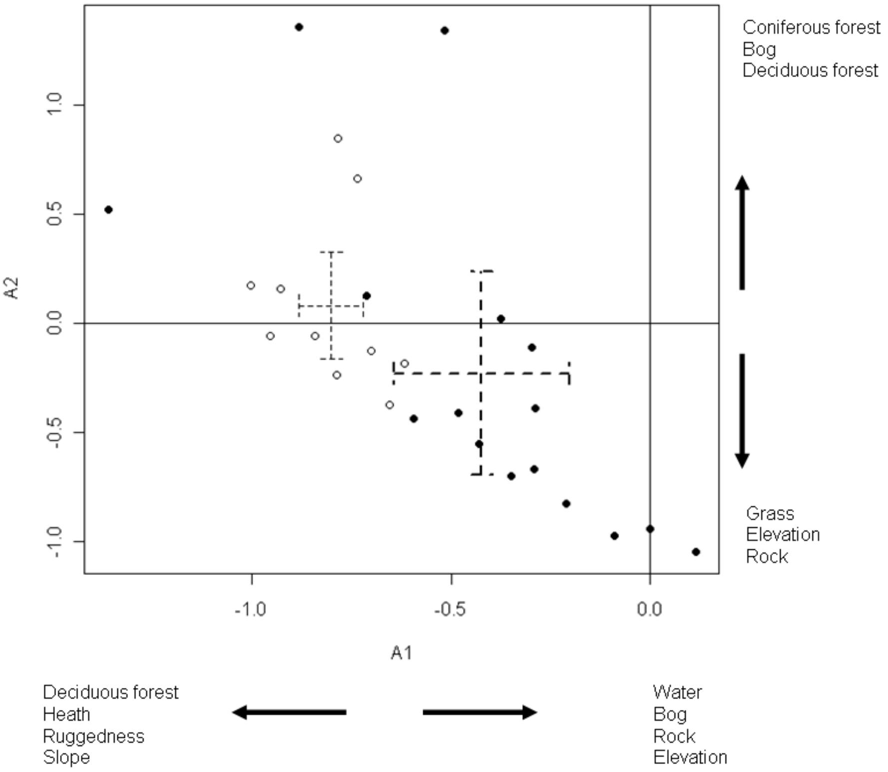

Figure 5. Result of the K-select analysis of selection for home ranges (second order selection) of lynx and wolverines in northern Sweden. The first axis A1 represents selection along the first principal component, comprising 49 % of the mean habitat selection (marginality), whereas A2 represents 24 %. 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 (β ± 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 ΔAIC column represents the change in AIC when removing the effect of national parks from the model.*

Mortality source	β ± SE	exp(β)	Δ_{AIC}
Brown bear			
Illegal	1.04 ± 0.46	2.8	2.9
Other	-0.46 ± 0.47	0.63	-0.96
Total mortality	0.23 ± 0.31	1.3	-1.3
Lynx			
Illegal	0.93 ± 0.46	2.5	2.3
Other	-0.31 ± 0.72	0.73	-1.8
Total mortality	0.55 ± 0.37	1.7	0.29
Wolverine			
Illegal	0.84 ± 0.36	2.3	3.5
Other	-0.084 ± 0.31	0.92	-1.9
Total mortality	0.38 ± 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.

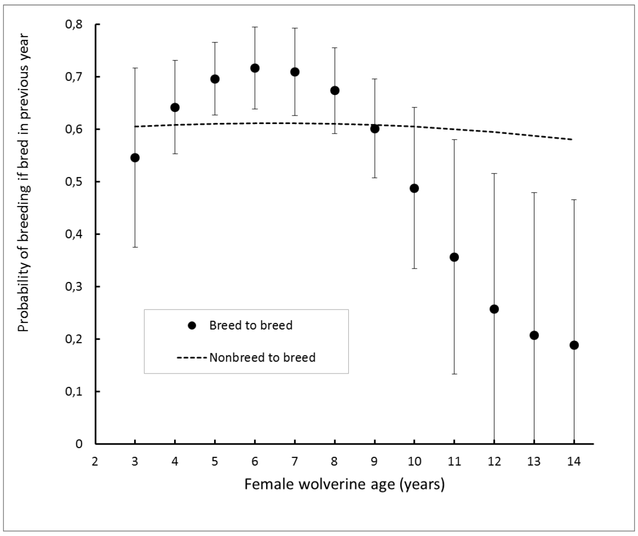

Figure 6. The probability to breed for female wolverines in relation to age for individuals that bred in previous year (point with 95 % CI) and for individual that not bred in previous year (dotted line).

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.

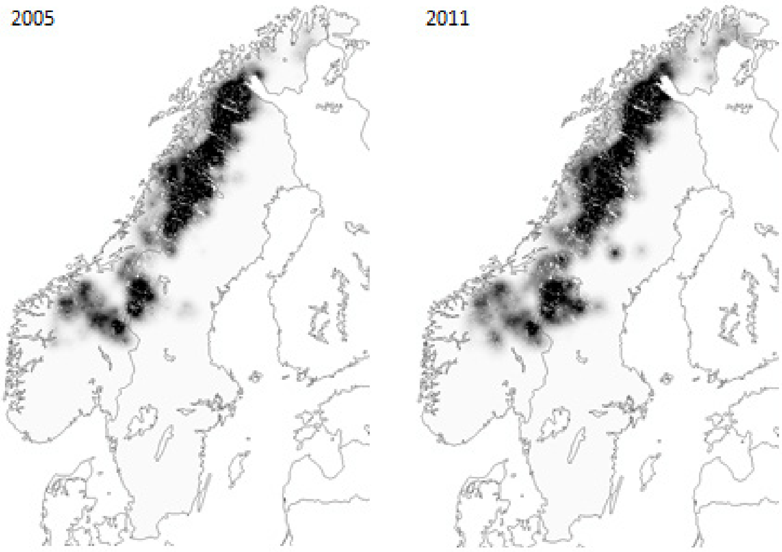

Figure 7. The predicted annual probability of wolverine reproductions in 2005 and 2011, based on the best logistic regression model.

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 themself, 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 perceptional 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.

Bjärvall, A., Franzen, R., Nordkvist, M. & Åhman, G. (1990). *Renar och rovdjur (Reindeer and predators, In Swedish)*. Solna, Sweden: Naturvårdsverket förlag.

Bjärvall, 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.

Falcucci, 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. & Lariviere, 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., Mysterud, A., May, R., Flagstad, O., Bröseth, 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 + Buisness 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 **systene, 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 friliftsliv 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 ufrogløymelege 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 resultet. 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 herligheiter.

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 Argentinaturen. 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 familen Stokke: **Rune, Elli-Kari, Nils-Anders og Jonas**. Spesielt til Rune for fine betraktningar, og for demonstrasjon av Formel1-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-feltatbeid 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 altenative synspunkt.

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

Jens - järvmannen 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!