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Spatial Ecology of Wolverines in Scandinavia

Thesis for the degree philosophiae doctor

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Norwegian University of Science and Technology
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Preface

This thesis is submitted to the Faculty of Sciences and Technology of the Norwegian University of Science and Technology (NTNU) for the degree of philosophiae doctor (PhD).The thesis consists of five papers and an introduction that summarizes the work. The research founding the basis of the thesis has been carried out at the Norwegian Institute for Nature Research (NINA) and the PhD study was affiliated to the Department of Biology, NTNU. My work formed part of the research project *Wolverines in a Changing World* of the Norwegian Wolverine Project that was financed by the Research Council of Norway (*Landskap i endring* program), the Norwegian Directorate for Nature Management, NINA, Sparebank–1 Midt-Norge, various Norwegian counties, and Alertis – fund for bear and nature conservation.

The thesis has been supervised by Arild Landa (NINA) and Reidar Andersen (NTNU). I sincerely thank my supervisors for all help, encouragement and fruitful discussions during the study period. I would also like to express my gratitude to John Linnell, Erling Solberg and Olav Strand for their ideas and support which greatly enhanced my learning curve and lifted this work. Also, thanks to my colleagues both at the Division for Terrestrial Ecology at NINA and at the Institute for Biology at NTNU for contributing to such a stimulating and pleasant environment.

Most of this work could not have been carried out without the enthusiastic help of many students, field personnel, Statens Naturoppsyn employees, and foremost Roy Andersen. His indispensable role as field coordinator has made it possible to capture and equip our study wolverines with GPS collars, and has been a pleasure to work with throughout.

To my family, thanks for letting me grumble to you when I was frustrated. Last, but most importantly, I would like to express my dearest thanks to Jiska van Dijk and Timmy. Jiska had to cope with me 24 hours a day, both as a colleague and as my wife. She helped me with all aspects of my work throughout the thesis and I am very grateful for all her patience, encouragement, and for loving me no matter what. Timmy, I should have spent more with you walking in nature instead of modelling it…but…

Alles komt altijd

Op z'n pootjes terecht

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II. **May, R.**, Landa, A., Dijk, J., van, & Andersen, R. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. – *Wildlife Biology*, 12, 285-295.

III. **May, R.**, Dijk, J., van, Andersen, R. & Andersen, R. & Landa, A. (manuscript). Ecotonal patch choice in a perceived mountain species: spatio-temporal ranging behaviour of female wolverines in southern Norway.

IV. Landa, A., **May, R**., Andersen, R., Segerström, P., Dijk, J., van & Persson, J. (submitted manuscript). Maternal care in wolverines; activity patterns from the den to cub independence. – *Journal of Mammalogy*.

V. **May, R.**, Gorini, L., Dijk, J., van, Brøseth, H., Linnell, J. D. C., Landa, A., & Andersen, R. (submitted manuscript). Reproductive den site selection in Norwegian wolverines at different spatial scales. – *Journal of Wildlife Management*.

Introduction

Large carnivores in Europe

During the last centuries, wilderness areas in Europe have changed into multiple-use landscapes in the face of human development and urbanisation. Today, impacts from the changing landscapes are considered to be the most important threat to biological diversity in terrestrial ecosystems (Entwistle & Dunstone, 2000). Predictions about which species are expected to be especially sensitive and which environmental changes have the greatest effects will provide valuable guidelines for management measures.

Many mammalian carnivores possess characteristics that may make them particularly vulnerable to landscape changes (Noss *et al.*, 1996; Woodroffe & Ginsberg, 1998; Crooks & Soulé, 1999; Sunquist & Sunquist, 2001). As they play a central role in the maintenance of the biodiversity, stability, and integrity of various communities (Noss *et al.*, 1996; Berger, 1999; Crooks & Soulé, 1999), conservation of such sensitive species is a challenge worldwide. Successfully conserving populations, species, or biological diversity involves a better understanding of ecosystem dynamics and the role of predator species in a community context (Landa, 1997). By accelerating the rate and expanding the scope of disturbance and habitat change, man has undermined the resilience and viability of large carnivore populations causing widespread declines (Weaver *et al.*, 1996; Weber & Rabinowitz, 1996). Europe once offered a wide range of natural habitats for its large carnivore species. Whereas the other large northern carnivores (brown bear *Ursus arctos*, wolf *Canis lupus* and Eurasian lynx *Lynx lynx*) historically roamed throughout most of Europe, the distribution of wolverines *Gulo gulo* was limited southwards to Norway, the southern parts of Sweden, Estonia, Lithuania, and northeast Poland (Landa *et al.*, 2000).

Wolverine's adaptability to ecosystem changes

Within their geographic range, wolverines occupy a variety of habitats. General characteristics of wolverines are their large area requirements, low densities and remoteness from human development (Landa *et al.*, 2000; Sunquist & Sunquist, 2001), which make them particularly vulnerable to landscape changes. Also, compared to the other northern large carnivores, wolverines are more sensitive to anthropogenic effects (Carroll *et al.*, 2001; Rowland *et al.*, 2003) and more selective about habitat quality (Banci & Harestad, 1988; Weaver *et al.*, 1996), especially for reproducing females (Magoun & Copeland, 1998; Heinemeyer *et al.*, 2001). Among carnivores, complex systems of interactions, such as intra-guild competition exist (Caro, 1994; Creel & Creel, 1996). In an intra-guild context, wolverines have evolved as scavengers utilising remains left by other, more efficient predators such as the wolf, lynx and brown bear, in addition to carcasses of animals which have died from accidents or diseases (Haglund, 1966; Magoun, 1987; Novikov, 1994; Landa & Skogland, 1995; Landa *et al.*, 1997). In addition, large carnivores, and especially wolverines, are increasingly involved in conflicts with human interests because of their depredation on semi-domestic reindeer throughout the year in Fennoscandia, and on free-ranging domestic sheep *Ovis aries* during summer in Norway. In order to minimize conflict levels licensed hunting, depredation control and compensation schemes have been employed (Landa *et al.*, 2000; Swenson & Andrén, 2005), as well as regional zoning of large carnivores (Linnell *et al.*, 2005).

Given the extensive habitat needs of wolverines, their perceived susceptibility to human disturbance and the continuing encroachment of human activity on wilderness areas, provision of adequate habitat where there is no potential for conflict could be difficult (Landa, 1997). However, ensuring effective wolverine conservation depends on maintaining sustainable management aimed at minimising the potential for conflicts with human activities in the multiple-use landscapes. If conservation and management are to be successful, knowledge on multiple-scale habitat requirements and their adaptability to changing environments is of critical importance to minimise conflicts and maintain or restore viable populations (Landa *et al.*, 1998).

Relevance to conservation and management

Conserving large carnivores is a complex and dynamic problem, involving ecological, economic, institutional, political, and cultural factors. The wolverine is protected by the Bern Convention and should therefore be preserved in viable populations. Still, the Scandinavian wolverine population is locally at risk and large stretches of its range are fragmented (Landa *et al.*, 2000; Flagstad *et al.*, 2004). One of the most important issues to be addressed in realising a sustainable management of large carnivores will be minimising the existing conflicts with human activities in the natural environment. Conservation and management of the wolverine can only become successful when sufficient emphasis is put on understanding the effects of both spatial and temporal changes in the use and management of our natural environment. Changes in the way wolverines use the natural environment may occur at different hierarchical scales, from selection of natal dens and patch choice (micro-scale), home range placement and use (meso-scale), to community-based distribution patterns (macro-scale). The rate of change in their behaviour, however, has to be viewed in relation with the limits of acceptable changes in multiple-use landscapes. Understanding the exact nature of habitat requirements in wolverines and its effect on use and management of the natural environment will render invaluable information, new perspectives and alternative solutions for future conservation and management of the wolverine.

Aims of the thesis

The principal objective of the research project *Wolverines in a Changing World* was to gain better insights into the ecological role of wolverines in ecosystem dynamics, their adaptation to ecosystem change and its implications for sustainable management of the natural environment. The aim of this thesis, within these settings, was to investigate the habitat requirements of wolverines at different hierarchical scales and their adaptability to changing environments to predict availability of suitable habitat for wolverines in Scandinavia. This aim was addressed by focussing on the following research questions.

1. Is the large carnivore community differentiated in habitat tolerances and distribution, and what effect does this have on regional zoning of large carnivores?
2. To which extent are wolverines behaviourally influenced by human infrastructure; or more specifically, do wolverines show clear selection for certain habitats and avoid infrastructure both in home range location and within their home ranges?
3. How does the spatio-temporal ranging behaviour of female wolverines with dependent cubs change over the season, and how is this related to foraging strategies?
4. Which spacing strategies (i.e., maternal care) do female wolverines employ to successfully rear their offspring, and how do these activity patterns relate to cub growth and timing of independence?
5. Which topographic elements are crucial to suitability of natal den sites, at which spatial scale are these selected, and can variation in reproductive frequency from different denning localities be related to specific habitat characteristics?

Methodological approach

The wolverine

The wolverine is the largest terrestrial member of the family mustelidae. Its compact posture, coupled with its extraordinary strength and stamina are all adaptations to the harsh environments it inhabits. With their robust and broad skull and powerful jaws and teeth wolverines can scavenge on frozen carcasses and crush bones of large ungulates (Pasitschniak-Arts & Larivière, 1995). With their heavily furred, large paws wolverines can traverse deep and soft snow, enabling them to kill larger prey like reindeer *Rangifer tarandus* or occasionally even moose *Alces alces* (Haglund, 1966). Compared to similar-sized carnivores, wolverines have large home ranges to fulfil their energetic needs. Home ranges range from 40–100 km^2 for reproducing females to 200–1,500 km^2 for females without cubs and adult males, whereas sub-adults and reproductively senescent individuals may even roam over several thousand square kilometres (Landa *et al.*, 2000). Mating occurs during the summer; however, delayed implantation makes it possible for the wolverine to give birth in early spring (Landa *et al.*, 2000; Ferguson *et al.*, 2006) when they give birth to an average of two cubs (Persson *et al.*, 2006). The wolverine has a circumpolar, holarctic distribution covering the tundra and boreal forest (taiga) biomes of the northern hemisphere (Landa *et al.*, 2000). Its Palaearctic distribution is mainly north of latitude 60ºN and is sympatric with that of wild and semi-domestic reindeer (Landa *et al.*, 2000). Present populations of wolverines in Scandinavia are found in the central to northern parts of Norway and Sweden, and are mainly concentrated in mountain areas (Landa & Skogland, 1995). In south-central Norway, the wolverine has during the last decade extended its distribution eastwards into the boreal forests (Flagstad *et al.*, 2004), following the re-colonisation of the wolf in this area (Landa & Skogland, 1995). In Norway, the density of wolverines in 2005 was estimated to be 3.15 ± 0.33 (SE) per 1,000 km^2 (unpublished data). The wolverine is labelled by the IUCN as a vulnerable species (Hilton-Taylor, 2000), and is considered to be endangered in Norway (Norwegian Red List: Kålås *et al.*, 2006).

Study area

The main study area was located in south-central Norway (62^{o}N 9^{o}E). This area encloses many different ecological conditions, from remote mountainous areas in the west and centre where high densities of free-ranging sheep graze unattended in their summer pastures (June – September) to more accessible forest areas in the east where wolverines co-exist with wolves, lynx and brown bears. In the mountainous regions some of the largest remaining European populations of wild reindeer are found. In the north-eastern part of the study area, herding of semi-domestic reindeer is practised. Carcasses of reindeer and moose constitute wolverines' most important source of winter food. Also, roe deer *Capreolus capreolus,* mountain hare *Lepus timidus,* grouse *Lagopus* spp., lemming *Lemmus lemmus* and various rodents and insectivores form possible sources of food for the wolverine (Myhre & Myrberget, 1975; Magoun, 1987; Landa *et al.*, 1997). The habitat in the mountain ranges consist of mountain plateaus with peaks up to 2,286 m with bare rock (high alpine zone down to 1,800 m), which give way to alpine tundra with heath (e.g., heather *Caluna* spp., crowberry *Empetrum* spp.) and lichen (*Cladonia* spp.) vegetations (midalpine zone down to 1,400 m). At lower elevations, alpine shrub land (e.g., willow *Salix* spp., dwarf birch *Betula nana*) can be found down towards the treeline at 900 – 1,000 m (low alpine zone). From the treeline downwards, forests are comprised of mountain birch *Betula pubescens* (sub-alpine zone), Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* with a varied undercover (e.g., blueberry *Vaccinium* spp., grasses *Molina* spp. / *Deschampsia* spp., mosses *Sphagnum* spp.). The low alpine zone and the sub-alpine zone form the forest–alpine tundra ecotone (Grytnes, 2003). The mountain ranges are divided by steep valleys. The forest region is mostly characterized by hills or lower mountains up to 1,200 m and wider valleys. The vegetation here is comprised of mixed forests of birch, spruce and pine, interspersed with open marches, natural meadows and heath. In the study area, snow is present from October/November until May/June depending on elevation. Human infrastructure is mainly concentrated at lower elevations in the valley bottoms. Recreational cabins can be found at higher elevations as well. Activities may consist of hunting, hiking and camping, and cross-country skiing.

Parts of this thesis were also based on radio-tracking and denning activity data collected in Troms County in northern Norway (68^{o}N 19^{o}E), with some additional data on denning activity from Sarek, northern Sweden (67^{o}N 17^{o}E). The landscape, habitats, and climate of the northern areas are broadly similar to the south-central Norway, except that treeline is lower (600 – 700 m) and climate is more continental. Semi-domestic reindeer are herded throughout both northern areas by Sámi herders and few domestic sheep are grazed in inner Troms, but not in Sarek. In addition, lynx, which are a major predator of semi-domestic reindeer (Pedersen *et al.*, 1999), and brown bears, which can occasionally kill moose and reindeer, are present in both northern areas, but occur at higher densities in Sarek (Swenson *et al.*, 2000).

Study designs

The papers included within this thesis were based on data from radio-marked individuals in the different study areas, locations of predator-killed free-ranging sheep and locations of natal den sites. The last two data sources were taken from the national carnivore database “Rovbase”. Radio-tracking data included both GPS data collected between 2002 and 2005, and previously collected VHF data. Within the different papers different spatial models have been used, which were best suited for the questions asked (i.e., resource selection functions (I), compositional analyses (II), discrete choice models (III and V)). When studying habitat requirements of animals in the wild several fundamental issues are important to consider, being: scale of investigation, spatial and temporal autocorrelation, and individual preferences.

The scale (i.e., grain/resolution and domain/extent) of investigation in such studies is important, as ecological processes can occur at different spatio-temporal scales, which influence the strength of habitat preferences (Boyce, 2006). Therefore, the extent should be large enough to encompass, and the resolution should be fine enough to capture the regional/local dynamics of the species under study. Various spatial and temporal processes (e.g., inter-specific interactions, human activities, seasonal changes) may affect the space use of a species at various spatial and temporal scales, ranging from delineation of distribution patterns, landscape-scale home range placement, to habitat and patch use (Boyce, 2006; Meyer & Thuiller, 2006). Each of these investigations requires their own type of data. Paper I best fit a population approach, where we chose to study patterns of selection of geographical ranges within the landscape (first order selection, Johnson, 1980). Paper II focused on the placement of home ranges in the landscape and habitat use within these home ranges (second and third order selection, respectively). Here we were especially interested in studying each individual's requirements at a home range scale. Paper IV did not relate use with any environmental conditions, but rather investigated activity patterns of wolverine family groups. This analysis can, however, be placed at the third order hierarchical scale (i.e., patches within home ranges). Paper III and V also investigated the use of patches within home ranges, but more specifically focused on selection of microhabitat within these patches. The hierarchical scale of these studies was placed at the patch/local scale (fourth order selection) and was investigated using a fine resolution.

Radio-tracking animals in the wild, especially with the emergence of new GPS technology, opened up a lot of new opportunities to study elusive animals. However, it also generated new problems mostly connected to spatial and temporal autocorrelation of collected data (Legendre, 1993; De Solla *et al.*, 1999; Nielsen *et al.*, 2002). In our modelling efforts we controlled for the autocorrelated structure of our data by using specific models (Paper III and V), or only including functionally independent locations (i.e., with at least 24 hours between locations) so as to minimise autocorrelation (Paper I and II) and reduce the difference between GPS and VHF data (Paper I).

Radio-tracking data have a nested structure of correlated positions within individuals. Possible individual preferences may well affect habitat selection, especially when heterogeneity among few individuals is large (Crawley, 2002). We therefore took individual preferences into account in our modelling efforts (Paper II, III). In models which are based on large numbers of measurements on a few individuals, it is possible to get an accurate model on these animals' habitat requirements. However, there is less power for testing the significance of selection effects, especially if variation among individuals is large (Crawley, 2002). Still, if conservation of rare and shy species is to be successful, information based on a few individuals will prove to provide us with crucial knowledge of its biology.

Results and discussion

Although large carnivores are able to persist in multiple-use landscapes (e.g., Hellgren & Maehr, 1992; Haight *et al.*, 1998; Maehr *et al.*, 2003), many mammalian carnivores possess characteristics (e.g., large area requirements, low densities, longevity, trophic position) that may make them particularly vulnerable to landscape changes (Woodroffe & Ginsberg, 1998; Crooks & Soulé, 1999; Sunquist & Sunquist, 2001; Crooks, 2002). Carnivore species may react differently to fragmentation however, due to differences in their behaviour and ecology (Sunquist & Sunquist, 2001; Crooks, 2002). An animal's location in space and time, the way it perceives the surrounding landscape and its subsequent behaviour together determine what resources are available to it and what it chooses among the available resources (Arthur *et al.*, 1996; Hjermann, 2000; Olden *et al.*, 2004). This not only reflects the situation the animal finds itself in, but especially reflects the animal's reaction to that situation. An animal's selection of resources thus influences the shaping of decision-making processes at different spatial scales (e.g., Lima & Zollner, 1996; Olden *et al.*, 2004; Vuilleumier & Metzger, 2005), including movement behaviour (Paper III, IV), habitat patch choice (Paper II, III, V) and distribution in the landscape (Paper I, II). Ultimately this influences biological processes at higher levels of organization (Hassell & May, 1985; Wiens *et al.*, 1993; Sutherland, 1998; Russell *et al.*, 2003), such as reproductive strategies (Paper III, IV, V), intra-guild relationships (Paper I) or species persistence in multiple-use landscapes (Paper II, V). Habitat requirements, however, do not only differ among species but different resources may also be selected at different spatial scales. The scale at which a resource is selected forms an index of the relative importance that it has on the overall selection probability.

Specifically, the larger the scale at which a resource is selected, the higher its importance (Rettie & Messier, 2000). Thus, it can be considered a *hierarchical* process which is important when considering management and conservation actions (Rettie & Messier, 2000; McLoughlin *et al.*, 2004; Meyer & Thuiller, 2006). To understand how landscape heterogeneity mediates animal movements and consequent resource selection it is important to consider the complex interactions between landscape patterns and resource selection at different hierarchically structured spatial scales (Fauchald, 1999; Olden *et al.*, 2004; Vuilleumier & Metzger, 2005, and references therein). The answers to the following questions will shed light on the spatial processes wolverines are facing in the multiple-use landscapes of Scandinavia.

Question 1: *Is the large carnivore community differentiated in habitat tolerances and distribution, and what effect does this have on regional zoning of large carnivores? [Paper I]*

Within an intra-guild community setting, sympatry of the wolverine with the three forest-dwelling carnivore species, the lynx, wolf and brown bear, appears to depend on the availability of mountain ranges as a spatial refuge (Paper II, V) and the presence of wolves to provide scavenging opportunities (van Dijk *et al.* unpublished data). Whereas the presence of brown bears, wolves and lynx was generally associated with rugged, forested areas at lower elevations, did wolverines select open, rugged terrain at higher elevations. This result fits well with the perception that the wolverine is a carnivore of remote alpine regions (Paper II, Carroll *et al.*, 2001; Rowland *et al.*, 2003). The wolf is likely to be least affected much by intra-guild aggression; it may rather instigate it (i.e., intra-guild predator, Palomares & Caro, 1999). However, although intra-guild predation on wolverines has been documented (Burkholder, 1962; Boles, 1977; Hornocker & Hash, 1981; Magoun & Copeland, 1998), the wolf may also facilitate other species, like the wolverine, with scavenging opportunities (Selva *et al.*, 2003; Wilmers *et al.*, 2003). Despite their similar potential distribution patterns, also the three forest-dwelling species had clear differences in choice of habitat and kill sites. It is likely that high prey densities, low large carnivore densities and decreased dietary overlap have led to a situation with reduced exploitative exclusion (c.f., Karanth & Sunquist, 1995; Holt & Polis, 1997; Heithaus, 2001). In a broader regional context our study area encompasses similar habitat/land use compositions and prey densities as can be found in large stretches of southern Norway and Sweden, and has comparable carnivore management regimes within Norway. The spatial extent of regional planning depends on the scale at which population processes are occurring. Our estimates for the carrying capacity of the study area may render insight into the minimum area required for viable populations, and therefore the appropriate scale of regional zoning. However, to explain present distributions, habitat preferences and differentiation among Scandinavian large carnivores, historical management and the role of humans as a top predator in these multiple-use ecosystems should not be underestimated. The main reason for the decline in large carnivore populations in Scandinavia was human-induced mortality caused by (over)exploitation, persecution because of livestock/game conflicts, and fear (Swenson *et al.*, 1995; Linnell *et al.*, 2002; Linnell *et al.*, 2005). Today, a geographically differentiated management policy has been adopted in Norway, aimed at conserving viable populations of large carnivores while minimizing the potential for conflicts. Although nearly one third of the study area was suitable for sympatry of the three forest carnivore species, only 5% was suitable for all four species. Successful regional zoning of all four carnivores may therefore rely on establishing zones spanning an elevational gradient. Zoning of all four species into this region may thus enhance the conservation of an intact guild of large carnivores in the boreal forest ecosystem (Wabakken, 2001). On the other hand, sympatry of all four species may well increase conflict levels and resistance to carnivore conservation locally (Wabakken, 2001; Linnell *et al.*, 2005).

Question 2: *To which extent are wolverines behaviourally influenced by human infrastructure; or more specifically, do wolverines show clear selection for certain habitats and avoid infrastructure both in home range location and within their home ranges? [Paper II]*

Although wolves may provide wolverines with scavenging opportunities, further wolverine recovery in forest ecosystems might be difficult, given the concentrated human development in forested areas at lower elevations (Paper I) and the continuing encroachment of human activity on wilderness areas (Landa, 1997). We showed that wolverines in Norway located their home ranges in relatively undeveloped high alpine areas (i.e., alpine tundra and rock/ice). The selection for alpine areas is consistent with previous studies on home range use and altitude selection by wolverines (Hornocker & Hash, 1981; Whitman *et al.*, 1986; Landa *et al.*, 1998). We found that habitat selectivity in developed habitats was low, indicating that infrastructure and not habitat was the primary factor for home range location. Also, wolverines were more selective about habitat quality in undeveloped areas when establishing their home range (c.f., Heinemeyer *et al.*, 2001). Within their home ranges however, wolverines used alpine shrub land and forest, irrespective of human development. Increased human development and activity in once remote areas may thus cause reduced ability of wolverines to perform their daily activities unimpeded, making the habitat less optimal or causing wolverines to avoid the disturbed area (Landa *et al.*, 1998; Vangen *et al.*, 2001). Wild and semi-domestic reindeer constitutes wolverines’ most important source of winter food (Haglund, 1966; Myhre & Myrberget, 1975; Magoun, 1987; Landa *et al.*, 1997), and can be found in mountainous areas. Reindeer is one of the ungulate species most sensitive to habitat fragmentation and human disturbance (Cameron *et al.*, 1992; Helle & Särkelä, 1993; Smith *et al.*, 2000; Vistnes & Nellemann, 2001; Vistnes *et al.*, 2001; Nellemann *et al.*, 2003). The sympatric distribution of wolverines with wild and semi-domestic reindeer may therefore indicate that wolverines are vulnerable to indirect loss of habitat (Landa *et al.*, 2000); a result also found in modelling studies in the USA (Carroll *et al.*, 2001; Rowland *et al.*, 2003). Although wolverines have been shown to travel through developed areas and transportation corridors (Landa *et al.*, 1998; Vangen *et al.*, 2001), they apparently locate their home ranges away from human disturbance (undeveloped habitat), and use habitat which provides them with enough shelter and food (alpine shrub land and forest).

Question 3: *How does the spatio-temporal ranging behaviour of female wolverines with dependent cubs change over the season, and how is this related to foraging strategies? [Paper III]*

In a fluctuating environment incorporation of spatio-temporal activity patterns and home range use in resource selection models enhances the biological meaning of behavioural choices animals make along their path. Especially for central place foragers like the wolverine, the nature and strength of the trade-off between providing protection for their dependent cubs and being away searching for food is likely to influence their spatio-temporal movement patterns throughout the summer. Assuming that travel speed (Pyke, 1984) is associated with patch choice, the daily activity pattern of wolverines clearly showed an increase in activity during the night. Whereas in the beginning of the summer cubs are placed at rendezvous sites, towards the end of the summer cubs grow more mobile and independent (Paper IV). The decrease in travel speed over the summer likely indicated a diminishing central place foraging movement pattern. At night wolverines preferred to forage in the lower-lying patches. Apparently, female wolverines are faced with a continuous, but diminishing, trade-off between providing food and shelter for their offspring throughout the summer. Recent studies are providing increasing evidence that boundaries between ecological communities (i.e., ecotones or edge habitats) may support higher densities of many prey species (e.g., Sekgororoane & Dilworth, 1995; Bayne & Hobson, 1998; Côté *et al.*, 2004) and may serve as hotspots for biodiversity (Brown, 2001; Lomolino, 2001; Rickart, 2001; Kark & van Rensburg, 2006). It seems that wolverines utilize this ecotone for foraging. A high abundance of species and high species richness, providing them with a variety of different prey species each having their own peculiarities, could well represent the patches with the highest expected profitability. Landa *et al.* (unpublished data) found that, given the assumption that biomass and productivity generally is higher at lower altitudes, wolverine home range sizes were inversely correlated with altitude within the same region/latitude. This would imply that wolverines living in higher and less optimal habitat would need larger home ranges to support their energetic needs (Macdonald, 1983; Ferguson *et al.*, 2006). This may explain the regional differences in movement patterns (i.e., activity patterns and home range use) we found in our study, and may well signify adaptations to the foraging strategies in reproducing wolverines harmonized to the surroundings they inhabit.

Question 4: *Which spacing strategies (i.e., maternal care) do female wolverines employ to successfully rear their offspring, and how do these activity patterns relate to cub growth and timing of independence? [Paper IV]*

In coping with the trade-off placed upon reproducing females (Paper III), they employ specific spacing strategies and maternal care. The adoption of a denning strategy (Paper V) followed by a more nomadic life style should be expected to allow the cubs to become nearly full-grown and reach independence before the onset of winter. In the parturition and weaning period, female wolverines relied on food caches and spent most of their time together with the cubs. At this time, denning females had a nocturnal daily activity pattern (see also Paper III). The activity pattern of females over the denning period correlated well with cub growth and presumably consumption of food caches. Over the rearing period, the intervening distances between mother and offspring increased significantly and by September, cubs were nearly full-grown and nutritionally independent from their mother. Cubs are likely to be most vulnerable to predation during the period when they are left unattended in the den (March – April), when they have just left the den site in early May (Magoun, 1985; Landa *et al.*, 1997), and when becoming independent in August – September (Vangen et al., 2001). In the parturition and weaning period, rapid growth of cubs and demands of lactation place increased energetic demands on the mother. When the risk of (intra-specific) predation is high for cubs which are left unattended at the den or rendezvous site, the choice of the female to stay away for longer periods might be driven by food depletion (Haglund, 1966; Vander

Wall, 1990; Pasitschniak-Arts & Larivière, 1995; Persson, 2003). The recorded hoarding behaviour is likely offering the female a possibility to spend as much as possible time in the vicinity of her offspring as well as compensating for the high energetic costs of raising cubs (Magoun, 1985; Landa *et al.*, 1997). After den abandonment, the cubs' ability to accompany the mother more and more puts less energetic costs on the mother, and simultaneously optimizes growth, foraging skills, and independence in the cubs. Autumn is the time of nutrimental independence for offspring in many other northern carnivores, birds and mammals. In general, timing of reproductive seasons is determined by availability of food as well as offspring growth and survival. Being solitary, theoretically is disadvantageous and strongly affects the ability to provide food and simultaneously offer protection for their offspring. Within the northern generalist carnivore guild, all the canids (arctic fox *Alopex lagopus*, red fox *Vulpes vulpes* and wolf) produce a higher number of cubs at a much narrower time window than the solitary wolverine. However, the constraints faced by wolverine females solitary raising cubs in relatively oligotrophic environments seems to be counteracted by having food caches, early birth in den sites when cubs are small and altricial, and prolonged maternal care until cubs are full-grown and independent before the onset of winter.

Question 5: *Which topographic elements are crucial to suitability of natal den sites, at which spatial scale are these selected, and can variation in reproductive frequency from different denning localities be related to specific habitat characteristics? [Paper V]*

Compared to other northern large carnivores, wolverines are thought to be more selective about habitat quality (Paper I, Paper II) and particularly sensitive to human disturbance during the natal denning period for reproductive females (Magoun & Copeland, 1998; Heinemeyer *et al.*, 2001). Successful reproduction, and thereby population viability, is therefore likely to be enhanced by the choice of suitable den sites. At a landscape scale, den sites were placed in steep, rugged terrain, facing north to northwest at 1,000 meters above sea level (i.e., just above tree line) and away from human infrastructure. At the site-specific scale, den sites in southern Norway were associated with steep, rugged terrain with bare rock and shrub vegetation, at distance from private roads. At both spatial scales, the overall ruggedness or steepness of the terrain appeared to be an important feature for den sites. Steep and rugged terrain enables wolverines to dig out den sites in snow drifts. It is also possible that steep and rugged terrain, especially when placed farther from human infrastructure, is perceived as providing security from humans or other potentially dangerous carnivores. This appears to be a general pattern for wolverines to prefer steep slopes, ravines or boulder fields (Pulliainen, 1968; Magoun & Copeland, 1998). The avoidance of infrastructure at both scales of wolverine den site selection corroborates well with previous authors who have expressed their concern that wolverines may be especially sensitive to disturbance during the natal denning period (Weaver *et al.*, 1996; Magoun & Copeland, 1998; COSEWIC, 2003). The preferences detected were all selected for at a very fine scale (50 m), indicating that the local requirements for a suitable den site are very stringent. Landa *et al.* (1997) hypothesised that differences in reproductive frequency are likely to be due to differences in habitat quality of the various denning localities. Wolverines are known to have low reproductive rates as compared to similar sized carnivore species. We estimated reproductive frequency from monitoring of denning localities at 0.56, which was similar to reproductive rates of radio-collared wolverines in Scandinavia

(Persson *et al.*, 2006). It is important to bare in mind that we have only examined areas that wolverines have used for reproduction at least once, indicating that all of them are suitable to some degree. There are clearly many areas that are not suitable for wolverines and where wolverines have never settled. However, those areas where wolverine did settle, we found that their reproductive frequency was positively influenced by placement at higher elevation, on gentler slopes and farther from humans (i.e., public roads). This indicates that the distribution of den sites, and possibly successful reproduction, may be partly influenced by direct disturbance or a higher risk of human-caused mortality associated with infrastructure (Thurber *et al.*, 1994; Landa *et al.*, 2000).

Future prospects

This thesis has rendered insight into the spatial ecology of wolverines in Scandinavia at different spatial scales. Scales of investigation influence the processes that guide habitat selection (e.g., foraging dictate patch use whereas landscape configurations affect placement of home ranges) (Boyce, 2006). This means that the appropriate scale (resolution and extent), data sets and models should be used in order to obtain meaningful results. The finest resolution which forms the basis for the spatial extent of movement patterns is the animal’s perception. An animal’s locomotor, visual, audile and olfactory properties influence the perceptual range in which it perceives the landscape (Olden *et al.*, 2004). The wolverine is known to have magnificent olfactory properties (Pasitschniak-Arts & Larivière, 1995), which may well give them a large perceptual range (Olden *et al.*, 2004). The resolution at which selection of habitat is strongest likely reflects the perception a wolverine has of its surroundings. The spatial domains in which a wolverine moves through the landscape should also be further investigated, and can be deduced from analyzing the fractal dimensions of their movement patterns based on snow tracking data (e.g., Nams & Bourgeois, 2004; Nams, 2005). As not all features of the landscape may be perceived in the same way it is important to get a better insight into the hierarchical selectiveness for different resources at different spatial scales (i.e., multi-grain selection, Meyer & Thuiller, 2006). This is especially important for animals with moderate dispersal abilities in habitat fragments embedded in an inhospitable environment (Meyer & Thuiller, 2006), and likely also to hold for animals moving in more than one spatial domain (e.g., moving through its territory while foraging along the way, Nams & Bourgeois, 2004; Nams, 2005); both of which may be applicable to the wolverine. At a larger scale, factors associated with individual establishment are often explored by delineating their home ranges using methods like minimum convex polygons (MCP) or kernels. However, what is often neglected is to detect to which extent the placement of a home range is defined, not by the available habitat inside, but rather by the habitat features around the home range borders. Natural or man-made borders, such as ecotones, rivers and deep valleys, or roads and power lines, may possibly provide better insight into the mechanisms behind wolverines' preferences and territoriality.

A species' habitat preferences and adaptability to changes in the landscape ultimately affects its population dynamics and in the long run even evolutionary trajectories (Hassell & May, 1985; Wiens *et al.*, 1993; Fahrig, 1997; Sutherland, 1998; Russell *et al.*, 2003; Vuilleumier & Metzger, 2005). Especially in fragmented landscapes, ecological processes of wolverines may be affected through reduced habitat connectivity, increased home range sizes, decreased densities, and lower dispersal success. This could then lead to increased energy expenditure associated with rearing young (Gittleman & Harvey, 1982), reduced reproductive rates (Miller, 1993), decreased survival (Persson, 2003), ultimately leading to increased inbreeding and probability of extinction (Fahrig, 1997; Sunquist & Sunquist, 2001; Vuilleumier & Metzger, 2005). However, if the landscape structure is changing faster (i.e., through anthropogenic activities) than the rate of change in behaviour, wolverines will be unable to persist in multiple-use landscapes. Generally, species distribution and habitat use are limited by available resources and adaptive constraints, and regulated by inter- and intra-specific competition and predation. However, large scale processes such as climate change and human activities may well increase resource availability and lift species-specific constraints, thus changing the dynamics of natural communities. This, and the ability of species to react to these changes may, among others, affect trophic and competitive interactions and community structure and homogenize ecosystem transitions, ultimately leading to degraded or simplified ecosystems (Creel *et al.*, 2001; Melian & Bascompte, 2002; Soulé *et al.*, 2003). Also, natural predation by large carnivores not only influences direct mortality in their prey, but also behaviour (i.e., vigilance) and spatial resource use by what is termed ‘the ecology of fear’ (Brown *et al.*, 1999; Ripple & Beschta, 2004). Especially the presence of more predator species in the same region (i.e., a functional guild of large predators) give stability to ecosystem processes (Chapin *et al.*, 1997; Ginsberg, 2001; Melian & Bascompte, 2002; Soulé *et al.*, 2003). How spatial processes affect demography (reproduction, survival, dispersal), intra-guild interactions (with wolf, lynx and red fox), and predator-prey relationships (e.g., wild and domestic reindeer, free-ranging sheep, foraging patches) will thus provide important insights into the population dynamics of the wolverine, which in turn enhances successful conservation and management of this elusive species in the future.

References

Arthur, S.M., Manly, B.F.J., McDonald, L.L., & Garner, G.W. (1996) Assessing habitat selection when availability changes. *Ecology*, **77**, 215-227.

Banci, V. & Harestad, A.S. (1988) Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Annales Zoologici Fennici*, **25**, 265-270.

Bayne, E.M. & Hobson, K.A. (1998) The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed wood forest. *Canadian Journal of Zoology,* **76**, 62-69.

Berger, J. (1999) Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proceedings of the Royal Society of London B*, **266**, 2261-2267.

Boles, B.K. (1977) Predation by wolves on wolverines. *Canadian Field Naturalist*, **19**, 68-69.

Boyce, M.S. (2006) Scale for resource selection functions. *Diversity & Distributions*, **12**, 269-276.

Brown, J.H. (2001) Mammals on Mountainsides: Elevational Patterns of Diversity. *Global Ecology and Biogeography*, **10**, 101-109.

Brown, J.S., Laundre, J.W., & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385-399.

Burkholder, B.L. (1962) Observations concerning wolverine. *Journal of Mammalogy*, **43**, 263-264.

Cameron, R.D., Reed, D.J., Dau, J.R., & Smith, W.T. (1992) Redistribution of calving caribou in response to oil field development on the arctic slope of Alaska. *Arctic*, **45**, 338-342.

Caro, T.M. (1994) *Cheetahs of the Serengeti Plains*. The University of Chicago press, Chicago and London.

Carroll, C., Noss, R.F., & Paquet, P.C. (2001) Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications*, **11**, 961-980.

Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., & Tilman, D. (1997) Biotic control over the functioning of ecosystems. *Science*, **277**, 500-504.

COSEWIC (2003) *COSEWIC assessment and updat status report on the wolverine Gulo gulo in Canada*. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics*, **35**, 113-147.

Crawley, M.J. (2002) *Statistical computing: an introduction to data analysis using S-Plus*. John Wiley & Sons Ltd., Chichester, U.K.

Creel, S. & Creel, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526-538.

Creel, S., Spong, G., & Creel, N. (2001) Interspecific competition and the population biology of extinction-prone carnivores. *Carnivore Conservation* (eds J.L.

Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), Vol. 5, pp. 35-60. Cambridge University Press, Cambridge.

Crooks, K.R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, **16**, 488-502.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature,* **400**, 563-566.

De Solla, S.R., Bonduriansky, R., & Brooks, R.J. (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, **68**, 221-234.

Entwistle, A. & Dunstone, N., eds. (2000) *Priorities for the Conservation of Mammalian Diversity. Has the Panda had its day?* Vol. 3. Cambridge University Press, Cambridge, UK.

Fahrig, L. (1997) Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management*, **61**, 603-610.

Fauchald, P. (1999) Foraging in a Hierarchal Patch System. *The American Naturalist,* **153**, 603-613.

Ferguson, S.H., Higdon, J.W., & Larivière, S. (2006) Does seasonality explain the evolution and maintenance of delayed implantation in the family Mustelidae (Mammalia: Carnivora)? *Oikos*, **114**, 249-256.

Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P., & Ellegren, H. (2004) Colonization history and non-invasive monitoring of a re-established wolverine (*Gulo gulo*) population. *Conservation Biology*, **18**, 676-688.

Ginsberg, J.R. (2001) Setting priorities for carnivore conservation: what makes carnivores different? *Carnivore Conservation. Conservation biology series 5* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), Vol. 5, pp. 498-523. The Zoological Society of London, Cambridge.

Gittleman, J.L. & Harvey, P.H. (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, **10**, 57-63.

Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291-300.

Haglund, B. (1966) De stora rovdjurens vintervanor. *Viltrevy*, **4**, 1-311.

Haight, R.G., Mladenoff, D.J., & Wydeven, A.P. (1998) Modeling disjunct gray wolf populations in semi-wild landscapes. *Comnservation Biology*, **12**, 879-888.

Hassell, M.P. & May, R.M. (1985) From individual behaviour to population dynamics. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 3-32. Blackwell Scientific, Oxford.

Heinemeyer, K.S., Aber, B.C., & Doak, D.F. (2001) *Aerial surveys for wolverine presence and potential winter recreation impacts to predicted wolverine denning habitats in the southwestern Yellowstone ecosystem*, GIS/ISC Laboratory, Dept. of Environmental Studies, University of California, Santa Cruz.

Heithaus, M.R. (2001) Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, **92**, 542-554.

Helle, T. & Särkelä, M. (1993) The effects of outdoor recreation on range use by semi-domesticated reindeer. *Scandinavian Journal of Forest Research*, **8**, 123-133.

Hellgren, E.C. & Maehr, D.S. (1992) Habitat fragmentation and black bears in the eastern United States. *Eastern Workshop Black Bear Management and Research*, **11**, 154-166.

Hilton-Taylor, C. (2000) *2000 IUCN Red List of Threatened Species*. IUCN, Gland/Cambridge, Switzerland/United Kingdom.

Hjermann, D.O. (2000) Analyzing habitat selection in animals without well-defined home ranges. *Ecology*, **81**, 1462-1468.

Holt, R.D. & Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745-764.

Hornocker, M.G. & Hash, H.S. (1981) Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology*, **59**, 1286-1301.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **59**, 1286-1301.

Karanth, K.U. & Sunquist, M.E. (1995) Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*, **64**, 439-450.

Kark, S. & van Rensburg, B.J. (2006) Ecotones: marginal or central areas of transition? *Israel Journal of Ecology & Evolution*, **52**, in press.

Kålås, J.A., Viken, Å., & Bakken, T., eds. (2006) *Norsk Rødliste 2006 - 2006 Norwegian Red List*. Artsdatabanken, Trondheim, Norway.

Landa, A. (1997) *Wolverines in Scandinavia : ecology, sheep depredation and conservation*. Norwegian University of Science and Technology Department of Zoology, Trondheim.

Landa, A., Lindén, M., & Kojola, I. (2000) *Action plan for the conservation of wolverines (Gulo gulo) in Europe*, Report to the Council of Europe Convention on the Conservation of European Wildlife and Natural Habitats. Council of Europe Press, Strasbourg.

Landa, A. & Skogland, T. (1995) The relationship between population density and body size of wolverines *Gulo gulo* in Scandinavia. *Wildlife Biology*, **1**, 165-175.

Landa, A., Strand, O., Linnell, J.D.C., & Skogland, T. (1998) Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology*, **76**, 448-457.

Landa, A., Strand, O., Swenson, J.E., & Skogland, T. (1997) Wolverines and their prey in southern Norway. *Canadian Journal of Zoology*, **75**, 1292-1299.

Legendre, P. (1993) Spatial autocorrelation: Trouble or New Paradigm? *Ecology*, **74**, 1659-1673.

Lima, S.L. & Zollner (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131-135.

Linnell, J.D.C., Løe, J., Okarma, H., Blancos, J.C., Andersone, Z., Valdmann, H., Balciauskas, L., Promberger, C., Brainerd, S., Wabakken, P., Kojola, I., Andersen, R., Liberg, O., Sand, H., Solberg, E.J., Pedersen, H.C., Boitani, L., & Breitenmoser, U. (2002) *The fear of wolves: A review of wolf attacks on humans*, NINA Oppdragsmelding 731, Norwegian Institute for Nature Research.

Linnell, J.D.C., Nilsen, E.B., Lande, U.S., Herfindal, I., Odden, J., Skogen, K., Andersen, R., & Breitenmoser, U. (2005) Zoning as a means of mitigating conflicts with large carnivores: principles and reality. *People and Wildlife, Conflict or Co-existence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), Vol. 9, pp. 162-175. Cambridge University Press, New York.

Lomolino, M.V. (2001) Elevation Gradients of Species-Density: Historical and Prospective Views. *Global Ecology and Biogeography*, **10**, 3-13.

Macdonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379-384.

Maehr, D.S., Kelly, M.J., Bolgiano, C., Lester, T., & McGinnis, H. (2003) Eastern cougar recovery is linked to the Florida panther: Cardoza and Lanlois revisited. *Wildlife Society Bulletin*, **31**, 849-853.

Magoun, A.J. (1985) *Population characteristics, ecology and management of wolverines in northwest Alaska*. PhD Thesis, University of Alaska, Fairbanks, Fairbanks, Alaska.

Magoun, A.J. (1987) Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. *Canadian Field Naturalist*, **191**, 392-397.

Magoun, A.J. & Copeland, J.P. (1998) Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management*, **62**, 1313-1320.

McLoughlin, P.D., Walton, L.R., Cluff, H.D., Paquet, P., & Ramsay, M.A. (2004) Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy*, **85**, 576-580.

Melian, C.J. & Bascompte, J. (2002) Food web structure and habitat loss. *Ecology Letters*, **5**, 37-46.

Meyer, C.B. & Thuiller, W. (2006) Accuracy of resource selection functions across spatial scales. *Diversity & Distributions*, **12**, 288-297.

Miller, S.D. (1993) *Impacts of Increased Hunting Pressure on the Density, Structure and Dynamics of Brown Bear Populations in Alaska's Game Management Unit 13.* Department of Fish & Game, Fairbanks, Alaska.

Myhre, R. & Myrberget, S. (1975) Diet of wolverine (*Gulo gulo*) in Norway. *Journal of Mammalogy*, **56**, 752-757.

Nams, V.O. (2005) Using animal movement paths to measure response to spatial scale. *Oecologia*, **143**, 179-188.

Nams, V.O. & Bourgeois, M. (2004) Fractal analysis measures habitat use at different spatial scales: an example with American marten. *Canadian Journal of Zoology*, **82**, 1738-1747.

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., & Newton, A. (2003) Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation*, **113**, 307-317.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., & Munro, R.H.M. (2002) Modelling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*, **13**, 45-56.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., & Paquet, P.C. (1996) Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, **10**, 949-963.

Novikov, B.V. (1994) The modern state of the population and numbers of the wolverine. *Lutreola*, **3**, 22-27.

Olden, J.D., Schooley, R.L., Monroe, J.B., & Poff, N.L. (2004) Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology*, **73**, 1190-1194.

Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492-508.

Pasitschniak-Arts, M. & Larivière, S. (1995) *Gulo gulo*. *Mammalian Species*, **499**, 1-10.

Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andrén, H., Lindén, M., & Segerström, P. (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildlife Biology*, **5**, 203-211.

Persson, J. (2003) *Population Ecology of Scandinavian Wolverines*. PhD, Swedish University of Agricultural Sciences, UMEÅ.

Persson, J., Landa, A., Andersen, R., & Segerström, P. (2006) Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy*, **87**, 75-79.

Pulliainen, E. (1968) *Breeding biology of the wolverine (Gulo gulo L.) in Finland*, Annales Zoologici Fennici. Department of Agricultural and Forest Zoology, Helsinki.

Pyke, G.H. (1984) Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, **15**, 523-575.

Rettie, W.J. & Messier, F. (2000) Hierarchal habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466-478.

Rickart, E.A. (2001) Elevational Diversity Gradients, Biogegraphy and the Structure of Montane Mammal Communities in the Intermountain Region of North America. *Global Ecology and Biogeography*, **10**, 77-100.

Ripple, W.J. & Beschta, R.L. (2004) Wolves and the ecology of fear: Can predation risk structure ecosystems? *Bioscience*, **54**, 755-766.

Rowland, M.M., Wisdom, M.J., Johnson, D.H., Wales, B.C., Copeland, J.P., & Edelmann, F.B. (2003) Evaluation of landscape models for wolverines in the interior northwest, United States of America. *Journal of Mammalogy*, **84**, 92-105.

Russell, R.E., Swihart, R.K., & Feng, Z. (2003) Population consequences of movement decisions in a patchy landscape. *Oikos*, **103**, 142-152.

Sekgororoane, G.B. & Dilworth, T.G. (1995) Relative Abundance, Richness, and Diversity of Small Mammals at Induced Forest Edges. *Canadian Journal of Zoology*, **73**, 1432-1437.

Selva, N., Jedrzejewska, B., Jedrzejewski, W., & Wajrak, A. (2003) Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). *Ecoscience*, **10**, 303-311.

Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C., & Hervieux, D. (2000) Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Canadian Journal of Zoology*, **78**, 1433-1440.

Soulé, M.E., Estes, J.A., Berger, J., & Del Rio, C.M. (2003) Ecological effectiveness: Conservation goals for interactive species. *Conservation Biology*, **17**, 1238-1250.

Sunquist, M.E. & Sunquist, F.C. (2001) Changing landscapes: consequences for carnivores. *Carnivore conservation. Conservation biology series 5* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), Vol. 5, pp. 399-418. Cambridge University Press, Cambridge.

Sutherland, W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour*, **56**, 801-809.

Swenson, J.E. & Andrén, H. (2005) A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. *People and Wildlife. Conflict of Coexistence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), Vol. 9, pp. 497+xvii. Cambridge University Press, Cambridge, UK.

Swenson, J.E., Gerstl, N., Dahle, B., & Zedrosser, A. (2000) *Action plan for the conservation of the brown bear (Ursus arctos) in Europe*, Report to the Council of Europe Convention on the Conservation of European Wildlife and Natural Habitats T-PVS (2000) 24.

Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R., & Söderberg, A. (1995) The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, **1**, 11-25.

Thurber, J.M., Peterson, R., Drummer, T.D., & Thomasma, S.A. (1994) Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin*, **22**, 61-68.

Vander Wall, S.B. (1990) *Food hoarding in animals*. University of Chicago Press, London.

Vangen, K.M., Persson, J., Landa, A., Andersen, R., & Segerström, P. (2001) Characteristics of dispersal in wolverines. *Canadian Journal of Zoology*, **79**, 1641-1649.

Vistnes, I. & Nellemann, C. (2001) Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management*, **65**, 915-925.

Vistnes, I., Nellemann, C., Jordhøy, P., & Strand, O. (2001) Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biology*, **24**, 531-537.

Vuilleumier, S. & Metzger, R. (2005) Animal dispersal modelling: Handling landscape features and related animal choices. *Ecological Modelling*, **190**, 159-170.

Wabakken, P. (2001) Flerarts- og soneforvaltning i rovdyr-saukonflikten. *Utmarksbeite og store rovdyr. Delrapport 3 fra forskningsprogrammet Bruk og forvaltning av utmark* (eds V. Jaren & J.P. Løvstad), Vol. 3, pp. 61-67. Norges forskningsråd, Oslo.

Weaver, J.L., Paquet, P.C., & Ruggiero, L.F. (1996) Resilience and conservation of large carnivore conservation in North America. *Conservation Biology*, **10**, 964-976.

Weber, W. & Rabinowitz, A. (1996) A global perspective on large carnivore conservation. *Conservation Biology*, **10**, 1046-1054.

Whitman, J.S., Ballard, W.B., & Gardner, C.L. (1986) Home range and habitat use by wolverines in southcentral Alaska. *Journal of Wildlife Management*, **50**, 450-463.

Wiens, J.A., Stenseth, N.C., Van Horne, B., & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., & Getz, W.M. (2003) Trophic facilitation by introduced top predators: gray wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology*, **72**, 909-916.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126-2128.

Paper I

Habitat differentiation within the large carnivore community of Norway's multiple-use landscapes

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Running title: Habitat differentiation in a large carnivore guild

Summary

1. The re-establishment of large carnivores in Norway has led to increased conflicts and the adoption of regional zoning. When planning the future distribution of large carnivores, it is important to consider details of their potential habitat tolerances, and the strength of inter-specific differentiation. Here, we study differentiation in habitat and kill sites within the community of large carnivores in south-eastern Norway.
2. We compared habitat selection of the brown bear, Eurasian lynx, wolf and wolverine, based on radio-tracking data. Differences in choice of kill sites were explored using locations of documented predator-killed sheep. We modelled each species' selection for, and differentiation in, habitat and kill sites on a landscape scale using resource selection functions and multinomial logistic regression. Based on the projected habitat suitability, we estimated the potential numbers that could fit in the study area given the amount of suitable habitat.
3. Although bears, lynx and wolves had overlapping distributions, we found a clear differentiation for all four species in both choices of habitat and kill sites. The presence of bears, wolves and lynx was generally associated with rugged, forested areas at lower elevations, whereas wolverines selected rugged terrain at higher elevations. Whereas one third of the study area was suitable for the three forest species, a mere 5% was suitable for all four large carnivore species.
4. *Synthesis and applications.* Sympatry of the wolverine with the three forest-dwelling carnivore species appears possible due to the availability of mountain ranges and scavenging opportunities. High prey densities, low carnivore densities, decreased dietary overlap and scavenging opportunities have likely led to reduced exploitative exclusion.
5. A geographically differentiated management policy has been adopted in Norway, aimed at conserving viable populations of large carnivores in Scandinavia, while minimizing the

potential for conflicts. Sympatry of viable populations of all four carnivores will be most successful when planning for regional zones of adequate size spanning an elevational gradient. Although regional sympatry enhances the conservation of an intact guild of large carnivores, it may well increase conflict levels and resistance to carnivore conservation locally.

Keywords: habitat and predation patterns, intra-guild competition, species co-existence, elevational zones, carrying capacity

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Introduction

During the last century, habitat fragmentation and increased human pressure have reduced populations of large carnivores throughout the world (Weber & Rabinowitz 1996; Woodroffe 2000; Sunquist & Sunquist 2001). Although large carnivores are able to persist in multiple-use landscapes (e.g., Hellgren & Maehr 1992; Haight, Mladenoff & Wydeven 1998; Maehr *et al.* 2003), many mammalian carnivores possess characteristics that may make them particularly vulnerable to landscape changes (Woodroffe & Ginsberg 1998; Crooks 2002; Sunquist & Sunquist 2001). Carnivore species may react differently to fragmentation however, due to differences in behaviour and ecology (Sunquist & Sunquist 2001; Crooks 2002).

In addition to this, inter-specific interactions may further increase the vulnerability of top predators (Holt *et al.* 1999; Melian & Bascompte 2002). Intra-guild competition is often asymmetrical and may have strong effects on the population dynamics of the subordinate competitor (Holt & Polis 1997; Creel, Spong & Creel 2001). Intra-guild predation may be expected to be fiercer when the predators have a higher dietary or spatial overlap (Heithaus 2001). Apart from direct competition for prey, possible sympatry of multiple carnivore species also depends on interference and intra-guild predation. Linnell & Strand (2000) hypothesized that interference may reduce population growth through temporal and spatial avoidance, changes in foraging efficiency, or direct killing, irrespective of dietary and habitat overlap. Intra-guild competition is thought to be density-dependent and the degree of intra-guild interference is thought to depend on body-size differences (Ruggiero *et al.* 1994; Buskirk 1999). Intra-guild competition and interference may ultimately lead to habitat differentiation (i.e., competitive exclusion). In addition, subordinate predators may also be suppressed in the absence of scavenging opportunities from top predators (Buskirk 1999).

Four species of large carnivores are present in Scandinavia: the brown bear *Ursus arctos* L., grey wolf *Canis lupus* L., Eurasian lynx *Lynx lynx* L. and wolverine *Gulo gulo* L. The conservation of large carnivores in Scandinavia is dependent upon co-existence with humans in a multiple-use landscape. The recovery of carnivore populations, however, has led to increased conflicts. The main causes of conflict are their depredation on semi-domestic reindeer *Rangifer tarandus* L. throughout the year in Fennoscandia, and on free-ranging domestic sheep *Ovis aries* L. during summer, primarily in Norway (Swenson & Andrén 2005). Although most predation on reindeer is caused by wolverines and lynx, all large carnivores in Norway kill free-ranging sheep. This has led to the adoption of a geographically differentiated management policy aimed at conserving viable populations of large carnivores in Scandinavia, while minimizing the potential for conflicts (Wabakken 2001; Ministry of Environment 2003; Linnell *et al.* 2005). When planning the future distribution of large carnivores, it is important to consider details of their potential habitat tolerances, and the strength of differentiation among the four species. The present population goals for large carnivores in Norway are specified for eight management regions (Ministry of Environment

2003; Committee on Energy and Environment 2004). The large carnivore region of Hedmark County, in which the major part of the study area was situated, is the only region that has populations of all four large carnivore species. We analysed data sets of large carnivore habitat use based on radio-telemetry and choice of kill sites based on documented predator-killed free-ranging sheep. Our initial expectation was that bears, wolves and lynx would have broadly similar patterns of habitat selection (forest species). By contrast, the wolverine has traditionally been viewed as a species linked closely to the mountains in Scandinavia, although in recent years they have also colonised more forested habitats (Landa & Skogland 1995; Flagstad *et al.* 2004). We expected that wolverines would be clearly differentiated in choices of habitat and kill sites from the other three species. However, through the effect of intra-guild competition, also the three forest-dwelling carnivore species were expected to show differentiation in habitat use and choice of kill sites.

Materials and methods

STUDY AREA

Norway is the country in mainland Europe with the lowest human population density (approx. 12/km^2) and with large continuous areas of semi-natural landscapes. Despite the low human density, wilderness areas have declined dramatically in the last century through resource extraction (i.e., livestock grazing, hunting, timber logging, including a network of gravel forest roads), infrastructure development (i.e., roads, recreational cabins and hydropower plants), and recreation. Our study area (18,336 km^2) was located in southeast Norway. It consists of ten municipalities in the northern parts of Hedmark County and three bordering municipalities in Oppland County (Fig. 1, inset), and was centred on the lake Storsjøen (latitude 61°27', longitude 11°18'). The river Glomma and the adjacent national highway RV3 run from north to south in the centre of the study area. The landscape is constituted of boreal forests interspersed with low mountain ranges. Areas above treeline, at 900-1,000 m, are mainly found in the west and north of the study area. Infrastructure is mainly found in the south and west of the study area, and in the valley bottoms. All four large carnivore species exist within the study area and the numbers in Hedmark County are estimated by the national large carnivore monitoring programme at 14-24 wolves (3-6 packs or scent-marking pairs), 20-30 wolverines (mainly within the study area) and 50-90 lynx (mainly south of the study area) (Brøseth & Andersen 2004; Brøseth, Odden & Linnell 2004; Wabakken *et al.* 2004). The total number of bears was estimated at 9-13 for southeast Norway (Østlandet) (Swenson *et al.* 2003). The populations of all four species are in the re-colonising stage, with the bear population in particular being dominated by males. The average winter densities of potential large prey species are 0.9/km^2 and 0.8/km^2 for moose *Alces alces* L. and roe deer *Capreolus capreolus* L., respectively (Solberg *et al.* 2003). However, roe deer are distributed less evenly over the area than moose. Other potential ungulate prey species are red deer *Cervus elaphus* L. and wild reindeer. Moreover, semi-domestic reindeer are herded in the north-eastern two municipalities of the study area. Other potential prey species are tetraonids and other bird species, mountain hare *Lepus timidus* L., beaver *Castor fiber* L., red squirrel *Sciurus vulgaris* L., small rodents and insectivores, as well as red fox *Vulpes vulpes* L., badger *Meles meles* L., pine marten *Martes martes* L. and small mustelids, which are all represented within the study area. Throughout the study area, with disjoint distribution and at highly variable densities, free-ranging, and mostly unattended domestic sheep and cattle *Bos taurus* L. are grazed in the forests and low mountain ranges during the summer (June-September) (Zimmermann, Wabakken & Dötterer 2003).

STUDY DESIGN AND SPATIAL SCALE

Distribution, habitat preferences and differentiation among guild members can be investigated with the use of resource selection functions (Johnson *et al.* 2000; Boyce 2006). The scale (i.e., grain/resolution and domain/extent) of investigation in such studies is important, as ecological processes can occur at different spatio-temporal scales, which influence the strength of habitat preferences (Boyce 2006). Inter-specific interactions may affect the space use of sympatric carnivores at various spatial and temporal scales, ranging from delineation of distribution patterns (e.g., Lande *et al.* 2003), landscape-scaled habitat differentiation, to spatio-temporal relationships among carnivores (e.g., Fedriani, Palomares & Delibes 1999). Each of these investigations requires their own type of data. To address differentiation among wide ranging large carnivore species, the resolution need not be very fine; a coarser grain will even out intra-specific spatial heterogeneity at finer resolutions leaving the inter-specific differences under study. However, the extent should be large enough to encompass the regional dynamics of the large carnivore community in the multiple-use landscapes. Our spatially, but not temporally, overlapping data sets (see Table 1 and under “Data sets”) on the large carnivore guild in one specific region of Norway best fit a landscape approach. We therefore chose to study patterns of use on the landscape using a grain of 1 x 1 km resource units (pixels), and investigated habitat differentiation within the large carnivore guild by comparing selection of geographical ranges among the species within the study area (first order selection, Johnson 1980).

BACKGROUND MAPS

Habitat differentiation among the four large carnivore species was investigated using seven habitat covariates: elevation, terrain ruggedness, percentage tree cover, distance to the forest edge, and distance to the nearest public road, private road and building. Elevation was obtained from a 100 x 100 m Digital Elevation Model (DEM; Norwegian Mapping Authority). Terrain ruggedness was calculated by taking the square root of the sum of squared differences in elevation of each pixel in the 100 x 100 m DEM to its 8 neighbours, thus rendering a terrain ruggedness index (Riley, DeGloria & Elliot 1999). Percentage tree cover was obtained from a MODIS map (Hansen *et al.* 2002). The four distance measures were obtained from digital 1:50,000 topographic maps (Norwegian Mapping Authority). All maps were finally converted into overlapping 1 x 1 km pixel grids.

DATA SETS

The study was based on radio-tracking data gathered from research projects on large carnivores (Table 1). Only functionally independent locations (i.e., with at least 24 hours between locations) were used so as to minimise autocorrelation and reduce the difference between GPS and VHF data (i.e., several positions per day versus up to one position per day, respectively). As the data were collected during different time periods, this study renders insight into spatial but not necessarily temporal sympatry of the four large carnivores.

Locations of documented predator-killed sheep falling within the boundaries of the study area from the period 1994-2004 were used as an independent data set for validation of the modelled results (see Fig. 1). In order to receive compensation for losses suffered by predators, it is economically important to the owners of free-ranging sheep to intensively search for carcasses throughout the summer grazing season (~100 days/yr). Carcasses are examined by trained personnel of the State Nature Inspectorate, who record the location and determine the species of the predator, based on well-documented species-specific kill patterns through autopsy (Landa 1999). Although the locations of sheep kills found are likely to be biased towards ease of detection, both with respect to sheep grazing preferences and human observability (e.g., proximity to roads, open areas), this bias can be expected to be irrespective of carnivore species.

MODELLING AND STATISTICAL ANALYSES

For each species we transformed the set of radio-tracking locations into presence maps, where each 1 x 1 km pixel indicated whether it included one or more locations (Fig. 1). This avoids unwanted spatial autocorrelation and pseudo-replication effects. We expected a pseudo-replication effect for the members of the two wolf packs, while travelling together. Also several animals were tracked over several years, possibly rendering the same effect. We thereafter modelled each species' habitat selection on a landscape scale following a resource selection function framework (Manly *et al.* 2002), using logistic regression models:

$$w(x) = \exp(\beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + ... + \beta_n \cdot X_n) \qquad \text{eqn 1}$$

with β_i as the model coefficient of the i^{th} of n habitat covariates, X_i. Availability was considered to be the same for all species, and was based on a 'presence' map generated from a dataset of 2,500 points randomly spread throughout the study area following the same procedure as mentioned above. Because the focus of this study was to elucidate habitat differentiation among large carnivores, we present the full models only.

The outcome of each resource selection function was projected to the entire study area, producing probability maps for each species using equation 2 (Manly *et al.* 2002).

$$\pi = \frac{\exp(\beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + ... + \beta_n \cdot X_n)}{1 + \exp(\beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + ... + \beta_n \cdot X_n)} \qquad \text{eqn 2}$$

Here we assumed that the intra-specific variation was insignificant compared to the inter-specific variation. Also, we assumed that the individuals used to calculate the probability maps represented the resource selection of the species. The mean probability over each map measured the general suitability of the study area for each species relative to the other species. The standard deviation gave a measure for the habitat breadth within the study area. In order to get a better insight into the scale of our study area versus necessary scales for regional zoning, we extrapolated the number of tracked individuals to possible potential numbers that could fit in the entire study area given the amount of suitable habitat. For each species *i*, we estimated the potential number N_i for the entire study area as follows:

$$N_i = \frac{A_{\bar{p}}}{a} \cdot n_i \qquad \text{eqn 3}$$

where $A_{\bar{p}}$ is the number of map pixels with a probability higher than the mean probability $\bar{p}$ within the presence pixels (Fig. 1); a is the number of presence pixels; and n_i is the number of tracked individuals (c.f., Boyce & McDonald 1999). The locations of documented predator-killed sheep were plotted on the probability maps for each species, to see how well this independent data source fit the maps. We also assessed choice of kill sites relative to used habitat (i.e., presence pixels) by employing resource selection functions.

We estimated the overall strength of differentiation among species both in habitat use and choice of kill sites by calculating the multivariate distance over the standardized resource selection functions coefficients. Standardized coefficients allow comparisons of the relative influence of resources on habitat use, regardless of the measurement scale quantifying the resource (Zar 1999; Marzluff *et al.* 2004). The standardized coefficients for each resource covariate β_i' were estimated as:

$$\beta_i' = \hat{\beta}_i \frac{S_{X_i}}{S_{resp}} \qquad \text{eqn 4}$$

where $\hat{\beta}_i$ is the maximum likelihood estimate of the coefficient for resource i; S_{X_i} is the standard deviation of the values of resource i; and S_{resp} is the estimate of the standard deviation of the response values. The standardized standard errors of the coefficients S_i' were calculated in a similar fashion. The multivariate distance between two species j and k was calculated as:

$$D_{jk} = -\left(\sum_{i=1}^{n} (\beta_{ij}' - \beta_{ik}')^2 \right)^{1/n} + 1 \qquad \text{eqn 5}$$

We incorporated the uncertainty from the resource selection functions by calculating the average multivariate distances from 1,000 iterated random draws from a distribution with the mean β_i' and standard error S_i'. The multivariate distance D_{jk} rendered a number between –1 and +1 for totally differentiated and identical habitat selection, respectively. Finally, we performed multinomial logistic regression on the presence data to investigate how the species were differentiated; for which covariates they differed, and how strongly. The species were taken as a categorical dependent variable, taking each species as a reference category in an iterative way. Thus, each unique species combination could be assessed. To investigate possible differences in choice of kill sites, the locations of predator-killed sheep were compared using the same approach.

Results

HABITAT USE AND CHOICE OF KILL SITES

The resource selection functions for bears, wolves and lynx indicated that the presence of these species was generally associated with rugged, forested areas at lower elevations, and relatively close to private roads (Table 2). Of these species, lynx preferred the lowest elevations, the densest forests, and kept closest to roads (Table 2, Table S1 in Supplementary Material). Wolverines on the other hand, selected rugged terrain at higher elevations and far from human infrastructure. They did not show any selection for tree cover. The probability maps for each species, based on the presented resource selection functions, are given in Fig. 2.

Kill sites of documented predator-killed sheep were for all four species found in more open terrain, farther from the forest edge and closer to private roads compared to their habitat use (Table 3), indicative of the expected bias of sheep grazing preferences and human observability. Whereas wolves killed sheep at lower elevations; kill sites for the other three species were generally found at higher elevations. The three forest-dwelling species killed sheep in less rugged terrain; no such effect was found for the wolverine. All species, except lynx, killed sheep farther from public roads.

PATTERNS OF INTRA-GUILD DISTRIBUTION

The wolf had the highest mean probability of presence in the study area; indicating that the study area was most suitable for wolves when considering habitat, given our data (Table 4). The lynx had the widest habitat breadth as measured by its high standard deviation, followed by the wolf. The wolverine and brown bear, on the other hand, had narrow habitat breadths and relatively low mean probabilities. The mean probabilities over the presence pixels for the brown bear, wolf, lynx and wolverine were clearly higher than the mean for the entire map (0.5, 0.7, 1.1 and 1.1 SD higher, respectively); indicating that they used the more suitable areas (Table 4). Also, kill sites of wolves, lynx and wolverines were found in more suitable areas (0.6, 0.8 and 0.9 SD higher, respectively). However this effect was not found in kill sites of bears (0.1 SD over the mean). Still, between 50 to 80% of all kill sites were found in pixels with a probability over the mean.

Whereas 22% of the study area was not suitable for any of the species (i.e., a pixel was defined as suitable when the pixel probability was higher than the mean probability for the entire study area); 26% was suitable for one of the four species. Sympatry was possible, given the results of our analyses, in 17%, 30% and 5% of the study area for two, three, or all four species, respectively. The high percentage for three species follows the high overlap in distribution for the three forest-dwelling species; the brown bear, wolf and lynx (33%; see also Fig. 2). The estimated potential numbers for the study area indicated higher numbers of wolf packs, lynx and bears than are now present in the study area (Table 4). The projected potential number of wolverines was similar to the approximate numbers at present.

DIFFERENTIATION IN HABITAT AND KILL SITES

Overall, wolverines differed in their habitat use compared to the three forest-dwelling carnivore species (Table 5). Also the brown bear, wolf and lynx had a slight differentiation in habitat use; none was found between wolf and lynx. Whereas wolverine presence was most probable in the more mountainous northwest of the study area, the presence of the other three species was more distributed in the south and along the Glomma Valley running from north to south in the centre of the study area (Fig. 2). The overall differentiation in choice of kill sites showed a clear difference for wolverine compared to the three forest-dwelling species; which, except for the brown bear – lynx, killed sheep in similar habitat (Table 5).

The multinomial logistic regression indicated a clear differentiation in use of habitat covariates among the four species (Table 6). The differences among species explained more than 27% of the variation in habitat selection (Nagelkerke $R^2 = 0.276$). The brown bear was found in less rugged terrain than the other three species. The strongest differentiation in preference was found for elevation. Lynx were found at the lowest elevations, followed in rising elevation by wolves, bears and wolverines (Table 6, Table S1). Also, a clear effect in differentiation was found for tree cover and distance to private roads. The lynx preferred pixels with a higher percentage of tree cover, and closer to private roads than the brown bear and wolf. The wolverine was found in more open areas far from private roads. The wolf and wolverine stayed farther from forest edges than the lynx and brown bear, but differentiated most concerning proximity to public roads.

The multinomial logistic regression on the locations of predator-killed sheep indicated a clear differentiation in habitat among species (Table 6). The differences among species explained more than 50% of the variation in kill site selection (Nagelkerke $R^2 = 0.518$). As for the differentiation in habitat, elevation of kill sites had the strongest differentiating and similar effect; except for the wolf – wolverine. For these two species ruggedness at the kill sites differed most. Lynx and wolverines killed sheep in more rugged terrain than bears and wolves. Wolverines killed sheep in more open areas, whereas bears chose more forested sites. Wolverine also stayed farther from forest edges and public roads than the other species. Proximity to private roads mainly had a differentiating effect on the forest species.

Discussion

The results from this study indicate that the three forest-dwelling large carnivore species, the lynx, wolf and brown bear had similar habitat preferences. All three species selected rugged, forested areas at lower elevations. In contrast, the wolverine clearly distinguished itself from the other three species. Wolverines selected open, rugged terrain at higher elevations. Also, they chose to kill sheep in similar terrain, but farther from infrastructure. This result fits well with the perception that the wolverine is a carnivore of remote alpine regions (Carroll, Noss & Paquet 2001; Rowland *et al.* 2003; May *et al.* 2006). Although intra-guild predation on wolverines has been documented (Burkholder 1962; Boles 1977; Hornocker & Hash 1981; Magoun & Copeland 1998), wolverines may also be positively affected by the scavenging opportunities that other large carnivores provide (Magoun 1987; Novikov 1994; Landa & Skogland 1995; Landa *et al.* 1997). The wolf is likely to be least affected by intra-guild aggression; it may rather instigate it (i.e., intra-guild predator, Palomares & Caro 1999). Wolves may furthermore facilitate other species, like the wolverine, with scavenging opportunities (Selva *et al.* 2003; Wilmers *et al.* 2003). Within the study area, sympatry of the wolverine with the three forest-dwelling carnivore species appears to depend on the availability of mountain ranges as a spatial refuge (May *et al.* 2006). However, sympatry may also be enhanced by the presence of wolves to provide scavenging opportunities (Landa & Skogland 1995; van Dijk *et al.* unpublished data).

Despite their similar potential distribution patterns, the three forest-dwelling species had clear differences in choice of habitat and kill sites. As expected the latter was biased towards more open areas closer to private roads, irrespective of carnivore species, but this did not affect our results on differentiation among species. Bears preferred less rugged and high-lying terrain than wolves and lynx, and chose more forested kill sites. However, although they may benefit to some extent from the presence of other predators through increased scavenging opportunities (MacNulty, Varley & Smith 2001; Smith, Peterson & Houston 2003), fierce exploitative competition is not likely to be of significance because of their omnivorous diet (Dahle *et al.* 1998). It should, however, also be taken into account that densities of both bears and wolves were very low in the study area at the time. Our study showed that wolves and lynx differed least in habitat use. Still, lynx used denser forests at low elevations. Lynx killed sheep in more rugged terrain at higher elevations than wolves; which may reflect differences in hunting techniques (i.e., stalking versus chase hunt), different habitat preference during hunting and avoidance of intra-guild predation. Also, lynx prey mainly on roe deer and small game (Odden, Linnell & Andersen 2006) in our study area, whereas wolves primarily feed on moose (Sand *et al.* 2005). It is therefore likely that high prey densities, low large carnivore densities (due to management actions) and decreased dietary overlap have led to a situation with reduced exploitative exclusion (c.f., Holt & Polis 1997; Heithaus 2001).

In a broader regional context our study area encompasses similar habitat/land use compositions and prey densities as can be found in large stretches of southern Norway and central Sweden, and has a carnivore management regime comparable to other regions in Norway. The spatial extent of regional planning depends on the scale at which population processes are occurring. Our estimates for possible potential numbers of large carnivores that would fit inside the entire study area may render insight into the minimum area required for viable populations, and scale of regional zoning. The potential numbers rendered from this study have, however, to be interpreted as a thought experiment. These numbers merely present an extrapolation of suitable areas to the study area and did not take into account species-specific population dynamics or habitat configurations (e.g., turnover, home range overlap, density-dependent home range sizes, habitat fragment sizes and connectivity; Boyce & McDonald 1999). Also, the brown bear in Norway is at the western edge of an expanding range, with relatively fewer females than in more central parts of the population (Swenson, Sandegren & Söderberg 1998). Because the study area is situated in-between two genetically isolated wolverine populations (Flagstad *et al.* 2004), population viability will be much enhanced if these two populations are allowed to connect (May *et al.* unpublished data).

To explain present distributions, habitat preferences and differentiation among Scandinavian large carnivores, historical management and the role of humans as a top predator in these multiple-use ecosystems should not be underestimated. The main reason for the decline in large carnivore populations in Scandinavia was human-induced mortality caused by (over)exploitation, persecution because of livestock/game conflicts, and fear (Swenson *et al.* 1995; Linnell *et al.* 2002; Linnell *et al.* 2005). The current forest-dominated distribution of bears in Scandinavia is based on re-colonization from a few remnant populations that survived in remote areas in Sweden (Swenson *et al.* 1995). Similarly, centuries of heavy persecution of wolverines all over Norway until 30 years ago may partly explain the habitat preferences and more remote distribution of wolverines found at present (Landa *et al.* 2000; May *et al.* 2006). Although the wolf was functionally extinct in the late 1960's, after decades of intensive persecution, they have now re-established in south-central Scandinavia (Wabakken *et al.* 2001; Vilà *et al.* 2003). After having been reduced to very low levels in the mid-20th century due to unregulated hunting and high bounties, changes in management have led to a recovery of lynx population in Scandinavia (Andrén *et al.* 2002).

Although nearly one third of the study area was suitable for sympatry of the three forest species, a mere 5% was suitable for all four species. Successful regional zoning of all four carnivores may therefore rely on establishing zones spanning an elevational gradient. Also, the estimated potential numbers indicate that regional zones should encompass more suitable habitat than was available within the study area. Zoning of all four species may, however, enhance the conservation of an intact guild of large carnivores in the boreal forest ecosystem (Wabakken 2001). On the other hand, fostering sympatry of all four species may well increase conflict levels and resistance to carnivore conservation locally (Wabakken 2001; Linnell *et al.* 2005). These conflicts may be reduced by discouraging extensive sheep husbandry (Zimmermann, Wabakken & Dötterer 2003; Milner *et al.* 2005), employing effective preventive and mitigation measures required for adequate compensation schemes, promoting different lifestyles and livelihood (e.g., ecotourism and outdoor recreation) and also allowing for limited control (Linnell *et al.* 2005; Swenson & Andrén 2005). However, the social context (non-material nature) of many of the large carnivore conflicts in Norway should never be forgotten (Skogen 2003). Our study results may hopefully provide guidance to managers attempting to design regional-scale zoning to facilitate recovery of large carnivores on the Scandinavian Peninsula.

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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 *Lynx lynx* population size from censuses of family groups. *Wildlife Biology*, **8**, 299-306.

Boles, B.K. (1977) Predation by wolves on wolverines. *Canadian Field Naturalist*, **19**, 68-69.

Boyce, M.S. (2006) Scale for resource selection functions. *Diversity & Distributions*, **12**, 269-276.

Boyce, M.S. & McDonald, L.L. (1999) Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution*, **14**, 268-272.

Brøseth, H. & Andersen, R. (2004) *Yngleregistreringer av jerv i Norge i 2004*, NINA Minirapport 016. Norwegian Institute for Nature Research, Trondheim.

Brøseth, H., Odden, J., & Linnell, J.D.C. (2004) *Minimum antall familiegrupper, bestandsestimat og bestandsutvikling for gaupe i Norge i 2004*, NINA Minirapport 073. Norwegian Institute for Nature Research, Trondheim.

Burkholder, B.L. (1962) Observations concerning wolverine. *Journal of Mammalogy*, **43**, 263-264.

Buskirk, S.W. (1999) Mesocarnivores of Yellowstone. *Carnivores in Ecosystems: The Yellowstone Experience* (eds T.W. Clark, A.P. Curlee, S.C. Minta & P.M. Kareiva), pp. 429+xii. Yale University Press, New Haven/London.

Carroll, C., Noss, R.F., & Paquet, P.C. (2001) Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications*, **11**, 961-980.

Committee on Energy and Environment (2004) *Innstilling fra energi- og miljøkomiteen om rovvilt i norsk natur*, Inst.S.nr.174 (2003-2004). Stortinget, 7th of May 2004, Oslo.

Creel, S., Spong, G., & Creel, N. (2001) Interspecific competition and the population biology of extinction-prone carnivores. *Carnivore conservation* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 35-60. Cambridge University Press, Cambridge.

Crooks, K.R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, **16**, 488-502.

Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E., & Sandegren, F. (1998) The diet of brown bears in central Scandinavia: effects of access to free-ranging domestic sheep. *Wildlife Biology*, **4**, 147-158.

Fedriani, J.M., Palomares, F. & Delibes, M. (1999) Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, **121**, 138-48.

Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P., & Ellegren, H. (2004) Colonization history and non-invasive monitoring of a re-established wolverine (*Gulo gulo*) population. *Conservation Biology*, **18**, 676-688.

Haight, R.G., Mladenoff, D.J., & Wydeven, A.P. (1998) Modeling disjunct gray wolf populations in semi-wild landscapes. *Conservation Biology*, **12**, 879-888.

Hansen, M.C., DeFries, R.S., Townsend, J.R.G., Sohlberg, R., Dimiceli, C., & Carroll, M. (2002) Towards an operational MODIS continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. *Remote sensing of environment*, **83**, 303-319.

Heithaus, M.R. (2001) Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, **92**, 542-554.

Hellgren, E.C. & Maehr, D.S. (1992) Habitat fragmentation and black bears in the eastern United States. *Eastern Workshop Black Bear Management and Research*, **11**, 154-166.

Holt, R.D., Lawton, J.H., Polis, G.A., & Martinez, N.D. (1999) Trophic rank and the species-area relationship. *Ecology*, **80**, 1495-1504.

Holt, R.D. & Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745-764.

Hornocker, M.G. & Hash, H.S. (1981) Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology*, **59**, 1286-1301.

Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L., & Kie, J.G. (2000) Resource selection and spatial separation of mule deer and elk during spring. *Journal of Wildlife Management*, **64**, 685-697.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **59**, 1286-1301.

Landa, A. (1999) *Spor og tegn. Et hefte til hjelp i bestemmelse av store rovdyr*. NINA•NIKU, Norwegian Institute for Nature Research, Trondheim.

Landa, A., Linnell, J.D.C., Swenson, J.E., Røskaft, E., & Moskness (2000) Conservation of Scandinavian wolverines in ecological and political landscapes. *Mustelids in a modern world: conservation aspects of small carnivore-human interactions* (ed H.I. Griffiths), pp. 1-20. Backhuys Publishers, Leiden, Netherlands.

Landa, A. & Skogland, T. (1995) The relationship between population density and body size of wolverines Gulo gulo in Scandinavia. *Wildlife Biology*, **1**, 165-175.

Landa, A., Strand, O., Swenson, J.E., & Skogland, T. (1997) Wolverines and their prey in southern Norway. *Canadian Journal of Zoology*, **75**, 1292-1299.

Lande, U.S., Linnell, J.D.C., Herfindal, I., Salvatori, V., Brøseth, H., Andersen, R., Odden, J., Andrén, H., Karlsson, J., Willebrand, T., Persson, J., Landa, A., May, R., Dahle, B. & Swenson, J. (2003) *Utredninger i forbindelse med ny rovvlitmelding. Potensielle* *leveområder for store rovdyr i Skandinavia: GIS-analyser på et økoregionalt nivå*, NINA Fagrapport 64. Norwegian Institute for Nature Research, Trondheim.

Linnell, J.D.C., Løe, J., Okarma, H., Blanco, J.C., Andersone, Z., Valdmann, H., Balciauskas, L., Promberger, C., Brainerd, S., Wabakken, P., Kojola, I., Andersen, R., Liberg, O., Sand, H., Solberg, E.J., Pedersen, H.C., Boitani, L., & Breitenmoser, U. (2002) *The fear of wolves: A review of wolf attacks on humans*, NINA Oppdragsmelding 731, Norwegian Institute for Nature Research, Trondheim.

Linnell, J.D.C., Nilsen, E.B., Lande, U.S., Herfindal, I., Odden, J., Skogen, K., Andersen, R., & Breitenmoser, U. (2005) Zoning as a means of mitigating conflicts with large carnivores: principles and reality. *People and Wildlife, Conflict or Co-existence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), Vol. 9, pp. 162-175. Cambridge University Press, New York.

Linnell, J.D.C. & Strand, O. (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity & Distributions*, **6**, 169-176.

MacNulty, D.R., Varley, N., & Smith, D.W. (2001) Grizzly Bear, *Ursus arctos*, usurps Bison calf, *Bison bison*, captured by Wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. *Canadian Field-Naturalist*, **115**, 495-498.

Maehr, D.S., Kelly, M.J., Bolgiano, C., Lester, T., & McGinnis, H. (2003) Eastern cougar recovery is linked to the Florida panther: Cardoza and Lanlois revisited. *Wildlife Society Bulletin*, **31**, 849-853.

Magoun, A.J. (1987) Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. *Canadian Field Naturalist*, **191**, 392-397.

Magoun, A.J. & Copeland, J.P. (1998) Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management*, **62**, 1313-1320.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second edition*. Kluwer Press, New York, New York, USA.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P. & Handcock, M.S. (2004) Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology*, **85**, 1411-1427.

May, R., Landa, A., Dijk, J., van, & Andersen, R. (2006) Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. *Wildlife Biology*, **12**, 285-295.

Melian, C.J. & Bascompte, J. (2002) Food web structure and habitat loss. *Ecology Letters*, **5**, 37-46.

Milner, J.M., Nilsen, E.B., Wabakken, P. & Storaas, T. (2005) Hunting moose or keeping sheep? – Producing meat in areas with carnivores. *Alces*, **41**, 49-61.

Ministry of Environment (2003) *Rovvilt i norsk natur*, Stortingsmelding nr. 15 (2003-2004). Trondheim.

Novikov, B.V. (1994) The modern state of the population and numbers of the wolverine. *Lutreola*, **3**, 22-27.

Odden, J., Linnell, J.D.C. & Andersen, R. (2006) Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of south-eastern Norway: the relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research*, **52**, 237-244.

Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492-508.

Riley, S.J., DeGloria, S.D., & Elliot, R. (1999) A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, **5**, 23-27.

Rowland, M.M., Wisdom, M.J., Johnson, D.H., Wales, B.C., Copeland, J.P., & Edelmann, F.B. (2003) Evaluation of landscape models for wolverines in the interior northwest, United States of America. *Journal of Mammalogy*, **84**, 92-105.

Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., & Zielinski, W.J. (1994) *The scientific basis for conserving forest carnivores: American marten, fisher, lynx and wolverine in the western United States*, General Technical Report RM-254. USDA Forest Service, Fort Collins, CO.

Sand, H., Zimmermann, B., Wabakken, P., Andrén, H. & Pedersen, H.C. (2005) Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, **33**, 914-925.

Selva, N., Jedrzejewska, B., Jedrzejewski, W., & Wajrak, A. (2003) Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). *Ecoscience*, **10**, 303-311.

Skogen, K. (2003) Adapting adaptive management to a cultural understanding of land use conflicts. *Society and Natural Resources*, **16**, 435-450.

Smith, D.W., Peterson, R.O., & Houston, D.B. (2003) Yellowstone after wolves. *BioScience,* **53**, 330-340.

Solberg, E.J., Sand, H., Linnell, J.D.C., Brainerd, S.M., Andersen, R., Odden, J., Brøseth, H., Swenson, J., Strand, O., & Wabakken, P. (2003) *Utredninger i forbindelse med ny rovviltmelding. Store rovdyrs innvirkning på hjorteviltet i Norge: Økologiske prosesser og konsekvenser for jaktuttak og jaktutøvelse*, NINA fagrapport 63. Norwegian Institute for Nature Research, Trondheim.

Sunquist, M.E. & Sunquist, F. (2001) Changing landscapes: consequences for carnivores. *Carnivore Conservation. Conservation biology series 5* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), Vol. 5, pp. 39-418. The Zoological Society of London, Cambridge.

Swenson, J., Dahle, B., Arnemo, J.M., Brunberg, S., Hustad, H., Nerheim, E., Sandegren, F., Solberg, K.H., & Söderberg, A. (2003) *Utredninger i forbindelse med ny rovvlitmelding. Status og forvaltning av brunbjørnen i Norge*, NINA fagrapport 60. Norwegian Institute for Nature Research, Trondheim.

Swenson, J.E. & Andrén, H. (2005) A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. *People and Wildlife. Conflict of Coexistence?* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), Vol. 9, pp. 497+xvii. Cambridge University Press, Cambridge, UK.

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**, 819-826.

Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R., & Söderberg, A. (1995) The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, **1**, 11-25.

Vilà, C., Sundquist, A.-K., Flagstad, Ø., Seddon, J., Björnefeldt S., 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 B*, **270**, 91-97.

Wabakken, P. (2001) Flerarts- og soneforvaltning i rovdyr-saukonflikten. *Utmarksbeite og store rovdyr. Delrapport 3 fra forskningsprogrammet Bruk og forvaltning av utmark* (eds V. Jaren & J.P. Løvstad), Vol. 3, pp. 61-67. Norges forskningsråd, Oslo.

Wabakken, P., Aronsson, Å., Sand, H., Rønning, H., & Kojola, I. (2004) *Ulv i Skandinavia. Statusrapport for vinteren 2002-2003*. Høgskolen i Hedmark, Hedmark.

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**, 710-725.

Weber, W. & Rabinowitz, A. (1996) A global perspective on large carnivore conservation. *Conservation Biology*, **10**, 1046-1054.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M. (2003a) Trophic facilitation by introduced top predators: gray wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology*, **72**, 909-916.

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**, 2126-2128.

Zar, J.H. (1999) *Biostatistical analysis. Fourth edition.* Prentice Hall Inc., Upper Saddle River, New Jersey.

Zimmermann, B., Wabakken, P., & Dötterer, M. 2003. Brown bear-livestock conflicts in a bear conservation zone in Norway: are cattle a good alternative to sheep? *Ursus*, **14**, 72-83.

Table 1. Sampling statistics of the radio-tracked large carnivores in the southeast Norwegian study area.

	Brown bear	**Wolf**	**Lynx**	**Wolverine**
Collection period	1988 – 2004	2001 – 2005	1995 – 2002	2003 – 2004
Collection methods (type of collars)	VHF, GPS	GPS	VHF, GPS	GPS
Number of individuals	20	4*	32	4
females	5	2	19	3
males	15	2	13	1
Individuals per year (± SD)	4.3 ± 1.5	2.6 ± 0.9	10.6 ± 7.4	3.5 ± 0.7
Total independent fixes	3,035	2,780	4,920	453
Number of fixes per individual (± SD)	152 ± 255	498 ± 305	154 ± 129	227 ± 88
Number of presence pixels (Fig. 1)	1,183	874	2,063	265

* two alpha pairs of two packs

Table 2. Resource selection functions for four carnivore species in southeast Norway. For each model, presence data was compared with 2,311 randomly selected pixels throughout the study area. Below each species the Nagelkerke R^2 for the model is given.

Species	Covariates	ß	SE	Wald	P
Brown bear	Intercept	-1.414	0.230	37.892	0.000
$R^2 = 0.139$	Elevation	$-4.9E^{-4}$	$2.6E^{-4}$	3.545	0.060
	Ruggedness	$5.2E^{-3}$	$1.4E^{-3}$	13.157	0.000
	Tree cover	$2.3E^{-2}$	$2.8E^{-3}$	71.211	0.000
	Distance to forest edge	$-4.8E^{-4}$	$1.1E^{-4}$	17.765	0.000
	Distance to public road	$-2.3E^{-5}$	$1.5E^{-5}$	2.178	0.140
	Distance to private road	$-3.2E^{-4}$	$6.2E^{-5}$	25.618	0.000
	Distance to building	$5.0E^{-4}$	$6.3E^{-5}$	62.680	0.000
Wolf	Intercept	-0.533	0.219	5.926	0.015
$R^2 = 0.129$	Elevation	$-2.0E^{-3}$	$2.7E^{-4}$	53.142	0.000
	Ruggedness	$8.0E^{-3}$	$1.4E^{-3}$	30.657	0.000
	Tree cover	$1.2E^{-2}$	$2.7E^{-3}$	20.373	0.000
	Distance to forest edge	$-9.6E^{-6}$	$1.0E^{-4}$	0.009	0.926
	Distance to public road	$3.6E^{-5}$	$1.7E^{-5}$	4.811	0.028
	Distance to private road	$-2.7E^{-4}$	$6.5E^{-5}$	17.104	0.000
	Distance to building	$1.9E^{-4}$	$7.3E^{-5}$	6.723	0.010
Lynx	Intercept	0.702	0.176	15.928	0.000
$R^2 = 0.378$	Elevation	$-3.4E^{-3}$	$2.4E^{-4}$	201.811	0.000
	Ruggedness	$9.7E^{-3}$	$1.4E^{-3}$	49.494	0.000
	Tree cover	$2.4E^{-2}$	$2.2E^{-3}$	121.845	0.000
	Distance to forest edge	$1.8E^{-4}$	$1.2E^{-4}$	2.379	0.123
	Distance to public road	$1.9E^{-6}$	$1.7E^{-5}$	0.013	0.910
	Distance to private road	$-3.8E^{-4}$	$7.9E^{-5}$	22.807	0.000
	Distance to building	$-1.5E^{-4}$	$7.1E^{-5}$	4.410	0.036
Wolverine	Intercept	-4.412	0.477	85.684	0.000
$R^2 = 0.142$	Elevation	$2.7E^{-3}$	$4.8E^{-4}$	31.082	0.000

	Ruggedness	$5.4E^{-3}$	$2.4E^{-3}$	4.978	0.026
	Tree cover	$2.3E^{-3}$	$5.7E^{-3}$	0.157	0.692
	Distance to forest edge	$6.0E^{-5}$	$9.4E^{-5}$	0.414	0.520
	Distance to public road	$-1.5E^{-4}$	$2.5E^{-5}$	36.581	0.000
	Distance to private road	$-2.2E^{-6}$	$7.7E^{-5}$	0.001	0.978
	Distance to building	$4.5E^{-4}$	$9.5E^{-5}$	21.945	0.000

Table 3. Comparison between habitat use and kill sites of documented predator-killed sheep in southeast Norway. The Wald statistics represent the strength of selection for kill sites relative to habitat used; the sign indicates the direction of the effect. One, two or three asterisks indicate $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively.

	Brown bear	**Wolf**	**Lynx**	**Wolverine**
Intercept	-7.291^{***}	-1.667	-6.723^{***}	-2.412^{*}
Elevation	5.707^{***}	-3.150^{**}	4.213^{***}	1.861
Ruggedness	-6.605^{***}	-6.215^{***}	-4.814^{***}	1.860
Tree cover	-3.268^{**}	-5.807^{***}	-6.704^{***}	-1.558
Distance to forest edge	11.628^{***}	10.251^{***}	12.713^{***}	8.370^{***}
Distance to public road	2.399^{*}	5.265^{***}	-5.929^{***}	7.187^{***}
Distance to private road	-0.934	-7.137^{***}	0.128	-4.837^{***}
Distance to building	-6.216^{***}	-5.068^{***}	-9.513^{***}	-4.543^{***}

Table 4. Statistics for the probability maps and kill sites of four carnivore species in southeast Norway, both for the entire maps shown in Fig. 2 and a subset of this for the presence pixels and kill sites as shown in Fig. 1.

	Brown bear	***Wolf***	***Lynx***	***Wolverine***
Statistics habitat use				
mean probability map (± SD)	0.211 ± 0.115	0.246 ± 0.128	0.368 ± 0.272	0.102 ± 0.086
mean presence pixels only (± SD)	0.270 ± 0.103	0.329 ± 0.127	0.668 ± 0.187	0.198 ± 0.149
number of suitable pixels[†] (%)	5,016 (27%)	4,798 (26%)	3,517 (19%)	1,902 (10%)
extrapolated potential numbers	85	11[‡]	55	29
approx. present numbers	~9 – 13	3[‡]	~ 14 – 26	~ 20 – 30
Statistics kill sites				
number of sheep carcasses	1,554	415	855	357
mean probability (± SD)	0.218 ± 0.085	0.321 ± 0.117	0.585 ± 0.225	0.178 ± 0.125
% carcasses in suitable pixels[&]	51 (25)	78 (49)	79 (45)	66 (33)

[†] suitable pixels are defined as having a probability higher than the mean in the presence pixels.

[‡] number of packs or scent-marking pairs.

[&] suitable pixels are defined as having a probability higher than the mean for the entire map; higher than the mean in the presence pixels only are given between brackets.

Table 5. Strength of differentiation in habitat use and choice of kill sites between species as measured by the multivariate distances between the standardized partial regression coefficients, given in Table 1 and 2. Negative mean values indicate differentiation and positive values similar use/choices. When the 95% CI includes zero; neither could be determined.

Species pairs		**Mean**	**SD**	**95% CI**
Habitat use				
brown bear	wolf	-0.099	0.043	-0.183 – -0.014
brown bear	lynx	-0.227	0.030	-0.286 – -0.169
brown bear	wolverine	-0.426	0.046	-0.517 – -0.335
wolf	lynx	-0.037	0.047	-0.128 – 0.054
wolf	wolverine	-0.515	0.041	-0.596 – -0.435
lynx	wolverine	-0.571	0.037	-0.644 – -0.498
Kill sites				
brown bear	wolf	-0.001	0.016	-0.031 – 0.030
brown bear	lynx	-0.054	0.008	-0.069 – -0.039
brown bear	wolverine	-0.152	0.005	-0.162 – -0.141
wolf	lynx	0.283	0.038	0.208 – 0.357
wolf	wolverine	-0.087	0.016	-0.118 – -0.056
lynx	wolverine	-0.111	0.008	-0.127 – -0.096

Table 6. Multinomial logistic regression results for comparisons among four carnivore species in southeast Norway. The Wald statistics represent the strength of differentiation between species. The sign indicates the direction of the effect relative to the species in the first column which was used as reference category. Only unique species combinations are presented. One, two or three asterisks indicate $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively.

Species pairs		**Intercept**	**Elevation**	**Ruggedness**	**Tree cover**	**Distance to**			
						forest edge	**public road**	**private road**	**building**
Differentiation in habitat use ($R^2 = 0.295$)									
brown bear	wolf	14.148***	-33.139***	6.436*	-8.825**	12.342***	11.833***	1.395	-16.710***
brown bear	lynx	105.162***	-138.202***	7.349**	5.237*	2.343	0.048	-0.084	-91.774***
brown bear	wolverine	-45.866***	38.565***	1.482	-10.931***	15.682***	-6.791**	9.275**	0.117
wolf	lynx	38.184***	-25.905***	-0.017	33.011***	-4.589*	-9.969**	-1.751	-22.810***
wolf	wolverine	-71.977***	83.613***	-0.076	-3.331	1.145	-22.011***	4.196*	8.612**
lynx	wolverine	-123.355***	139.228***	-0.045	-18.532***	6.509*	-6.778**	8.504**	35.583***
Differentiation in kill sites ($R^2 = 0.531$)									
brown bear	wolf	56.186***	167.334***	4.805*	35.177***	26.416***	15.159***	6.666**	37.048***
brown bear	lynx	66.172***	117.94***	81.965***	7.543**	13.024***	27.073***	0.352	43.793***
brown bear	wolverine	100.047***	66.715***	33.728***	15.752***	27.456***	16.266***	0.693	4.274*
wolf	lynx	0.022	20.86***	65.027***	14.094***	59.528***	52.303***	3.454	0.848
wolf	wolverine	151.914***	188.525***	36.146***	1.671	0.24	0.253	7.672**	12.119***
lynx	wolverine	155.48***	147.31***	0.129	7.903**	42.949***	47.03***	0.969	9.462**

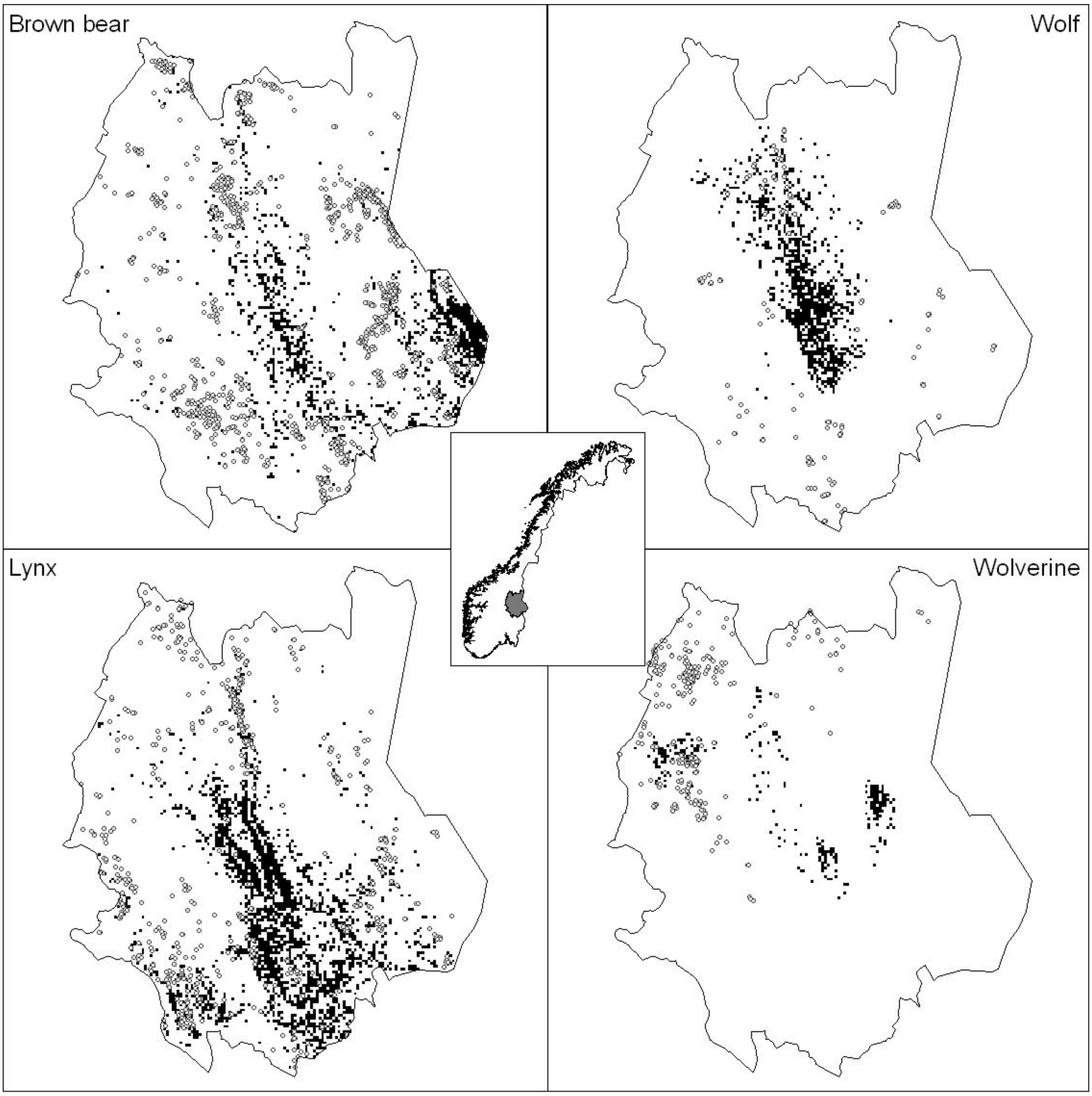

Figure 1. Presence maps for four large carnivore species within the study area in southeast Norway (see inset). The presence pixels from the radio-tracking data are given in black; locations of predator-killed sheep are given as white circles.

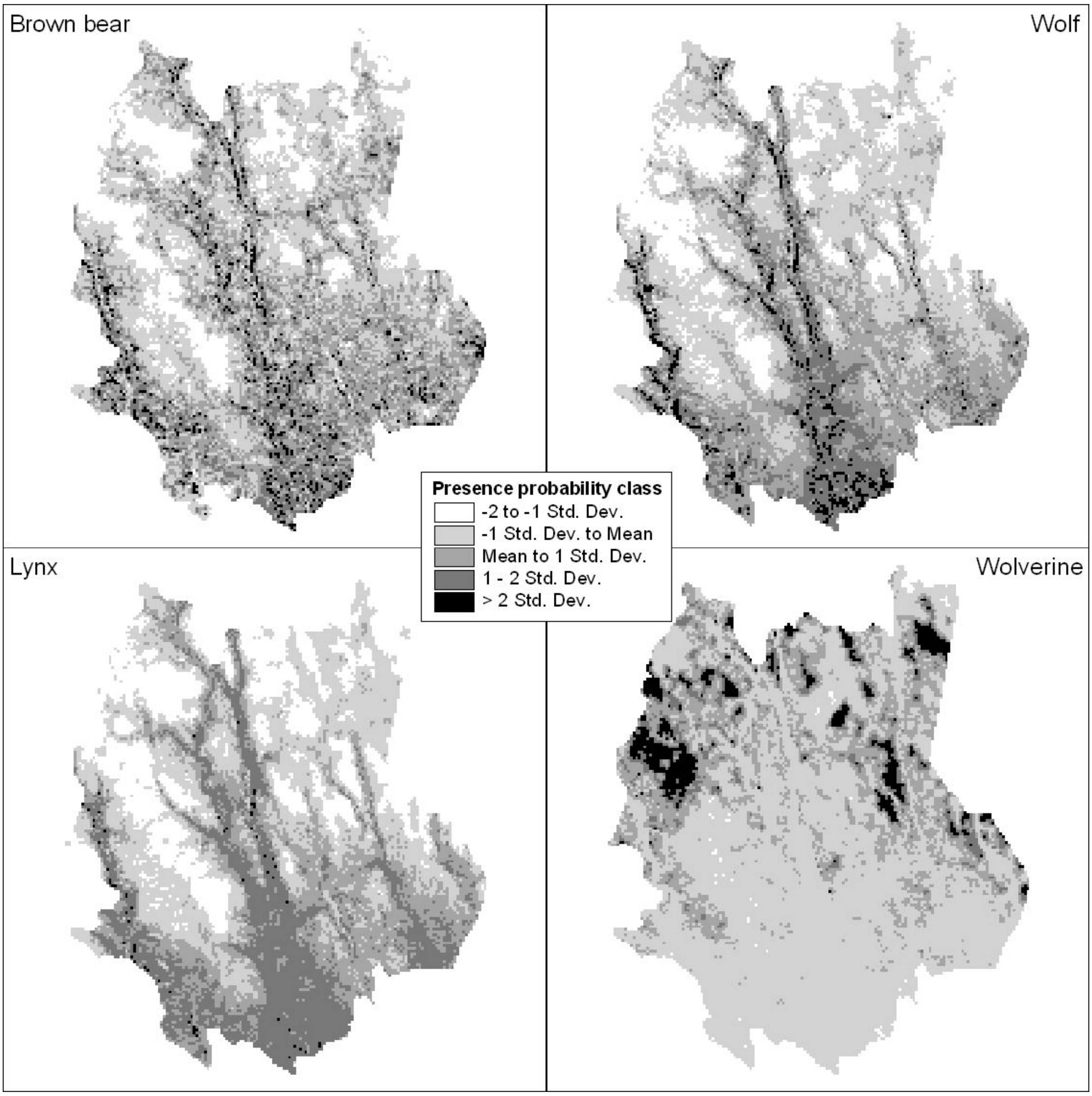

Figure 2. Probability maps for four large carnivore species within the study area in southeast Norway. The probability distributions were based on species-specific resource selection function models given in Table 1.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online from www.Blackwell-Synergy.com:

Table S1. Habitat statistics for habitat use and locations of predator-killed sheep within the probability maps of four carnivore species in southeast Norway. The rows give the mean and standard deviation for the habitat covariates used in the resource selection functions given in Table 1 and 2 of the main manuscript.

	Brown bear	**Wolf**	**Lynx**	**Wolverine**
Habitat use				
Elevation (m)	597 ± 168	559 ± 195	457 ± 172	855 ± 223
Ruggedness	31 ± 27	34 ± 32	32 ± 29	35 ± 24
Tree cover (%)	41 ± 16	41 ± 18	49 ± 18	21 ± 17
Distance to forest edge (m)	87 ± 287	133 ± 362	95 ± 298	633 ± 1,099
Distance to public road (m)	2,615 ± 2,226	2,654 ± 2,393	1,655 ± 2,001	3,788 ± 1,848
Distance to private road (m)	396 ± 660	357 ± 724	135 ± 388	1,445 ± 1,345
Distance to building (m)	763 ± 726	636 ± 616	370 ± 515	1,482 ± 1,022
Kill sites				
Elevation (m)	715 ± 170	515 ± 244	541 ± 219	1,066 ± 183
Ruggedness	28 ± 20	24 ± 21	38 ± 29	38 ± 24
Tree cover (%)	34 ± 17	39 ± 22	42 ± 18	9 ± 12
Distance to forest edge (m)	1,331 ± 562	1,487 ± 648	1,275 ± 525	2,431 ± 1,642
Distance to public road (m)	3,397 ± 2,943	2,247 ± 3,617	1,418 ± 2,400	8,362 ± 4,835
Distance to private road (m)	454 ± 919	76 ± 407	104 ± 413	1,747 ± 1,392
Distance to building (m)	677 ± 712	226 ± 560	234 ± 504	1,404 ± 1,015

Paper II

Impact of infrastructure on habitat selection of wolverines *Gulo gulo*

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Compared to the other northern large carnivores, wolverines *Gulo gulo* are thought to be the most sensitive species with regard to habitat changes and human disturbance. Nowadays wolverines in Scandinavia are found in remote high alpine areas, and we investigated whether human development through presence of infrastructure has relegated them to these areas. We analysed wolverine habitat selection and the impact of infrastructure in two study areas in Norway using compositional analysis. We found that alpine tundra with low human development was important for wolverines to locate their home ranges. Human development formed a more important factor for home range location than did habitat, because habitat selectivity was much higher in undeveloped habitats than in developed habitats. Within their home ranges, wolverines used alpine shrubland and forest, irrespective of human development. The sympatric distribution of wolverines with wild and semi-domestic reindeer *Rangifer tarandus* indicates that wolverines are vulnerable to indirect loss of habitat. However, we hypothesise that wolverine distribution may be partly influenced by direct disturbance or higher risk of human-caused mortality associated with infrastructure. Increased human development and activity in once remote areas may thus cause reduced ability of wolverines to perform their daily activities unimpeded, making the habitat less optimal or causing wolverines to avoid the disturbed area. Our results suggest that the potential exists for further wolverine recovery in forest ecosystems with low levels of infrastructural development.

Key words: compositional analysis, Gulo gulo, habitat use, home range location, human development, infrastructure, Norway, wolverine

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Because of their place on top of the food chain, large carnivores occupy large home ranges which make them potentially more vulnerable than other species to habitat fragmentation resulting from human infrastructural development and habitat conversion (Woodroffe & Ginsberg 2000). The wolverine *Gulo gulo* is one of the least known carnivores of the northern Hemisphere. Wolverines inhabit the arctic and subarctic zones in Alaska, Canada, Siberia and Scandinavia, as well as temperate forests in North America (Landa et al. 2000a, COSEWIC 2003).

They have disappeared from their southernmost distribution during the last centuries, probably due to the combined pressures of persecution, deforestation and human development (Banci 1994, Landa et al. 2000a). In a global perspective, wolverine distribution still seems to be declining, although in some areas legislative protection has led to recovery (Landa et al. 2000a,b).

The present population of wolverines in Eurasia is mainly north of 60°N, and unlike in North America and Siberia, wolverines in western Europe live in relatively fragmented habitat (Landa et al. 1998). Wolverines once occupied a much wider range of natural habitats in Europe. Before 1850, wolverines were found in most of Norway, from north to the southern parts of Sweden, Finland and the Baltic States (Landa et al. 2000a). During the last century they have mainly occupied alpine areas in central Norway, along the Norwegian-Swedish border from the county of Hedmark and northwards, and in northeast Finland (Landa et al. 2000a). As a result of their use of remote areas, low densities, shyness (Banci 1994), and present habitat occupied (Landa et al. 2000a, Walker et al. 2001), the wolverine has acquired a reputation of being a high alpine dweller in modern Scandinavian folklore.

The wolverine is often viewed as an opportunistic carnivore inhabiting higher elevations above the tree line, but with no clear association to topographic or vegetation characteristics (Kelsall 1981, Whitman et al. 1986, Banci & Harestad 1990, Henaug 2000). However, compared to the other northern large carnivores, such as the wolf *Canis lupus*, lynx *Lynx lynx* and brown bear *Ursus arctos*, wolverine history and recovery in Europe indicate that it is likely to be the most sensitive species with regard to anthropogenic effects, including mortality, habitat changes and human disturbance (Andersen et al. 2003, Lande et al. 2003, Linnell et al. 2003, Pedersen et al. 2003, Swenson et al. 2003, Sæther et al. 2003). In this study, we aimed to quantify the extent to which wolverines are behaviourally influenced by human infrastructure. We hypothesised that wolverines select areas which are inaccessible to humans. Because human accessibility into natural areas is linked to the presence of infrastructure, the objective of our study was to assess whether wolverines show clear selection for certain habitats and avoid infrastructure both in home range location and within their home ranges.

Material and methods

Study areas

Our study was conducted in two mountainous areas in Norway (Table 1). One study area was situated in south-central Norway at 62°N 9°E; the other in the county of Troms, northern Norway at 68°N 19°E. South-central Norway consists of high alpine plateaus with peaks above 2,000 m a.s.l. separated by steep valleys. The tree line lies between 800 and 1,000 m a.s.l. The valleys surrounding the high alpine plateaus contain public and private roads, railways, summer dairy farms, permanent settlements and clusters of recreational cabins. The main human activities are hiking, cross-country skiing, wild reindeer *Rangifer tarandus* hunting (in autumn) and free-range sheep *Ovis aries* grazing (in summer; Landa et al. 1999). The landscape of Troms is broadly similar to south-central Norway except that the tree line is lower (600-700 m a.s.l.). Infrastructure is less widespread in the northern regions and few domestic sheep graze in Troms. In addition, semi-domesticated reindeer are found in the county.

Both study areas consisted of forest, alpine shrubland, alpine tundra and mountain peaks (see Table 1). Forest is dominated by Scots pine *Pinus sylvestris* and Norwegian spruce *Picea abies* at the lowest elevations. At high-

Table 1. Proportional composition of undeveloped habitat and habitat with infrastructure within the south-central Norway (10,839 km^2) and Troms (10,652 km^2) study areas.

	Undeveloped	Private roads	Public roads	Human structures	Total	% developed
South-central Norway						
Forest	0.099	0.038	0.025	0.068	0.230	57.0
Alpine shrubland	0.321	0.049	0.013	0.013	0.396	18.9
Alpine tundra	0.345	0.007	0.000	0.001	0.353	2.3
Rock/ice	0.021	0.000	0.000	0.000	0.021	0.0
Total	0.786	0.094	0.038	0.082		
Troms						
Forest	0.140	0.021	0.023	0.043	0.227	38.3
Alpine shrubland	0.136	0.004	0.008	0.011	0.149	8.7
Alpine tundra	0.596	0.007	0.003	0.002	0.608	2.0
Rock/ice	0.016	0.000	0.000	0.000	0.016	0.0
Total	0.888	0.032	0.034	0.056		

er elevations, alpine shrubland with mountain birch *Betula pubescens* forms a band between forest and alpine tundra. Alpine tundra consists of heath land and bogs. Mountain peaks are comprised of rock, snow and ice. In both study areas, infrastructure (i.e. houses, cabins, settlements, public and private roads) was mainly concentrated in the forest down in the valleys.

Radio-tracking and home ranges

In south-central Norway, 10 wolverines were radio-tracked during 1990-1995 (eight males, two females). In Troms, 27 wolverines were radio-tracked during 1996-2001 (four males, 23 females). Animals were tracked from fixed-wing aircraft (55%), helicopter (1%), car (22%), snowmobile (2%), and by foot (20%). From the ground, positions of the animals were determined by triangulation. The positions of each tracked animal constitute a subsample of the animal's individual behaviour and past history through space and time (Aebischer et al. 1993a,b). In wolverines this is closely associated with the age class of the animal; juveniles first cohabit with their mothers after which they undergo an exploratory phase as yearlings before settling as adults. Therefore we assigned the positions of each radio-tracked animal to the different age classes prior to data analyses. Thus one animal tracked as a juvenile, yearling and adult was identified as three individuals in the analyses. This rendered a total of 16 tracked juvenile, nine yearling and 22 adult individuals in the analyses (Table 2). Per individual, a minimum of 20 biologically independent tracking points (maximum of one per 24 hours) was used to calculate multi-annual home ranges. Home ranges were calculated in Ranges 6 using the 95% minimum convex polygon (MCP; Mohr 1947) method, peeled around the kernel centre to avoid strong outlier effects (Worton 1989, Harris et al. 1990). Using multi-annual home ranges reduces possible short-term within-individual variations in habitat composition occurring because of differences in annual/seasonal weather conditions, or reproductive versus non-reproductive years for females (Aebischer et al. 1993a). Because ca 95% of all tracking points are daytime locations (09:00-22:00), the results are therefore biased towards activities of wolverines during the day.

Definition of habitat availability

Frequently, habitat availability is defined by selecting arbitrary study area boundaries (Aebischer et al. 1993b, McClean et al. 1998). Following animals at different sites or in different years complicates the definition of available habitat. To avoid this problem we defined a general region of probable wolverine movement for both study areas (Schadt et al. 2002). The area available to the wolverines is represented by the 100% MCP polygon drawn around all independent tracking points. To include the area possibly available to 'boundary individuals', the MCP was enlarged by the upper limit of the

Table 2. Specifications of the radio-tracked wolverines in the two study areas.

ID	Sex	Age class	# fixes
South-central Norway			
1	F	Yearling	25
1	F	Adult	25
2	M	Adult	42
4	F	Adult	28
5	M	Yearling	37
7	M	Adult	73
8	M	Adult	71
9	M	Yearling	33
11	M	Adult	23
12	M	Juvenile	38
13	M	Juvenile	30
Troms			
1	M	Adult	117
2	F	Adult	69
3	F	Juvenile	49
3	F	Yearling	43
3	F	Adult	43
4	F	Adult	36
5	F	Juvenile	27
7	F	Juvenile	22
10	M	Juvenile	24
11	F	Juvenile	37
11	F	Yearling	33
11	F	Adult	32
12	F	Adult	64
13	F	Adult	30
14	F	Juvenile	34
14	F	Yearling	34
14	F	Adult	43
15	F	Juvenile	26
16	F	Adult	52
17	F	Adult	189
18	M	Juvenile	37
19	F	Juvenile	37
19	F	Yearling	31
19	F	Adult	29
25	F	Yearling	26
26	F	Adult	61
27	F	Adult	45
31	M	Juvenile	21
32	F	Juvenile	26
33	F	Juvenile	28
34	F	Adult	27
39	F	Adult	22
45	F	Juvenile	44
45	F	Yearling	39
46	F	Juvenile	36
49	F	Adult	20

one-tailed 95% confidence interval of the mean activity radius (mean activity radius + t *SE) over the tracked wolverine population. Activity radii were calculated as the mean linear distance between each independent tracking point and the geographical centre (arithmetic mean) of each individual's multi-annual home range. The buffers were 13.5 km (10.2 + 1.812*1.8; N = 11) in south-central Norway and 7.4 km (6.5 + 1.689*0.5; N = 36) in Troms. The study areas therefore encompassed a total of 10,839 km^2 in south-central Norway and 10,652 km^2 in Troms.

Background maps

Two different background maps were available for this analysis. First, a habitat map was based on a land cover (a classified AVHRR image) which was downloaded from the homepage of United States Geological Survey (http://edcdaac.usgs.gov/glcc/background.html). Habitats were grouped into four broad classes: forest (including both boreal forest and the birch forest zone that occurs at the tree line), alpine shrubland, alpine tundra and rock/ice. Water, including lakes and rivers, was excluded from the analysis. The map was on a 1×1 km pixel resolution.

Secondly, a 1:250,000 vector map of Norwegian infrastructure was available from the Norwegian State Mapping Authority (Statens Kartverk). For analysis, infrastructure classes were grouped as structures (houses, cabins or settlements), public roads and private roads (mainly unpaved forest roads). The vector data were converted to 1×1 km pixels for comparison with the habitat map. When more than one type of infrastructure was present in a pixel, the pixel was classified as the type associated with maximum human disturbance potential (i.e. a structure pixel might also contain roads of either type, a public road pixel might also contain private roads, whereas a private road pixel would only contain private roads). Pixels without any infrastructure were termed undeveloped.

These maps were then combined to produce a composite map with a potential of eight pixel categories: developed (any type of infrastructure) or undeveloped (no infrastructure) pixels for each of the four habitat classes. In effect there were only seven pixel categories because there were no rock/ice pixels containing any form of infrastructure.

Compositional analysis

Compositional analysis (Aitchison 1986, Aebischer et al. 1993a, Aebischer et al. 1993b) can be used to compare utilised with available habitats at two levels, examining home-range location within the overall study area (habitat requirements, or second order selection), and habitat use within the home range (resource usage, or third order selection; Johnson 1980). At each level, we ranked habitat types according to relative use (if they differed from random) and conducted significance tests.

Because a zero numerator or denominator in the log-ratio transformation in the proportional habitat use (composition) is invalid, proportions of habitat not utilised were substituted with a small positive value less than the smallest recorded non-zero proportion. For individuals with non-utilised habitat proportions, the habitat composition was calculated as follows. Based on n grid cells in their home range distributed over D habitat types, the proportional use of habitat I was calculated as $[(n_i + 0.5 / D) / (\Sigma n + 0.5)]$. The substituted zero-values were all smaller than the smallest non-zero value in the study area.

The overall test of significance was based on comparing the fit of differential versus identical habitat use by multivariate analysis of variance using the generalised likelihood ratio statistic Λ (Chatfield & Collins 1980, Kendall 1980, Aebischer et al. 1993b). Because the distribution of the log-transformed habitat compositions was not multivariate normal, we applied randomisation tests to obtain the level of significance (Manly 1997). We compared the test statistic with a simulated distribution based on 10,000 data sets, by resampling the original bootstrap population under the null hypothesis (i.e. use = available; Pendleton et al. 1998). We concluded that habitat was used non-randomly if the observed test statistic constituted the lowest 5% in the simulated distribution.

Thereafter the habitat types were ranked in order of use, from least to most used (Aebischer et al. 1993b), based on standardised log-ratio differences (mean log-ratio differences over the standard error of the difference). To determine which habitat types were actually selected, we calculated the 2-tailed simultaneous 90% CI for population selection ratios (ratio of totals) using the Bonferroni inequality with a confidence level of 97.5% (α/D) for the D different intervals (Manly et al. 2002).

We conducted three sets of compositional analysis. First, we conducted a compositional analysis for habitat type (four pixel categories: forest, shrubland, tundra and rock/ice). Secondly, we conducted a compositional analysis for infrastructure type (four pixel categories: undeveloped, human structures, public road and private road). Thirdly, we conducted a compositional analysis with the composite map (seven pixel categories: developed and undeveloped forest, developed and undeveloped shrublands, developed and undeveloped tundra and undeveloped rock/ice). All analyses were conducted sep-

Table 3. Habitat selection in home range location of wolverines in the study areas. South-central Norway (SCN) is given in the upper right half, and Troms in the lower left. The standardised log-ratio differences (mean log-ratio difference over the standard error of the difference) are presented. Asterisks represent significant deviation from random (P < 0.05). The last column ranks the habitat categories from least (0) to most used (3) in south-central Norway. The ranks in italics indicate selected habitats (P < 0.05).

	Forest	Alpine shrub	Alpine tundra	Rock/ ice	Rank SCN
Forest		-3.753*	4.637*	-4.784*	0
Alpine shrubland	0.816		-5.030*	-2.257*	1
Alpine tundra	2.446*	4.355*		-0.161	*2*
Rock/ice	-1.000	-2.039*	-6.993*		*3*
Rank Troms	1	2	*3*	0	

Table 4. Relative avoidance of infrastructure in home range location of wolverines in the study areas. South-central Norway (SCN) is given in the upper right half, and Troms in the lower left. The standardised log-ratio differences (mean log-ratio difference over the standard error of the difference) are presented. Asterisks represent significant deviation from random (P < 0.05). The last column ranks the habitat categories from least (0) to most used (3) in south-central Norway. The ranks in italics indicate selected habitats (P < 0.05).

	Human structures	Public roads	Private roads	Un- developed	Rank SCN
Human structures		-1.715	-2.281*	-5.865*	0
Public roads	2.238*		-1.043	-5.055*	1
Private roads	-0.664	-2.040*		-5.196*	2
Undeveloped	4.663*	3.473*	6.007*		*3*
Rank Troms	1	2	0	*3*	

arately for both study areas, and at the 'home-range location' and 'use within home range' levels.

The effects of sex on habitat selection could not be explored, because sample sizes in each study area were not adequate for sound statistical analyses (see also Table 1; *cf.* Aebischer et al. 1993a). Because the sample from south-central Norway was dominated by males, whereas the sample from Troms was dominated by females, we therefore cannot rule out that differences in habitat selection between the two areas are to some extent due to sexual differences in habitat selection. However, based on what is known about sexual differences in habitat use of wolverines (Lofroth 2001), we regard this to be of less importance than the effects of human development (Landa et al. 2000a, COSEWIC 2003). In Troms, sample sizes on female wolverines (11 juveniles, six yearlings, and 15 adults) made careful analyses possible on the effect of age class on habitat differentiation. To establish whether habitat selection in Troms had the tendency to differ by age class we compared a full model including age class as fixed factor with a restricted model in which age class was excluded (Aebischer et al. 1993a).

Results

Home range location

South-central Norway

Home ranges in south-central Norway were located in areas with rock/ice and alpine tundra ($\Lambda = 0.251$, $P = 0.004$; Table 3). Alpine shrubland was less selected, and forests were avoided. Related to infrastructure, wolverines located their home ranges in undeveloped areas ($\Lambda = 0.196$, $P = 0.002$; Table 4). Areas with private roads, public roads and human structures were, in descending order, less selected. The impact of human development on habitat selection was equal for alpine shrubland and alpine tundra; for both types undeveloped habitats were selected over developed habitats ($\Lambda = 0.093$, $P = 0.010$; Table 5). Wolverines did not locate their home ranges in forest, irrespective of human devel-

Table 5. Impact of human development on habitat selection in home range location of wolverines in the study areas. South-central Norway (SCN) is given in the upper right half, and Troms in the lower left. The standardised log-ratio differences (mean log-ratio difference over the standard error of the difference) are presented. Asterisks represent significant deviation from random (P < 0.05). The last column ranks the habitat categories from least (0) to most used (6) in south-central Norway. The ranks in italics indicate selected habitats (P < 0.05).

	Undeveloped				Developed			
	Forest	Alpine shrub	Alpine tundra	Rock/ice	Forest	Alpine shrub	Alpine tundra	Rank SCN
Undeveloped								
Forest		-2.931*	-3.501*	-3.309*	1.124	-0.422	0.380	2
Alpine shrub	0.383		-4.735*	-1.617	5.145*	4.310*	4.061*	4
Alpine tundra	2.612*	4.479*		0.056	5.506*	4.946*	6.461*	*6*
Rock/ice	-1.960*	-2.857*	-7.395*		5.601*	5.268*	3.863*	*5*
Developed								
Forest	-3.833*	-2.533*	-4.700*	0.070		-2.930*	-0.106	0
Alpine shrub	-1.818*	-2.712*	-4.963*	0.904	1.064		1.005	3
Alpine tundra	-1.363	-1.557	-4.639*	1.604	1.690*	0.408		1
Rank Troms	4	5	*6*	0	1	2	3	

opment. The relative selectivity for undeveloped over developed habitat, measured by the average (± SE) over the standardised log-ratio differences between undeveloped-developed habitat pairs (i.e. for forest, alpine shrubland and alpine tundra), was strong (3.965 ± 1.550). Relative selectivity for habitat, measured by the average (± SE) over the standardised log-ratio differences among (un)developed habitat categories, in undeveloped (3.722 ± 0.532) areas was nearly thrice the selectivity in developed areas (1.347 ± 0.833).

Troms

In Troms, wolverines located their home ranges in areas with alpine tundra ($\Lambda = 0.240$, $P < 0.001$; see Table 3). Alpine shrubland, forest and rock/ice were selected less. Related to infrastructure, wolverines located their home ranges in undeveloped areas ($\Lambda = 0.419$, $P < 0.001$; see Table 4). Areas with public roads were selected less. Areas with private roads and human structures were avoided. The impact of human development on habitat selection was equal for all habitat types; all undeveloped habitats except rock/ice were selected over developed habitats ($\Lambda = 0.165$, $P < 0.001$; see Table 5). Relative selectivity for undeveloped over developed habitat was strong (3.728 ± 0.559). Relative selectivity for (un)developed habitat, was more than twice as high in undeveloped (2.492 ± 1.184) as in developed areas (1.054 ± 0.370). Wolverines were least sensitive for human development in alpine tundra; no significant differences in relative selectivity were found between developed alpine tundra and undeveloped forest and alpine shrubland.

Use within home ranges

South-central Norway

Habitat use within home ranges showed a clear selection for alpine shrubland and forests; alpine tundra was less used and rock/ice was not used ($\Lambda = 0.142$, $P = 0.002$; Table 6). Within their home ranges wolverines used the available area randomly with regard to infrastructure ($\Lambda = 0.568$, $P = 0.522$). The available habitat within their home ranges tended to be used non-randomly with regard to human development ($\Lambda = 0.069$, $P = 0.087$; Table 7). Rock/ice was avoided altogether. All other habitat types showed no significant differences in ranking and were all, apart from undeveloped alpine tundra, selected. Relative selectivity for undeveloped over developed habitat was not strong (0.005 ± 1.293).

Table 6. Habitat selection of wolverines within their home ranges. South-central Norway (SCN) is given in the upper right half, and Troms in the lower left. The standardised log-ratio differences (mean log-ratio difference over the standard error of the difference) are presented. Asterisks represent significant deviation from random ($P < 0.05$). The last column ranks the habitat categories from least (0) to most used (3) in south-central Norway. The ranks in italics indicate selected habitats ($P < 0.05$).

	Forest	Alpine shrub	Alpine tundra	Rock/ ice	Rank SCN
Forest		-0.483	1.050	3.061*	*2*
Alpine shrub	-3.083*		5.717*	4.820*	*3*
Alpine tundra	-3.775*	-0.039		2.899*	1
Rock/ice	-1.966*	0.533	-0.983		0
Rank Troms	*3*	1	1	1	

Troms

Within their home ranges wolverines showed a tendency to use the available habitat non-randomly ($\Lambda = 0.543$, $P = 0.073$; see Table 6). Forests tended to be selected above the other habitat types. Also alpine shrubland tended to be selected, although it was not significantly different from the other habitat types. With regard to infrastructure they used the available area within their home ranges randomly ($\Lambda = 0.760$, $P = 0.460$). Wolverines tended to use the available habitat within their home

Table 7. Impact of human development on habitat selection within home ranges of wolverines in the study areas. South-central Norway (SCN) is given in the upper right half, and Troms in the lower left. The standardised log-ratio differences (mean log-ratio difference over the standard error of the difference) are presented. Asterisks represent significant deviation from random ($P < 0.05$). The last column ranks the habitat categories from least (0) to most used (6) in south-central Norway. The ranks in italics indicate selected habitats ($P < 0.05$).

	Undeveloped				Developed			
	Forest	Alpine shrub	Alpine tundra	Rock/ice	Forest	Alpine shrub	Alpine tundra	Rank SCN
Undeveloped								
Forest		-0.138	1.126	2.517*	0.837	1.041	0.828	*5*
Alpine shrub	-3.675*		5.921*	4.586*	1.243	1.709	-0.805	*5*
Alpine tundra	-4.584*	1.167		3.039*	-0.071	0.086	-2.531	2
Rock/ice	-1.935*	0.137	-1.591		-1.928*	-2.360*	-2.119	0
Developed								
Forest	-1.767*	0.606	-0.357	0.502		0.168	-1.519	*3*
Alpine shrub	-5.120*	-2.974*	-2.026*	-0.866	-1.334		-3.606*	*1*
Alpine tundra	-0.824	-0.895	-0.344	0.527	0.265	1.567		*5*
Rank Troms	*6*	1	4	2	3	0	5	

ranges non-randomly with regard to human development ($\Lambda = 0.248$, $P = 0.068$; see Table 7). Undeveloped forest, undeveloped alpine shrubland, and developed alpine tundra tended to be selected. Still, all habitat types, except developed alpine shrubland which tended to be avoided, did not render significant differences in ranking. Relative selectivity for undeveloped over developed habitat in Troms was weak (1.466 ± 0.970).

Habitat differentiation by age of female wolverines in Troms

Age had a significant effect on location of home ranges ($\Lambda = 0.823$, $P = 0.027$); yearling females tended to be found more in areas with forest and less in areas with alpine shrubland than both adults and juveniles. Within their home ranges, juveniles used higher lying habitats than adults (i.e. less forest and more alpine shrubland, and less alpine tundra and more rock/ice; $\Lambda = 0.857$, $P = 0.064$) whilst yearlings used less alpine tundra (and therefore more alpine shrubland and rock/ice) than adults. Related to infrastructure, age did not seem to have a clear effect on home range location ($\Lambda = 0.876$, $P = 0.101$), but yearlings seemed to locate their home ranges in areas with more private roads and less human settlements than both adults and juveniles. Within their home ranges, however, juveniles used less private roads than adult females, whereas yearlings were found to use more developed area (i.e. public roads and human settlements) than adults ($\Lambda = 0.833$, $P = 0.035$). Age affected the impact of development on habitat selection in home range location ($\Lambda = 0.565$, $P < 0.001$). Relative to adults, juveniles had more developed alpine tundra (and less undeveloped forest and developed alpine shrubland) in their home ranges. Yearlings included more forest, more rock/ice, but less developed alpine shrubland in their home ranges than did adults. Within their home ranges ($\Lambda = 0.671$, $P < 0.001$), juveniles used more rock/ice and less developed alpine tundra and forest than did adults. Yearlings used much more developed alpine shrubland and less alpine tundra (both developed and undeveloped) than did adults.

Discussion

This is the first study to investigate the impact of infrastructure on habitat selection of wolverines in Eurasia. It is important to note that compositional analysis does not give insight into the amount of time spent in each habitat type, nor on the exact distance wolverines keep from infrastructure. Compositional analysis ranks the relative use of habitat and infrastructure compared to the availability in the entire study area or within the home ranges. Several assumptions underlie the compositional analysis of habitat use (Aitchison 1986, Aebischer et al. 1993a,b). One important assumption is that each animal provides an independent measure of habitat use within the population. Caution is needed with territorial and social species. Wolverines are solitary and use large home ranges (Landa et al. 1998). Only during the mating season do males show territoriality (Landa et al. 2000a). Resident females with juveniles maintain exclusive home ranges during summer (Landa et al. 2000a). Unfortunately, the small tracked population in south-central Norway and the skewed population in Troms made it impossible to asses the effect of sex on habitat selection in our study. However, the similar results rendered from the male-biased population in south-central Norway and the female-biased population in Troms indicate that sex-specific habitat differentiation was not considerable. Based on the limited available data, we did explore in which direction there was a tendency for an age effect for female wolverines in Troms. Habitat selection did not change drastically between the age classes. General differences between the age classes showed that, relative to adult females, juveniles tended to select habitats on higher altitudes, whilst yearlings tended to use habitats at lower altitudes. However, because of the marginal sample sizes, these directions have to be taken cautiously. The results are in concordance with Lofroth (2001) who found that in mountainous areas in Canada adult females tend to use higher elevations and steeper terrain more than other sex and age classes, whereas adult males and subadults of both sexes make extensive use of low elevation habitats. Inclusion of family groups (i.e. juveniles accompanied by their mother) may to some extent overemphasise habitat selection within their joint home range. This, however, does not have to be negative; wolverines are believed to be especially selective about habitat quality (Magoun & Copeland 1998) and particularly sensitive to human disturbance (Heinemeyer et al. 2001) during the natal-denning period for reproductive females.

Our results indicate that wolverines in Norway located their home ranges in relatively undeveloped high alpine areas (i.e. alpine tundra and rock/ice). The selection for alpine areas is consistent with previous studies on home range use and altitude selection by wolverines (Whitman et al. 1986, Fangel 1997, Landa et al. 1998). We found that habitat selectivity in developed habitats was low, indicating that infrastructure and not habitat was the primary factor for home range location. Also, wolverines were more selective about habitat quality in undeveloped areas when establishing their home range (*cf.* Heinemeyer et al. 2001). At the home range level the tracked wolverines avoided areas with human structures (i.e. houses, cabins and settlements). This may be explained by the fact that human structures were mostly concentrated in the forested valley bottoms (83 and 77% in south-central Norway and Troms, respectively). Public and especially private roads reach further into wolverine habitat (i.e. alpine shrubland and alpine tundra). Within their home ranges, wolverines used alpine shrubland and forest. No strong effect was found with regard to avoidance of human development. The hypothesis that wolverines avoid human infrastructure at a large scale (i.e. home range location) was supported both in the northern and southern study area.

Wild and semi-domestic reindeer which constitutes the wolverines' most important source of winter food (Haglund 1966, Myrhe & Myrberget 1975, Magoun 1987, Landa et al. 1997), can also be found in alpine areas (Skogland 1994, Mysterud & Mysterud 1995). Wild reindeer is one of the ungulate species most sensitive to habitat fragmentation and human disturbance (Cameron et al. 1992, Smith et al. 2000, Vistnes et al. 2001, Nellemann et al. 2003). Similar results have been found for semi-domestic reindeer (Helle & Särkelä 1993, Vistnes & Nellemann 2001). The sympatric distribution of wolverines with wild and semi-domestic reindeer may therefore indicate that wolverines are vulnerable to indirect loss of habitat (Landa et al. 2000a); a result also found in modelling studies in the USA (Carroll et al. 2001, Rowland et al. 2003). Besides avoiding areas with anthropogenic disturbance, reindeer and caribou also avoid areas with higher risks of predation. In Troms, selection of habitat by semi-domestic reindeer was, however, more attuned to the avoidance of lynx than of wolverine (Henaug 2000). I. Vistnes (unpubl. data) found that wolverine-caused depredation on semi-domestic reindeer was highest in areas away from infrastructure and human settlements. Wolverine depredation on free-ranging domestic sheep during the summer in south-central Norway was found to increase with increasing distance to infrastructure although sheep abundance was highest in areas close to infrastructure (Taugbøl et al. 2001). Our study indicates that wolverine distribution may be partly influenced by direct disturbance or higher risk of human-caused mortality associated with infrastructure (Thurber et al. 1994, Landa et al. 2000a). Increased human development (e.g. houses, cabins, settlements and roads) and activity (e.g. recreation and husbandry) in once remote areas may thus cause reduced ability of wolverines to perform their daily activities unimpeded, making the habitat less optimal or causing wolverines to avoid the disturbed area (Landa & Skogland 1995, Landa et al. 2000a). Although wolverines have been shown to travel through developed areas and transportation corridors (Landa et al. 1998, Vangen et al. 2001), they apparently locate their home ranges away from human disturbance (undeveloped habitat), and use habitat which may provide them with enough shelter (alpine shrubland and forest).

Because infrastructure is mainly found in forested areas at lower elevations, wolverines seem to avoid the densely populated valleys in general. In south-central Norway especially, wolverines avoided locating home ranges in forest altogether regardless of infrastructure. Still, they did select forest and alpine shrubland within their home ranges. Little is known about wolverine ecology in forest ecosystems in Scandinavia (Landa et al. 1998), but since the wolf has returned to the forests of Hedmark the wolverine has followed and re-established in the area (Brøseth & Andersen 2003). This may offer the potential for further wolverine recovery in relatively unfragmented and undisturbed forests in Norway. However, many of the forested areas have changed due to increased human development in the last centuries. Forestry practices and recreational development have changed large tracts of forest. But because prey is still relatively abundant throughout Norway (Landa et al. 2000b), large tracts of forest in Norway may still offer the potential for wolverine recovery.

Even in less densely populated countries like Norway (Norway has the lowest human population density in western Europe), wilderness areas are embedded in multi-use landscapes with varying degrees of development. Given the extensive habitat needs of large carnivores and the continuing encroachment of human activity on natural areas, provision of adequate habitat, where there is no potential for conflict, could be difficult (Landa et al. 1997, Linnell et al. 2003). Ensuring effective conservation of large carnivores, however, depends on maintaining sustainable management aimed at minimising the potential for conflicts with human activities in multi-use landscapes. Also mitigation of fragmentation and isolation of the declining natural areas will form important measures in conserving species that are especially sensitive to habitat changes and human disturbance. Now that wilderness areas have become more developed as a result of increased infrastructure and human mobility, the direct and indirect effect of human activities on sensitive species, like the wolverine, should be better understood to enable proper and holistic management for future conservation. Consolidation of wolverine populations at a viable level can only be maintained when infrastructural development of wilderness areas is minimised, and placement of infrastructure and human activities are carefully zoned.

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References

Aebischer, N.J., Marcström, V., Kenward, R.E. & Karlbom, M. 1993a: Survival and Habitat Utilisation: A Case for Compositional Analysis. - In: Lebreton, J-D. & North, P.M. (Eds.); Marked Individuals in the Study of Bird Population. Birkhäuser Verlag, Basel, Switzerland, pp. 343-353.

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993b: Compositional analysis of habitat use from animal radio-tracking data. - Ecology 74: 1313-1325.

Aitchison, J. 1986: The statistical analysis of compositional data. - Chapman and Hall, London, 416 pp.

Andersen, R., Linnell, J.D.C., Odden, J., Andrén, H., Sæther, B-E., Moa, P., Herfindal, I., Kvam, T. & Brøseth, H. 2003: Utredninger i forbindelse med ny rovviltmelding. Gaupe - Bestandsdynamikk, bestandsutvikling og høstingsstrategier. (In Norwegian with an English summary: Reports for the large Predator Policy Statement. Lynx - Population dynamics, population development and harvesting strategies). - Norwegian Institute for Nature Research, Fagrapport 59: 1-28.

Banci, V. 1994: Wolverine. - In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J. & Zielinski, W.J. (Tech. Eds.); The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. General Technical Report RM-254, Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Fort Collins, CO, pp. 99-127.

Banci, V. & Harestad, A. 1990: Home range and habitat use of wolverines Gulo gulo in Yukon Canada. - Holarctic Ecology 13: 195-200.

Brøseth, H. & Andersen, R. 2003: Yngleregistreringer av jerv i Norge i 2003. - Norwegian Institute for Nature Research, Minirapport 016: 1-9. (In Norwegian).

Cameron, R.D., Reed, D.J., Dau, J.R. & Smith, W.T. 1992: Redistribution of calving caribou in response to oil field development on the Arctic Slope of Alaska. - Arctic 45: 338-342.

Carroll, C., Noss, R.F. & Paquet, P.C. 2001: Carnivores as focal species for conservation planning in the Rocky Mountain region. - Ecological Applications 11: 961-980.

Chatfield, C. & Collins, A.J. 1980: Introduction to Multivariate Analysis. - Chapman and Hall, London, 248 pp.

COSEWIC 2003: COSEWIC assessment and update status report on the wolverine Gulo gulo in Canada. - Committee on the Status of Endangered Wildlife in Canada, Ottawa, 41 pp.

Fangel, K. 1997: Winter micro- habitat selection of wolverine (Gulo gulo) in a northern boreal forest, Norway. - M.Sc. thesis, University of Tromsø, 36 pp.

Haglund, B. 1966: De stora rovdjurens vintervanor. - Viltrevy 4: 1-311. (In Norwegian)

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T. & Wray, S. 1990: Home range analysis using radio tracking data: a review of problems and techniques particularly as applied to the study of mammals. - Mammal Review 20: 97-123.

Heinemeyer, K.S., Aber, B.C. & Doak, D.F. 2001: Aerial surveys for wolverine presence and potential winter recreation impacts to predicted wolverine denning habitats in the southwestern Yellowstone ecosystem. - GIS/ISC Laboratory, Department of Environmental Studies, University of California, Santa Cruz, 21 pp. Available at: http://gis.ucsc.edu/Projects/gulo2000/gulo2000.htm [accessed May 2003].

Helle, T. & Särkelä, M. 1993: The effects of outdoor recreation on range use by semi-domesticated reindeer. - Scandinavian Journal of Forest Research 8: 123-133.

Henaug, C. 2000: A view to a kill. The use of habitat characteristics in semi-domestic reindeer related to predation vulnerability. - M.Sc. thesis, University of Tromsø, Tromsø, Norway, 25 pp.

Johnson, D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. - Ecology 59: 1286-1301.

Kelsall, J.P. 1981: Status report on the wolverine, Gulo gulo, in Canada in 1981. - Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, 47 pp.

Kendall, M. 1980: Multivariate Analysis. Second edition. - Griffin, London, 218 pp.

Landa, A., Gudvangen, K., Swenson, J.E. & Røskaft, E. 1999: Factors associated with wolverine Gulo gulo predation on domestic sheep. - Journal of Applied Ecology 36: 963-973.

Landa, A., Lindén, M. & Kojola, I. 2000a: Action plan for the conservation of wolverines in Europe (Gulo gulo). - Council of Europe Press, Strasbourg, 45 pp.

Landa, A., Linnell, J.D.C., Swenson, J.E., Røskaft, E. & Moskness, A. 2000b: Conservation of Scandinavian wolverines in ecological and political landscapes. - In: Griffiths, H.I. (Ed.); Mustelids in a modern world: conservation aspects of small carnivore-human interactions. Backhuys Publishers, Leiden, Netherlands, pp. 1-20.

Landa, A. & Skogland; T. 1995: The relationship between population density and body size of wolverines Gulo gulo in Scandinavia. - Wildlife Biology 1: 165-175.

Landa, A., Strand, O., Linnell, J.D.C. & Skogland, T. 1998: Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. - Canadian Journal of Zoology 76: 448-457.

Landa, A., Strand, O., Swenson, J.E. & Skogland, T. 1997: Wolverines and their prey in southern Norway. - Canadian Journal of Zoology 75: 1292-1299.

Lande, U.S., Linnell, J.D.C., Herfindal, I., Salvatori, V., Brøseth, H., Andersen, R., Odden, J., Andrén, H., Karlsson, J., Willebrand, T., Persson, J., Landa, A., May, R., Dahle, B. & Swenson, J. 2003: Utredninger i forbindelse med ny rovviltmelding. Potensielle leveområder for store rovdyr i Skandinavia: GIS-analyser på et økoregionalt nivå. (In Norwegian with an English summary: Reports for the Large Predator Policy Statement. Potential habitat for large carnivores in Scandinavia: a GIS analysis at the regional level). - Norwegian Institute for Nature Research, Fagrapport 64: 1-31.

Linnell, J.D.C., Lande, U.S., Skogen, K., Hustad, H. & Andersen, R. 2003: Utredninger i forbindelse med ny rovviltmelding. Scenarier for en geografisk differensiert forvaltning av store rovdyr i Norge. (In Norwegian with an English summary: Reports for the Large Predator Policy Statement. Management scenarios for large carnivores in Norway). - Norwegian Institute for Nature Research, Fagrapport 65: 1-43.

Lofroth, E. 2001: Wolverine ecology in plateau and foothill landscapes, 1996-2001. 2000/01 Year end report, northern wolverine project. - Forest Renewal Activity No. 712260, Ministry of Environment, Lands and Parks, Victoria, B.C., 98 pp.

Magoun, A.J. 1987: Summer and winter diets of wolverines, Gulo gulo, in arctic Alaska. - Canadian Field-Naturalist 191: 392-397.

Magoun, A.J. & Copeland, J.P. 1998: Characteristics of wolverine reproductive den sites. - Journal of Wildlife Management 62: 1313-1320.

Manly, B.F.J. 1997: Randomization, bootstrap and Monte Carlo methods in biology. Second edition. - Chapman and Hall, London, 399 pp.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. 2002: Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second edition. - Kluwer Academic Publishing, Dordrecht, Netherlands, 221 pp.

McClean, S., Rumble, M.A., King, R.M. & Baker, W.L. 1998: Evaluation of resource selection methods with different definitions of availability. - Journal of Wildlife Management 62: 793-801.

Mohr, C.O. 1947: Table of equivalent populations of North American small mammals. - American Midland Naturalist 37: 223-249.

Myhre, R. & Myrberget, S. 1975: Diet of wolverines (Gulo gulo) in Norway. - Journal of Mammalogy 56: 752-757.

Mysterud, I. & Mysterud, I. 1995: Perspektiver på rovdyr, ressurser og utmarksnæringer i dagens- og framtidens Norge: en konsekvensutredning av rovviltforvaltningens betydning for småfenæring, reindrift og viltinteresser. - Sluttrapport, KUR-prosjektet, Norsk sau og geitalslag, pp. 1-336. (In Norwegian).

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O. & Newton, A. 2003: Progressive impact of piecemeal infrastructure development on wild reindeer. - Biological Conservation 113: 307-317.

Pedersen, H.C., Brainerd, S.M., Liberg, O., Sand, H. & Wabakken, P. 2003: Utredninger i forbindelse med ny rovviltmelding. Ulv - Bestandsdynamikk, levedyktighet of effekter av uttak. (In Norwegian with an English summary: Reports for the Large Predator Policy Statement. Wolf - Population dynamics, viability and effects of alpha-individual loss.) - Norwegian Institute for Nature Research, Fagrapport 61: 1-89.

Pendleton, G.W., Titus, K., DeGayner, E., Flatten, C.J.& Lowell, R.E. 1998: Compositional Analysis and GIS for Study of Habitat Selection by Goshawks in Southeast Alaska. - Journal of Agricultural, Biological and Environmental Statistics 3: 280-295.

Rowland, M.M., Wisdom, M.J., Johnson, D.H., Wales, B.C., Copeland, J.P. & Edelmann, F.B. 2003: Evaluation of landscape models for wolverines in the interior northwest, United States of America. - Journal of Mammalogy 84: 92-105.

Sæther, B-E., Engen, S., Persson, J., Brøseth, H., Landa, A. & Willebrand, T. 2003: Utredninger I forbindelse med ny rovviltmelding. Levedyktighetsanalyser av skandinavisk jerv. (In Norwegian with an English summary: Reports for the Large Predator Policy Statement. Viability analyses for Scandinavian wolverines). - Norwegian Institute for Nature Research, Fagrapport 62: 1-28.

Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., Koubek, P., Huber, T., Stanisa, C. & Trepl, L. 2002: Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. - Journal of Applied Ecology 39: 189-203.

Skogland, T. 1994: Villrein: fra urinnvåner til miljøbarometer. - Teknologisk Forlag, Oslo, 143 pp. (In Norwegian).

Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C. & Hervieux, D. 2000: Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. - Canadian Journal of Zoology 78: 1433-1440.

Swenson, J., Dahle, B., Arnemo, J.M., Brunberg, S., Hustad, H., Nerheim, E., Sandegren, F., Solberg, K.H. & Söderberg, A. 2003: Utredninger i forbindelse med ny rovviltmelding. Status og forvaltning av brunbjørnen i Norge. (In Norwegian with an English summary: Reports for the Large Predator Policy Statement.Status and management of brown bears in Norway). - Norwegian Institute for Nature Research, Fagrapport 60: 1-19.

Taugbøl, T., Vistad, O.I., Nellemann, C., Kaltenborn, B.P., Flyen, A.C., Swensen, G., Nybakken, A., Horgen, B.C., Grefsrud, R., Lein, K., Sivertsen, J.B. & Gurigarad, K. 2001: Hyttebygging i Norge. En oppsummering og vurdering av ulike miljø- og samfunnsmessige effekter av hyttebygging i fjell- og skogtraktene i Sør-Norge. (In Norwegian with an English summary: Construction of recreational homes in Norway. A summary and evaluation of different environmental and social effects of constructing recreational homes in the mountainous and forested areas in southern Norway). - Norwegian Institute for Nature Research Oppdragsmelding 709: 1-65.

Thurber, J.M., Peterson, R.O., Drummer, T.D. & Thomasma, S.A. 1994: Gray wolf response to refuge boundaries and roads in Alaska. - Wildlife Society Bulletin 22: 61-68.

Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Segerström, P. 2001: Characteristics of dispersal in wolverines. - Canadian Journal of Zoology 79: 1641-1649.

Vistnes, I. & Nellemann, C. 2001: Avoidance of cabins, roads, and power lines by reindeer during calving. - Journal of Wildlife Management 65: 915-925.

Vistnes, I., Nellemann, C., Jordhøy, P. & Strand, O. 2001: Wild reindeer: impacts of progressive infrastructure development on distribution and range use. - Polar Biology 24: 531-537.

Walker, C.W., Vilà, C., Landa, A., Lindén, M. & Ellegren, H. 2001: Genetic variation and population structure in Scandinavian wolverine (Gulo gulo) populations. - Molecular Ecology 10: 53-63.

Whitman, J.S., Ballard, W.B. & Gardner, C.L. 1986: Home range and habitat use by wolverines in south-central Alaska. - Journal of Wildlife Management 50: 460-462.

Woodroffe, R. & Ginsberg, J.R. 2000: Ranging behaviour and vulnerability to extinction in carnivores. - In: Gosling, L.M. & Sutherland, W.J. (Eds.); Behaviour and conservation. Cambridge University Press, Cambridge, United Kingdom, pp. 125-140.

Worton, B.J. 1989: Kernel methods for estimating the utilisation distribution in home range studies. - Ecology 70: 164-168.

Paper III

Ecotonal patch choice in a perceived mountain species: spatio-temporal ranging behaviour of female wolverines in southern Norway

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Running title: Spatio-temporal ranging behaviour in wolverines

Abstract

1. Conservation of carnivores in an increasingly changing environment is much enhanced by understanding the decision-making processes underlying habitat patch choice. In a fluctuating environment incorporation of spatio-temporal activity patterns and home range use in resource selection models enhances the biological meaning of behavioural choices animals make along their path. Especially for central place foragers, such as the wolverine *Gulo gulo* L., the nature and strength of the trade-off between central place foraging and optimal foraging are likely to influence both spatio-temporal movement patterns and patch choice.
2. We investigated the spatio-temporal ranging behaviour of seven reproductive female wolverines in south-central Norway, based on GPS data collected in 2002-2005. The study was conducted using autoregressive models and discrete choice models, which incorporated individual preferences. Travel speed, home range use and selection for elevation were analysed in relation to spatial and temporal covariates (time-of-day and date).
3. Wolverines were more active during the night and in the home range periphery. The stronger selection for higher elevations towards the periphery of the wolverines' home ranges may be explained in two ways: (1) the location of the optimal central place lies in the "centre of gravity" of the food distribution, or (2) peripheral locations represent ranging movements for the purpose of transportation from patch to patch or central place. Over the summer, travel speed decreased and preference for lower-lying patches at day time increased, indicating a diminishing central place foraging movement pattern. At night wolverines selected similar patches at lower elevations all through the summer, enabling them to forage in the forest–alpine tundra ecotone; likely to be the patch with the highest expected profitability.

4. The elevation preferences throughout the summer clearly showed a change from central place foraging to optimal foraging in wolverines with dependent cubs. Whereas in the beginning of the summer cubs are placed at rendezvous sites, towards the end of the summer cubs grow more mobile and independent. Apparently, female wolverines are faced with a continuous, but diminishing, trade-off between providing food and shelter for their offspring throughout the summer.

Keywords: forest–alpine tundra ecotone, individual preferences, foraging strategies, random effects resource selection function, selective trade-off

Introduction

Human activities have resulted in worldwide habitat alterations, causing increased rates of habitat degradation, habitat loss, and fragmentation (Houghton, 1994; Noss, O'Connell & Murphy, 1997). Today, habitat alteration is generally considered to be the single greatest threat to species and ecosystems worldwide (Laurance & Bierregaard, 1997; Noss & Cooperrider, 1994). Many mammalian carnivores possess characteristics that may make them particularly vulnerable to landscape changes (Crooks & Soulé, 1999; Noss *et al.*, 1996; Sunquist & Sunquist, 2001; Woodroffe & Ginsberg, 1998). Being at the top of the food chain, carnivores have often specialized food requirements, tend to live at relatively low densities, occupy large home ranges, are long-lived, have low reproductive output, and long dispersal distances (Bennett, 1999; Sunquist & Sunquist, 2001). As they play a central role in the maintenance of the biodiversity, stability, and integrity of various communities (Berger, 1999; Crooks & Soulé, 1999; Noss *et al.*, 1996; Terborgh *et al.*, 1999), conservation of such sensitive species is a challenge worldwide. An important aspect in such cases is to understand the decision-making processes underlying habitat patch choice.

Probably the most important determinants of carnivore habitat choice are food and shelter. Foraging theory may thus give us insight into spatio-temporal choices that animals make. Or, as Sunde & Redpath (2006, and references therein) mentioned, behavioural responses to habitat heterogeneity have been used to identify essential resources and to quantify environmental constraints within heterogeneous landscapes. The optimal foraging theory states that habitat patches with the highest profitability should be preferred (Stephens & Krebs, 1986), where an unproductive and unpredictable environment necessitates a wide-ranging movement pattern and/or broader diet (MacArthur & Pianka, 1966). In a patchy environment, where prey has a non-random and aggregated distribution, the search pattern of the predator therefore is important for successful foraging (Fauchald, 1999; Grünbaum, 1998; Stephens & Krebs, 1986). Yet, habitat quality may also change with time (i.e., time-of-day or seasonal); changing its profitability. In a fluctuating environment the predator therefore has to continually evaluate ('sample') prey availability and profitability of patches in order to make optimal decisions (Krebs & Davies, 1984; Stephens & Krebs, 1986). The success of most foragers will thus be constrained by limits to their sensory perception, memory, and locomotion (Grünbaum, 1998), where an animal should forage in the patch with the highest *expected* profitability (Krebs & Davies, 1984; Pyke, 1984). Animals that depend on a central place (e.g., den site, rendezvous site, shelter) are faced with an extra trade-off, between habitat profitability and the travel distance to those patches. Often the optimal central place is not the one that only minimizes travel time among patches, but the one that also gives them (and their offspring) security from other predators and shelter from adverse weather (Magoun & Copeland, 1998; Orians & Pearson, 1979). Nonetheless, few animals are central place foragers throughout their life cycles, and the nature and strength of the selective trade-off between central place foraging and optimal foraging are likely to influence both movement patterns and patch choice (Orians & Pearson, 1979).

In this study we assessed the patch choices in a central place foraging predator of the northern hemisphere, the wolverine *Gulo gulo* L., by investigating their spatio-temporal ranging behaviour. The wolverine is a wide-ranging carnivore of the northern hemisphere. The wolverine is often viewed as an opportunistic carnivore inhabiting remote alpine areas (Banci & Harestad, 1990; Kelsall, 1981; Landa *et al.*, 1998; Whitman, Ballard & Gardner, 1986). As a result of their shyness and present habitat occupied, the wolverine has acquired a reputation as being a high alpine dweller (Carroll, Noss & Paquet, 2001; Landa, Lindén & Kojola, 2000; May *et al.*, 2006; Rowland *et al.*, 2003). May *et al.* (2006) argued that wolverines, although often characterized as habitat generalists, were especially selective about habitat quality in undeveloped areas when establishing their home range. Moreover, wolverines are particularly selective about habitat quality during the natal-denning period for reproductive females (Heinemeyer, Aber & Doak, 2001; Magoun & Copeland, 1998). When having cubs, female wolverines are forced to adopt a central place foraging strategy to provide her offspring protection and nourishment. However, to be able to find enough nourishment for both herself and her cubs, the mainly nocturnal wolverine females need to search for food where the chances of success are highest; in the most profitable patches.

Contrary to the general perception, wolverines in Norway preferred to use alpine shrub land and forest at lower elevations within their home ranges (May *et al.*, 2006). In addition, recent studies are providing increasing evidence that boundaries between ecological communities serve as hotspots for biodiversity (Brown, 2001; Kark & van Rensburg, 2006; Lomolino, 2001; Rickart, 2001). Ecotones or edge habitats may support higher densities of many prey species (e.g., Alverson, Waller & Solheim, 1988; Bayne & Hobson, 1998; Côté *et al.*, 2004; Kark & van Rensburg, 2006, and references therein; Sekgororoane & Dilworth, 1995) and ultimately a higher species abundance (Harris & Silva-Lopez, 1992; Ries *et al.*, 2004). In Scandinavia, the transition from alpine shrub land down towards the birch forest below the tree line forms the forest–alpine tundra ecotone (Grytnes, 2003). If this ecotone represents the area with the highest expected profitability, then we can expect wolverines to concentrate their movements within this transition zone. Also, given that mountain areas are relatively oligotrophic and stochastic environments, implies that they need large home ranges to support their energetic needs. Following the resource dispersion hypothesis, higher-lying areas would then be expected to be mainly used for transportation from patch to patch. We furthermore hypothesize that female wolverines face a trade-off between central place foraging and optimal foraging when having dependent cubs. In the beginning of the summer season, female wolverines are expected to show a strong daily response between using terrain at higher elevations where the cubs are placed at rendezvous sites, and using more profitable lower-lying hunting grounds at night time. As the season advances the need for central place foraging decreases as the cubs grow more mobile and independent. The daily response diminishes and their movement pattern more and more follows the optimal foraging strategy.

Material and methods

Study area

The study area was located in south-central Norway (Fig. 1). The area encloses many different ecological conditions, from remote mountainous areas in the west and centre where high densities of free-ranging sheep *Ovis aries* L. graze unattended in their summer pastures (June – September), to more accessible forest areas in the east where the wolverine co-exists with wolf *Canis lupus* L., lynx *Lynx lynx* L. and brown bear *Ursus arctos* L. In the mountainous regions some of the largest European populations of wild reindeer *Rangifer tarandus* L. are found (11,800 – 14,200 animals). In the north-eastern part of the study area, herding of semi-domestic reindeer is practised. Carcasses of reindeer and moose *Alces alces* L. constitute wolverines' most important source of winter food (van Dijk *et al.* unpublished data; Landa *et al.*, 1997; Magoun, 1987; Myhre & Myrberget, 1975). Roe deer *Capreolus Capreolus* L., mountain hare *Lepus timidus* L., grouse *Lagopus* spp., lemming *Lemmus lemmus* L. and various rodents and insectivores form possible sources of food for the wolverine; either as hunted prey or through scavenging. The habitat in the mountain ranges consists of mountain plateaus with peaks up to 2,286 m with bare rock (high alpine zone down to 1,800 m), which give way to alpine tundra with heath (e.g., heather *Caluna* spp., crowberry *Empetrum* spp.) and lichen (*Cladonia* spp.) vegetations (mid-alpine zone down to 1,400 m). At lower elevations, alpine shrub land (e.g., willow *Salix* spp., dwarf birch *Betula nana* L.) can be found down towards the treeline at 900 – 1,000 m (low alpine zone). From the treeline downwards, forests are comprised of mountain birch *Betula pubescens* L. (sub-alpine zone), Norway spruce *Picea abies* L. and Scots pine *Pinus sylvestris* L. with a varied undercover (e.g., blueberry *Vaccinium* spp., grasses *Molina* spp. / *Deschampsia* spp., mosses *Sphagnum* spp.). The low alpine zone and the sub-alpine zone form the forest–alpine tundra ecotone (Grytnes, 2003). The mountain ranges are divided by steep valleys. The forest region is mostly characterized by hills or lower mountains (up to 1,200 m) and wider valleys. The vegetation here is comprised of mixed forests of birch, spruce and pine, interspersed with open marches, natural meadows and heath. In the study area, snow is present from October/November until May/June depending on elevation. Human infrastructure is mainly concentrated at lower elevations in the valley bottoms. Recreational cabins can be found at higher elevations as well. Activities may consist of hunting, hiking and camping, and cross-country skiing.

GPS-data

Between 2002 and 2005 seven adult females have been (re-)captured at their secondary den sites in spring (Table 1). All individuals were outfitted with Televilt Prosrec 300 or Lotek 3300SL GPS collars. Usually these collars were programmed to render 7 positions per day over a period of 3 months, or 15 positions per day over a period of 1.5 months. The Lotek collar was programmed to render 3 positions per day until half of July, and 19 positions per day thereafter. The collars rendered on average 52 % ± 7 S.D. of the programmed positions, due to technical limitations (i.e., battery failure, premature drop-off) or due to lack of satellite contact (e.g., the animal being under ground, limited sky view).

Availability

At each position where the animal was recorded, the availability of resources was based on the previous position. Availability was defined within a circular area around the previous position, with a varying radius. This area was defined as the area of probable movement which was available to the animal at that point in time. Based on these areas of probable movement, each choice set consisted of 9 randomly chosen, non-used positions and one used position. The radius was based on the average speed of each animal throughout each tracked period and the time travelled from position t to position $t+1$. By using average speed, we incorporated the initial assumption that the animal had a fixed activity pattern throughout the day and over the season; enabling us to investigate temporal changes in their patch choice. Due to the time-interval between fixes and the loss of data, the speed measured between two consecutive positions is probably an underestimation of the actual speed travelled by the animal. To include this uncertainty in the area of probable movement for calculation of alternative positions available to the animal, we set the radius as:

$$r_{ij} = t_{ij} \cdot \left(\hat{s}_j + \frac{24 - p_j}{24 - f_{ij}} \cdot 2 \cdot \hat{\sigma}_j \right) \qquad \text{eqn 1}$$

For choice set *i* of animal *j* the radius r_{ij} is the product of the elapsed time from the previous fix (t_{ij}) with the average speed ($\hat{s}_j$) enlarged by the upper 95 % confidence limit ($2 \cdot \hat{\sigma}_j$) multiplied by a quality factor. This quality factor takes into account the effect of the tracking programme calculated as the number of positions taken per day (p_j; i.e., 3, 7, 15 or 19 positions per day), and the fix quality measured as the number of segments that could have been recorded between to consecutive positions given the tracking programme (f_{ij}, i.e., number of failed fixes). The average speed and standard deviation were calculated using only those positions which had a maximum f_{ij} of respectively 1, 2, and 3 for the tracking programmes of 7, 15 and 19 positions per day. This rendered an average maximum travel time of 3.15 hours (range 0 – 5 hours). Because average speed could not accurately be assessed for the tracking programme of 3 positions per day, we used the average speed and standard deviation from the tracking programme of 19 positions per day from the same collar (see Table 1). Due to loss of some data points, which increases the uncertainty of the actual moved distances, we only included those positions in the modelling which had a maximum f_{ij} of respectively 1, 2, 4 and 5 for the tracking programmes of 3, 7, 15 and 19 positions per day. This gave an average maximum travel time of 7.0 hours (range 5 – 9 hours).

Individual, temporal, spatial and topographic information

Movement data have a nested structure of correlated positions within individuals. Possible individual preferences may well affect habitat selection, especially when heterogeneity among few individuals is large (Crawley 2002). Individual resource use was, however, assumed to be constant over the years. Individual preferences and replications across years were taken into account in our modelling effort by including an individual grouping factor. Temporal and spatial information on each tracked individual were included in the model to reflect the effect of spatio-temporal behaviour; being time-of-day, day-of-the-year, and spatial location. Time-of-day (TIME) for each choice set *i* of animal *j* was calculated as:

$$TIME_{ij} = \frac{\cos(h_{ij} \cdot 15) + 1}{2} \qquad \text{eqn 2}$$

In equation 2, time-of-day for the choice set (h_{ij}) was defined as the recorded time in hours at the used position. This rendered a ratio between 0 at noon and 1 at midnight which follows the expected activity pattern of wolverines over the day (Landa *et al.,* unpublished data). Seasonal changes in ranging behaviour (day-of-the-year; PERIOD) were taken into account as a ratio which increased linearly over the summer season:

$$PERIOD_{ij} = d_{ij} / 365 \qquad \text{eqn 3}$$

with d_{ij} as Julian date of the used position in the choice set. The spatial location (SPACE) was measured for all observations within each choice set by the amount of dispersion relative to the harmonic mean centre (c.f., Dixon & Chapman, 1980), and was calculated as:

$$SPACE_{ij} = MIN_{i=1}^{n}(M_i) / M_i \qquad \text{eqn 4}$$

where

$$M_i = \left(\tfrac{1}{n-1} \sum_{k=1}^{n} \frac{1}{d_{ik}} \right)^{-1} \qquad \text{eqn 5}$$

and d_{ik} represents the distance between position *i* and *k* for all *n* positions. Because of the reciprocity of d_{ik} in the calculation, we added 1 m for distances <1 m. This measures equals 1 at the harmonic mean home range centre, and approaches 0 towards the periphery. Topographic features of all observations within each choice set were captured with elevation (ELEV), which was obtained from a 100x100 m Digital Elevation Model (DEM; Norwegian Mapping Authority). Because of the ecological differences between the mountain and forest areas, all locations for each individual received a regional coding (REGION; Table 1).

Spatio-temporal changes in activity patterns

The animal's movement pattern, and therefore patch choice, was assumed to be related to their travel speed (c.f., Pyke, 1984). Spatial and temporal changes in travel speed were investigated using linear autoregressive mixed effect regression. Travel speed was modelled with the spatial and temporal covariates: REGION, SPACE, TIME and PERIOD. Because a change in daily activity pattern over the season was suspected, the interaction term between TIME and PERIOD was also included. As travel speed is dependent on the sampling rate of the data and may vary among individuals, we included a random effect of travel time (in seconds) between positions (TRAVTIME) clustered over individuals (ID). First, the best fitting autoregressive order (*AR*) was established by comparing the fit among the full models with increasing *AR* orders. Thereafter, using the most parsimonious *AR* order, the model that best explained spatio-temporal travel speed in wolverines was constructed. For the analysis the lme function with corARMA correlation structure of the lme4 package was used (Bates & Sarkar, 2005) in the statistical software programme R version 2.4.1 (R Development Core Team, 2006).

Discrete choices with changing availability

Spatio-temporal activity patterns do, however, not tell us what patches (i.e., which part of the home range or what resources) were preferred when and where relative to availability in respect of where the wolverine was at a given time. As resource availability changes continuously over time and for individual animals, especially for animals with large home ranges and distinctive behavioural patterns (Manly *et al.*, 2002), a discrete choice resource selection function was used to model the spatio-temporal ranging behaviour of wolverines. Using discrete choice models avoids the problem of autocorrelated observations because availability is defined separately for each observation (Arthur *et al.*, 1996). Discrete choice models can in general be described by the following log-linear model:

$$w(x_{ij}) = \exp(\beta_0 + \beta_1 x_{ij1} + \beta_2 x_{ij2} + \ldots + \beta_p x_{ijp} + \gamma_{ij}) \quad \text{eqn 6}$$

where β_0 is the fixed intercept, $\beta_1, \beta_2, \ldots, \beta_p$ are selection coefficients for a vector x_{ij} of p covariates and γ_{ij} is the random effect for the location j being selected during the i^{th} choice, x_{ijp}, for $p = 1, 2, \ldots n$, estimated using multinomial logit regression (Gillies *et al.*, 2006).

In all models we accounted for individual preferences by incorporating a random clustering on individual (ID), and the choice sets (SET) nested within each individual. Our modelling exercise included three components of spatio-temporal ranging behaviour of wolverines; activity pattern, home range use and resource use. The animal's activity pattern was included following Hjermann's (2000) approach, by incorporating a fixed effect on step length from the previous position (STEP) within each choice set (c.f., Manly *et al.*, 2002). In this way the effect travel speed has on the movement pattern is included (i.e., the elapsed time within each choice set is equal, only the distance travelled differs). Home range use was incorporated with the use of a spatially explicit covariate (i.e., SPACE), as proposed by Rhodes *et al.* (2005), which also further diminishes spatial autocorrelation. Resource use was covered by the inclusion of elevation (ELEV). The full model included STEP, the spatial location and elevation, and all possible spatial and temporal first order interactions. To capture possible changes in the daily selection pattern over the season, we also included the second order interaction term between TIME and PERIOD. In choosing the most parsimonious models, we followed the information theoretic approach of Burnham & Anderson (2002) and Anderson *et al.* (2000). Model selection was determined using a backward stepwise procedure. The most parsimonious model corresponded to the model with the lowest Akaike Information Criterion (*AIC*) score (Burnham & Anderson, 2002).The model that could not be simplified any more without dropping a significant effect or violating the hierarchy principle (i.e., non-significant lower-order effects cannot be removed if a significant higher-order interaction of the same factors is present) was selected as the final one (c.f., Wu & Hamada, 2000). Finally, an individual-explicit model was constructed which included an individual grouping factor in addition to the fixed effects of the most parsimonious model.

Although discrete choice models are based on nominal polytomous data with repeated (correlated) observations (Manly *et al.*, 2002), Chen & Kuo (2001) proved that the log likelihood for Poisson log-linear models with random effects is equivalent to that for multinomial logit models. The advantage of using a Poisson log-linear model above a 'tricked' stratified Cox proportional hazards model, as proposed earlier by Manly *et al.* (2002), is that it enables the easy incorporation of random effects in the model. This is especially important to capture the effect of individual preferences and enables investigation of functional responses (Gillies *et al.*, 2006; Rhodes *et al.*, 2005). Statistics were performed in the statistical software programme R using the lmer function with a Poisson distribution of the lme4 library (Bates & Sarkar, 2005). Model fit was calculated using the Laplace approximation of the maximum likelihood.

Results

To assess the temporal autocorrelative structure of our data for travel speed, we performed autoregressive regression on the full model given in Table 3 using different autoregressive levels. An autoregressive level of 3 (AR3) gave the lowest AIC value (Table 2). We therefore continued to assess what influenced travel speed using the AR3 level. The two most parsimonious models indicated that travel speed increased towards the periphery of the home range, was higher at night time and decreased over the summer (Table 3). We found a slight regional effect (model Best II), with lower speed in the forest region. Given an average travel speed of 0.268 – 0.319 m/s in the home range periphery (for the forest and mountain region, respectively; Table 3, model Best I), and given the average SPACE in the forest and mountain region (0.144 ± 0.006 S.E. and 0.117 ± 0.004 S.E., respectively), the average travel speed throughout the home range was 0.215 – 0.276 m/s, respectively. Averaged over all individuals, approximately 80 % of all locations were found in the periphery of the home range (i.e., unclustered locations with SPACE<0.2; Fig. 2).

The backward stepwise procedure in establishing the most parsimonious models explaining spatio-temporal ranging behaviour (Table 4) showed that selection was neither affected by daily changes in spatial location (SPACE*TIME and SPACE*TIME*PERIOD), nor by regional differences (SPACE*REGION). Similarly, regional and seasonal changes in travel speed did not affect selection (STEP*REGION and STEP*PERIOD, respectively). The most parsimonious models ($\Delta AIC \leq 2$; Table 5) indicated that selection for a specific location increased with decreased travel speed (STEP). At night time, however, travel speed did not have any effect on the selection probability (STEP*TIME), as this effect evened out with STEP. The negative effect of travel speed on selection was also smaller at more clustered locations (STEP*SPACE). The selection probability decreased towards the periphery (SPACE), an effect that became stronger later on in the summer season (SPACE*PERIOD). Overall, there was a slight regional effect in selection, where wolverines in the mountain region had a stronger selection compared to animals inhabiting the forest region (models III and IV).

By including STEP as a covariate, thus assuming that availability decreases with increasing distance to the circle centre, most differences among the individuals and between the two regions were captured (Table 5; model V). Using this approach, not only the variation in the availability and speed between individuals or regions was explained, but also possible variations in the movement patterns within individuals. Although barely any regional differences were visible (models III, IV), one individual (model V; forest individual ID–2203) still separated itself from the others. Apparently, despite regional differences (see "Study area", Table 1) may induce differing ranging behaviour in the animals, only one individual differed in its ranging behaviour from the other individuals given our models.

We found clear spatial and temporal patterns in the selection for elevation. Table 5 and Fig. 3 show how the elevation used by the animals changed according to the regional, spatial and temporal location of the animal. Generally, wolverines selected for higher elevations (ELEV). In the periphery wolverines selected higher elevations compared to the home range clusters (ELEV*SPACE), where the wolverines selected less strongly for elevation at night time relative to midday (ELEV*TIME, Fig. 3A.). In more clustered locations (Fig. 3B.), they preferred to use lower elevations during the night, whereas they used higher elevations at daytime. Both in the home range centre and at the end of the summer season wolverines preferred to use lower-lying patches throughout the day with barely any daily pattern in patch choice (Figs 3B. and C.). In all, over the summer season both the selection strength for elevation (i.e., they preferred lower elevations, ELEV*PERIOD) and the daily pattern diminished (i.e., in September, ELEV*TIME*PERIOD, Table 5). Despite the elevational differences between the two regions, the selection strength for elevation differed only slightly between the two regions (Table 5, model IV), where the individuals in the forest region selected higher elevations relative to what was available to them. Yet, only one of the two least parsimonious of the four models (ΔAIC = 2) included this, non-significant, regional elevation effect.

Discussion

In this study we have attempted to elucidate how patch choice varies in space and time. Incorporating spatially and temporally explicit activity patterns and home range use in resource selection models enhances the biological meaning of behavioural choices animals make along their path. An animal's location in space and time, the way it perceives the surrounding landscape and its subsequent behaviour together determine what resources are available to it and what it chooses among the available resources (Arthur *et al.*, 1996; Hjermann, 2000; Olden *et al.*, 2004). An animal's perception and behaviour thus influences in shaping fine-scale decision-making processes, including its movement behaviour, choice of search strategy and habitat patch choice (e.g., Lima & Zollner, 1996; Olden *et al.*, 2004; Vuilleumier & Metzger, 2005). Ultimately this influences biological processes at broader spatial scales and higher levels of organization, such as regulating predator-prey interactions or species persistence in fragmented landscapes (Hassell & May, 1985; Russell, Swihart & Feng, 2003; Sutherland, 1998; Wiens *et al.*, 1993). To understand how landscape heterogeneity mediates animal movements, it is therefore important to consider the complex interaction between landscape patterns and an animal's spatio-temporal ranging behaviour.

Assuming that travel speed is associated with patch choice (Pyke, 1984), the daily activity pattern of wolverines clearly showed an increase in activity during the night. The decrease in travel speed over the summer likely indicates a diminishing central place foraging movement pattern. To elaborate on this, throughout the summer the selection for elevation only changed during day time, with an increasing preference for lower-lying patches. At night, all through the summer, similar patches at lower elevations were preferred by the wolverines. Thus, the difference between day time and night time patches lessened over the summer. Apparently, wolverines are throughout the summer faced with a continuous, but diminishing, trade-off between providing food and shelter for their offspring. Also, wolverines seemed to prefer to forage in patches at lower elevations throughout the summer. The elevations used by the wolverines during night time (i.e., approximately between 1,230-1,330 m and 800-900 m in the mountain and forest region, respectively) lie within the range of the forest–alpine tundra ecotone (Grytnes, 2003). It seems that wolverines utilize this ecotone for resting and foraging. A high abundance of species and high species richness, providing them with a variety of different prey species each having their own peculiarities, could well represent the patches with the highest expected profitability. Landa *et al.* (unpublished data) found that, given the assumption that biomass and productivity generally is higher at lower elevations, wolverine home range sizes were inversely correlated with elevation within the same region/latitude. Thus implying that wolverines living in a higher and less optimal habitat would need a larger home ranges to support their energetic needs (Ferguson, Higdon & Larivière, 2006; Macdonald, 1983), probably due to a greater availability and predictability of small prey (Landa *et al.*, 1997) and carrion (Persson, 2003) in lower-lying habitat. This may explain the regional differences in movement patterns (i.e., activity patterns and home range use) we found in our study, and may well signify adaptations to the foraging strategies in wolverines harmonized to the surroundings they inhabit.

We found a stronger selection for higher elevations towards the periphery of the wolverines' home ranges. Although this may seem contra-intuitive it may be explained in two, not necessarily mutually exclusive, ways. First, if the optimal central place (i.e., den site or rendezvous sites) is one that minimizes travel time among patches, then that site should lie in the "centre of gravity" of the food distribution (Orians & Pearson, 1979). This would imply that the highest point clustering would be expected to be found at lower elevations. Yet, previous studies have shown that although reproductive den sites are generally found just above the treeline, they are also found in rugged places that give wolverines and their offspring security from other predators and shelter from adverse weather (Magoun & Copeland, 1998). There may, however, exist a certain hierarchical trade-off between both requirements (i.e., central place versus suitable den site). Secondly, peripheral locations may also represent ranging movements for the purpose of transportation from patch to patch or central place, as could explain the higher travel speed in the periphery perceived in our study. This would then indicate that wolverines would prefer to use (i.e., forage or find shelter in) lower-lying ecotonal habitat (c.f., May *et al.*, 2006). These two suppositions would clearly merit further research on the choice and use of home range boundaries, home range overlap and territoriality.

The emergence of new GPS technology opened up a lot of new opportunities to study spatio-temporal movements of animals in the wild. However, it also generated new problems mostly connected to spatial and temporal autocorrelation of collected data (De Solla, Bonduriansky & Brooks, 1999; Legendre, 1993; Nielsen *et al.*, 2002). Here, we controlled for the autocorrelated structure of our data by using a discrete choice model (Arthur *et al.*, 1996; Hjermann, 2000; Manly *et al.*, 2002). Such a model stratifies the data per location, and compares each with what was locally available (in a moving circle centred on the previous location) to the animal at that time, thus minimizing temporal autocorrelation. The inclusion of a spatial covariate diminishes the spatial autocorrelative structure of the data (c.f., Rhodes *et al.*, 2005). Our study was based on an extensive GPS dataset for a mere seven individuals. Only one animal differed in its overall ranging behaviour from the other individuals; forest individual ID–2203. This wolverine's home range overlapped with the home range of a wolf pack. At the end of June, she and one of her cubs were (probably) killed by wolves only few kilometres from a wolf rendezvous site. Although we do not have any direct proof for this, its aberrant ranging behaviour may well have had a relation with the presence of this guild member (unpublished data). However, this was also the only animal which home range was largely placed below the treeline (791 m a.s.l., Table 1). In models which are based on large numbers of measurements on a few individuals, it is possible to get an accurate model of the way these animals' ranging behaviour change through space and time. However, there is less power for testing the significance of selection effects, especially if variation among individuals is large (Crawley, 2002). Still, to put this in perspective: our seven study individuals still represent over 8 % of all adult females in the southern Norwegian wolverine population (Flagstad *et al.*, 2006). If conservation of rare and elusive species is to be successful, information based even on a few individuals will prove to provide us with crucial knowledge of its biology in space and time.

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References

Alverson, W.S., Waller, D.M., & Solheim, S.L. (1988) Forests too deer: edge effects in Northern Wisconsin. *Conservation Biology*, **2**, 348-358.

Anderson, D.R., Burnham, K.P., & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912-923.

Arthur, S.M., Manly, B.F.J., McDonald, L.L., & Garner, G.W. (1996) Assessing habitat selection when availability changes. *Ecology*, **77**, 215-227.

Banci, V. & Harestad, A.S. (1990) Home range and habitat use of wolverines Gulo gulo in Yukon, Canada. *Holarctic Ecology*, **13**, 195-200.

Bates, D. & Sarkar, D. (2005) *lme4: Linear Mixed-Effects Models Using S4 Classes*, URL: http://CRAN.R-project.org, R package version 0.9975-0.

Bayne, E.M. & Hobson, K.A. (1998) The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed wood forest. *Canadian Journal of Zoology*, **76**, 62-69.

Bennett, A.F. (1999) *Linkages in the Landscape* IUCN, Gland, Switzerland / Cambridge, U.K.

Berger, J. (1999) Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proceedings of the Royal Society of London B*, **266**, 2261-2267.

Brown, J.H. (2001) Mammals on Mountainsides: Elevational Patterns of Diversity. *Global Ecology and Biogeography*, **10**, 101-109.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical informtaion-theoretic approach. 2nd edition* Springer-Verlag, New York, New York, USA.

Carroll, C., Noss, R.F., & Paquet, P.C. (2001) Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications*, **11**, 961-980.

Chen, Z. & Kuo, L. (2001) A note on the estimation of the multinomial logit model with random effects. *The American Statistician*, **55**, 89-95.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics*, **35**, 113-147.

Crawley, M.J. (2002) *Statistical computing: an introduction to data analysis using S-Plus* John Wiley & Sons Ltd., Chichester, U.K.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563-566.

De Solla, S.R., Bonduriansky, R., & Brooks, R.J. (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, **68**, 221-234.

Dixon, K.R. & Chapman, J.A. (1980) Harmonic mean measure of animal activity areas. *Ecology*, **61**, 1040-1044.

Fauchald, P. (1999) Foraging in a Hierarchal Patch System. *The American Naturalist*, **153**, 603-613.

Ferguson, S.H., Higdon, J.W., & Larivière, S. (2006) Does seasonality explain the evolution and maintenance of delayed implantation in the family Mustelidae (Mammalia: Carnivora)? *Oikos*, **114**, 249-256.

Flagstad, Ø., Andersen, R., Wärdig, C., Johansson, M., Brøseth, H., & Ellegren, H. (2006) Populasjonsovervåking av jerv i Skandinavia ved hjelp av DNA-analyse fra ekskrementer. Rapport 2005, Rep. No. 165. NINA, Trondheim.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., & Jerde, C.L. (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887-898.

Grünbaum, D. (1998) Using Spatially Explicit Models to Characterize Foraging Performance in Heterogenous Landscapes. *The American Naturalist*, **151**, 97-115.

Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291-300.

Harris, L.D. & Silva-Lopez, G. (1992) Fragmentation and the Conservation of Biological Diversity. In *Conservation biology. The theory and practice of nature conservation, preservation, and management* (eds P.L. Fiedler & S.K. Jain), pp. 197-237. Chapman and Hall, London.

Hassell, M.P. & May, R.M. (1985) From individual behaviour to population dynamics. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 3-32. Blackwell Scientific, Oxford.

Heinemeyer, K.S., Aber, B.C., & Doak, D.F. (2001) Aerial surveys for wolverine presence and potential winter recreation impacts to predicted wolverine denning habitats in the southwestern Yellowstone ecosystem.

Hjermann, D.O. (2000) Analyzing habitat selection in animals without well-defined home ranges. *Ecology*, **81**, 1462-1468.

Houghton, R.A. (1994) The worldwide extent of land-use change. *BioScience*, **44**, 305-313.

Kark, S. & van Rensburg, B.J. (2006) Ecotones: marginal or central areas of transition? *Israel Journal of Ecology & Evolution*, **52**, in press.

Kelsall, J.P. (1981) Status report on the wolverine, Gulo gulo, in Canada in 1981. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa.

Krebs, J.R. & Davies, N.B. (1984) *Behavioural Ecology. An Evolutionary Approach. Second Edition* Blackwell Scientific Publications, Oxford, U.K.

Landa, A., Lindén, M., & Kojola, I. (2000) Action plan for the conservation of wolverines (*Gulo gulo*) in Europe. Council of Europe Press, Strasbourg.

Landa, A., Strand, O., Linnell, J.D.C., & Skogland, T. (1998) Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology*, **76**, 448-457.

Landa, A., Strand, O., Swenson, J.E., & Skogland, T. (1997) Wolverines and their prey in southern Norway. *Canadian Journal of Zoology*, **75**, 1292-1299.

Laurance, W.F. & Bierregaard, R.O. (1997) *Tropical forest remnants: ecology, management, and conservation of fragmented communities* Chicago University Press, Chicago.

Legendre, P. (1993) Spatial autocorrelation: Trouble or New Paradigm? *Ecology*, **74**, 1659-1673.

Lima, S.L. & Zollner (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131-135.

Lomolino, M.V. (2001) Elevation Gradients of Species-Density: Historical and Prospective Views. *Global Ecology and Biogeography*, **10**, 3-13.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist*, **100**, 603-609.

Macdonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379-384.

Magoun, A.J. (1987) Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. *Canadian Field Naturalist*, **191**, 392-397.

Magoun, A.J. & Copeland, J.P. (1998) Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management*, **62**, 1313-1320.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second edition* Kluwer Press, New York, New York, USA.

May, R., Landa, A., Dijk, J., van, & Andersen, R. (2006) Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. *Wildlife Biology*, **12**, 285-295.

Myhre, R. & Myrberget, S. (1975) Diet of wolverine (*Gulo gulo*) in Norway. *Journal of Mammalogy*, **56**, 752-757.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., & Munro, R.H.M. (2002) Modelling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*, **13**, 45-56.

Noss, R.F. & Cooperrider, A.Y. (1994) *Saving nature's legacy: protecting and restoring biodiversity* Island Press, Washington D.C.

Noss, R.F., O'Connell, M.A., & Murphy, D.D. (1997) *The science of conservation planning* Island Press, Washington, D.C.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., & Paquet, P.C. (1996) Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, **10**, 949-963.

Olden, J.D., Schooley, R.L., Monroe, J.B., & Poff, N.L. (2004) Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology*, **73**, 1190-1194.

Orians, G.H. & Pearson, N.E. (1979) On the theory of Central Place Foraging. In *Analysis of Ecological Systems* (eds D.J. Horn, G.R. Stairs & R.D. Mitchell), pp. 155-177. Ohio State University Press, Columbus, Ohio, U.S.A.

Persson, J. (2003) *Population Ecology of Scandinavian Wolverines*. PhD, Swedish University of Agricultural Sciences, UMEÅ.

Pyke, G.H. (1984) Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, **15**, 523-575.

R Development Core Team (2006) *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria, URL: http://www.R-project.org.

Rhodes, J.R., McAlpine, C.A., Lunney, D., & Possingham, H.P. (2005) A spatially explicit habitat selection model incorporating home range behavior. *Ecology*, **86**, 1199-1205.

Rickart, E.A. (2001) Elevational Diversity Gradients, Biogegraphy and the Structure of Montane Mammal Communities in the Intermountain Region of North America. *Global Ecology and Biogeography*, **10**, 77-100.

Ries, L., Fletcher, R.J., Jr., Battin, J., & Sisk, T.D. (2004) Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. *Annual Review of Ecology and Systematics*, **35**, 491-522.

Rowland, M.M., Wisdom, M.J., Johnson, D.H., Wales, B.C., Copeland, J.P., & Edelmann, F.B. (2003) Evaluation of landscape models for wolverines in the interior northwest, United States of America. *Journal of Mammalogy*, **84**, 92-105.

Russell, R.E., Swihart, R.K., & Feng, Z. (2003) Population consequences of movement decisions in a patchy landscape. *Oikos*, **103**, 142-152.

Sekgororoane, G.B. & Dilworth, T.G. (1995) Relative Abundance, Richness, and Diversity of Small Mammals at Induced Forest Edges. *Canadian Journal of Zoology*, **73**, 1432-1437.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory* Princeton University Press, Princeton, New Jersey, USA.

Sunde, P. & Redpath, S.M. (2006) Combining information from range use and habitat selection: sex-specific spatial responses to habitat fragmentation in tawny owls *Strix aluco*. *Ecography*, **29**, 152-158.

Sunquist, M.E. & Sunquist, F. (2001) Changing landscapes: consequences for carnivores. In *Carnivore Conservation. Conservation biology series 5* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), Vol. 5, pp. 399-418. The Zoological Society of London, Cambridge.

Sutherland, W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour*, **56**, 801-809.

Terborgh, J., Estes, J.A., Paquet, P.C., Ralls, K., Boyd-Heger, D., Miller, B., & Noss, R.F. (1999) The role of top carnivores in regulating terrestrial ecosystems. In *Continental Conservation: Scientific Foundations of Regional Reserve Networks* (eds M.E. Soulé & J. Terborgh), pp. 39-64. Island Press, Washington.

Vuilleumier, S. & Metzger, R. (2005) Animal dispersal modelling: Handling landscape features and related animal choices. *Ecological Modelling*, **190**, 159-170.

Whitman, J.S., Ballard, W.B., & Gardner, C.L. (1986) Home range and habitat use by wolverines in southcentral Alaska. *Journal of Wildlife Management*, **50**, 450-463.

Wiens, J.A., Stenseth, N.C., Van Horne, B., & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126-2128.

Wu, C.F.J. & Hamada, M. (2000) *Experiments: Planning, Analysis, and Parameter Design Optimization* John Wiley & Sons, Inc., New York, New York, USA.

Table 1. Overview of the radio-tracked female wolverines in south-central Norway in 2002-2005.

Animal ID	Collar type	Tracked period	Programme (fixes per day)	# positions (stored / programmed)	Region	Home range elevation (m)
ID–1402	Televilt	06.05.2002 - 21.07.2002	7	609 / 1135	Mountain	1,413 ± 190
	Lotek	28.06.2004 - 09.09.2004	3 + 19	603 / 1062		
	Televilt	26.04.2005 - 21.09.2005	7	612 / 1032		
ID–1703	Televilt	26.04.2003 - 27.07.2003	7	332 / 638	Forest	931 ± 115
	Televilt	27.04.2004 - 13.07.2004	15	610 / 1150		
ID–1903	Televilt	28.04.2003 - 22.05.2003	7	64 / 160	Mountain	1,271 ± 128
ID–2203	Televilt	29.04.2003 - 03.07.2003	7	210 / 450	Forest	791 ± 90
ID–2603	Televilt	29.04.2004 - 13.09.2004	7	566 / 950	Mountain	1,101 ± 148
ID–2903	Televilt	07.05.2003 - 25.08.2003	7	418 / 763	Mountain	1,272 ± 199
ID–5505	Televilt	28.06.2005 - 03.08.2005	7	105 / 248	Mountain	1,366 ± 166

Table 2. Autoregressive model for travel speed fitted with maximum likelihood based on the full model given in Table 3.

Model	**Autoregressive order**				**Deviance**	**AIC**	**ΔAIC**
	1	2	3	4			
AR0					2245	2265	367
AR1	0.311				1900	1922	24
AR2	0.289	0.074			1881	1905	7
AR3	0.285	0.059	0.051		1872	1898	0
AR4	0.285	0.060	0.051	-0.002	1872	1900	2

Table 3. Model structures of the third order autoregressive (AR3) models describing spatio-temporal changes in speed of female wolverines.

Model	**Model fit**		**Fixed effects**					**Random effects**	
			covariate	coefficient	std. error	t-value	p-value	ID effect	st. dev
Full	Deviance	1872	intercept	0.250	0.077	3.264	0.001	intercept	0.227
	AIC	1898	REGION–forest[†]	-0.048	0.031	1.568	0.178	TRAVTIME	$-1.1e^{-5}$
	ΔAIC	1	SPACE	-0.368	0.035	10.419	<0.001	residual	0.332
			TIME	0.273	0.089	3.055	0.002		
			PERIOD	-0.253	0.147	1.721	0.085		
			TIME*PERIOD	0.223	0.177	1.255	0.209		
Best I	Deviance	1873	intercept	0.319	0.053	6.060	<0.001	intercept	0.229
	AIC	1897	REGION–forest[†]	-0.051	0.031	1.638	0.162	TRAVTIME	$-1.1e^{-5}$
	ΔAIC	0	SPACE	-0.365	0.031	10.344	<0.001	residual	0.333
			TIME	0.163	0.018	9.074	<0.001		
			PERIOD	-0.394	0.095	4.138	<0.001		
Best II	Deviance	1876	intercept	0.277	0.050	5.582	<0.001	intercept	0.245
	AIC	1898	SPACE	-0.365	0.035	10.361	<0.001	TRAVTIME	$-1.1e^{-5}$
	ΔAIC	1	TIME	0.164	0.180	9.102	<0.001	residual	0.333
			PERIOD	-0.368	0.094	3.931	0.001		

[†] Regional effect is given relative to REGION–mountain.

Table 4. Model fits of the discrete choice models describing spatio-temporal ranging behaviour in female wolverines. The models were fit using a backward stepwise procedure. Model names represent each previous model without the named covariate. The ranks in column two refer to the model structures given in Table 5.

Model	**Rank**	**Deviance**	**AIC**	**ΔAIC**
Full model		14359	14399	9
– SPACE*TIME*PERIOD		14360	14398	8
– STEP*REGION		14360	14396	6
– SPACE*REGION		14360	14394	4
– STEP*PERIOD		14361	14393	3
– SPACE*TIME	IV	14362	14392	2
– ELEV*REGION	III	14364	14392	2
– REGION	I	14364	14390	0
– SPACE*PERIOD	II	14367	14391	1
Model I + ID	V	14353	14389	-1

Table 5. Model structures of the discrete choice models describing spatio-temporal ranging behaviour in female wolverines. Models I to IV are the most parsimonious models; model V represents an individual explicit derivate of model I. The numbers in the random effects columns give the standard deviation.

Model	**Fixed effects**					**Random effects**	
	covariate	value	std. error	t-value	p-value	grouping factor	intercept
I	intercept	-2.839	0.083	34.030	<0.001	ID	$2.2e^{-5}$
	STEP	$-2.5e^{-4}$	$1.6e^{-5}$	15.880	<0.001	SET in ID	$2.2e^{-5}$
	STEP*SPACE	$6.1e^{-5}$	$2.3e^{-5}$	2.680	0.007		
	STEP*TIME	$2.5e^{-4}$	$1.9e^{-5}$	12.620	<0.001	Estimated scale	1.082
	SPACE	4.063	0.443	9.170	<0.001		
	SPACE*PERIOD	1.661	0.948	1.750	0.080		
	ELEV	$1.4e^{-3}$	$1.7e^{-4}$	8.530	<0.001		
	ELEV*SPACE	$-1.3e^{-3}$	$3.9e^{-4}$	3.320	<0.001		
	ELEV*TIME	$-1.1e^{-4}$	$2.1e^{-4}$	5.230	<0.001		
	ELEV*PERIOD	$-1.3e^{-3}$	$2.9e^{-4}$	4.530	<0.001		
	ELEV*TIME*PERIOD	$1.2e^{-3}$	$3.9e^{-4}$	3.150	0.001		
II	intercept	-2.820	0.083	34.050	<0.001	ID	$2.2e^{-5}$
	STEP	$-2.5e^{-4}$	$1.6e^{-5}$	15.930	<0.001	SET in ID	$2.2e^{-5}$
	STEP*SPACE	$5.9e^{-5}$	$2.3e^{-5}$	2.590	0.010		
	STEP*TIME	$2.5e^{-4}$	$1.9e^{-5}$	12.700	<0.001	Estimated scale	1.085
	SPACE	4.400	0.398	11.050	<0.001		
	ELEV	$1.4e^{-3}$	$1.6e^{-4}$	8.360	<0.001		
	ELEV*SPACE	$-9.0e^{-4}$	$3.1e^{-4}$	2.850	0.004		
	ELEV*TIME	$-1.1e^{-4}$	$2.1e^{-4}$	5.140	<0.001		
	ELEV*PERIOD	$-1.2e^{-3}$	$2.8e^{-4}$	4.210	<0.001		
	ELEV*TIME*PERIOD	$1.2e^{-3}$	$3.9e^{-4}$	3.030	0.003		
III	intercept	-2.821	0.112	25.239	<0.001	ID	$2.2e^{-5}$
	STEP	$-2.5e^{-4}$	$1.6e^{-5}$	15.854	<0.001	SET in ID	$2.2e^{-5}$
	STEP*SPACE	$6.1e^{-5}$	$2.3e^{-5}$	2.672	0.008		
	STEP*TIME	$2.5e^{-4}$	$1.9e^{-5}$	12.626	<0.001	Estimated scale	1.082
	REGION–forest[†]	-0.013	0.053	0.241	0.809		
	SPACE	4.070	0.444	9.167	<0.001		
	SPACE*PERIOD	1.669	0.948	1.760	0.078		
	ELEV	$1.4e^{-3}$	$1.7e^{-4}$	8.378	<0.001		
	ELEV*SPACE	$-1.3e^{-3}$	$3.9e^{-4}$	3.324	<0.001		
	ELEV*TIME	$-1.1e^{-4}$	$2.1e^{-4}$	5.236	<0.001		
	ELEV*PERIOD	$-1.3e^{-3}$	$3.0e^{-4}$	4.526	<0.001		
	ELEV*TIME*PERIOD	$1.2e^{-3}$	$3.9e^{-4}$	3.149	0.002		
IV	intercept	-2.771	0.119	23.254	<0.001	ID	$2.2e^{-5}$
	STEP	$-2.5e^{-4}$	$1.6e^{-5}$	15.811	<0.001	SET in ID	$2.2e^{-5}$
	STEP*SPACE	$6.0e^{-5}$	$2.3e^{-5}$	2.622	0.009		
	STEP*TIME	$2.5e^{-4}$	$1.9e^{-5}$	12.622	<0.001	Estimated scale	1.078

	REGION–forest[†]	-0.269	0.221	1.219	0.223		
	SPACE	4.037	0.447	9.035	<0.001		
	SPACE*PERIOD	1.650	0.950	1.736	0.083		
	ELEV	$1.4e^{-3}$	$1.8e^{-4}$	7.954	<0.001		
	ELEV*REGION–forest[†]	$2.7e^{-4}$	$2.2e^{-4}$	1.198	0.231		
	ELEV*SPACE	$-1.3e^{-3}$	$3.9e^{-4}$	3.232	0.001		
	ELEV*TIME	$-1.1e^{-4}$	$2.1e^{-4}$	5.204	<0.001		
	ELEV* PERIOD	$-1.3e^{-3}$	$3.0e^{-4}$	4.486	<0.001		
	ELEV*TIME* PERIOD	$1.2e^{-3}$	$3.9e^{-4}$	3.111	0.002		
V	intercept	-2.836	0.135	21.034	<0.001	ID	$2.2e^{-5}$
	ID–1703[‡]	-0.051	0.064	0.787	0.432	SET	$2.2e^{-5}$
	ID–1903[‡]	0.047	0.164	0.286	0.775		
	ID–2203[‡]	0.233	0.107	2.169	0.030	Estimated scale	1.085
	ID–2603[‡]	-0.028	0.061	0.458	0.647		
	ID–2903[‡]	-0.013	0.062	0.209	0.834		
	ID–5505[‡]	0.087	0.110	0.792	0.429		
	STEP	$-2.5e^{-4}$	$1.6e^{-5}$	15.867	<0.001		
	STEP*SPACE	$5.6e^{-5}$	$2.3e^{-5}$	2.475	0.013		
	STEP*TIME	$2.5e^{-4}$	$2.0e^{-5}$	12.556	<0.001		
	SPACE	4.071	0.441	9.231	<0.001		
	SPACE*PERIOD	1.941	0.954	2.034	0.042		
	ELEV	$1.5e^{-3}$	$1.7e^{-4}$	8.370	<0.001		
	ELEV*SPACE	$-1.4e^{-3}$	$4.0e^{-4}$	3.557	<0.001		
	ELEV*TIME	$-1.1e^{-4}$	$2.1e^{-4}$	5.330	<0.001		
	ELEV*PERIOD	$-1.4e^{-3}$	$3.0e^{-4}$	4.583	<0.001		
	ELEV*TIME*PERIOD	$1.3e^{-3}$	$3.9e^{-4}$	3.255	0.001		

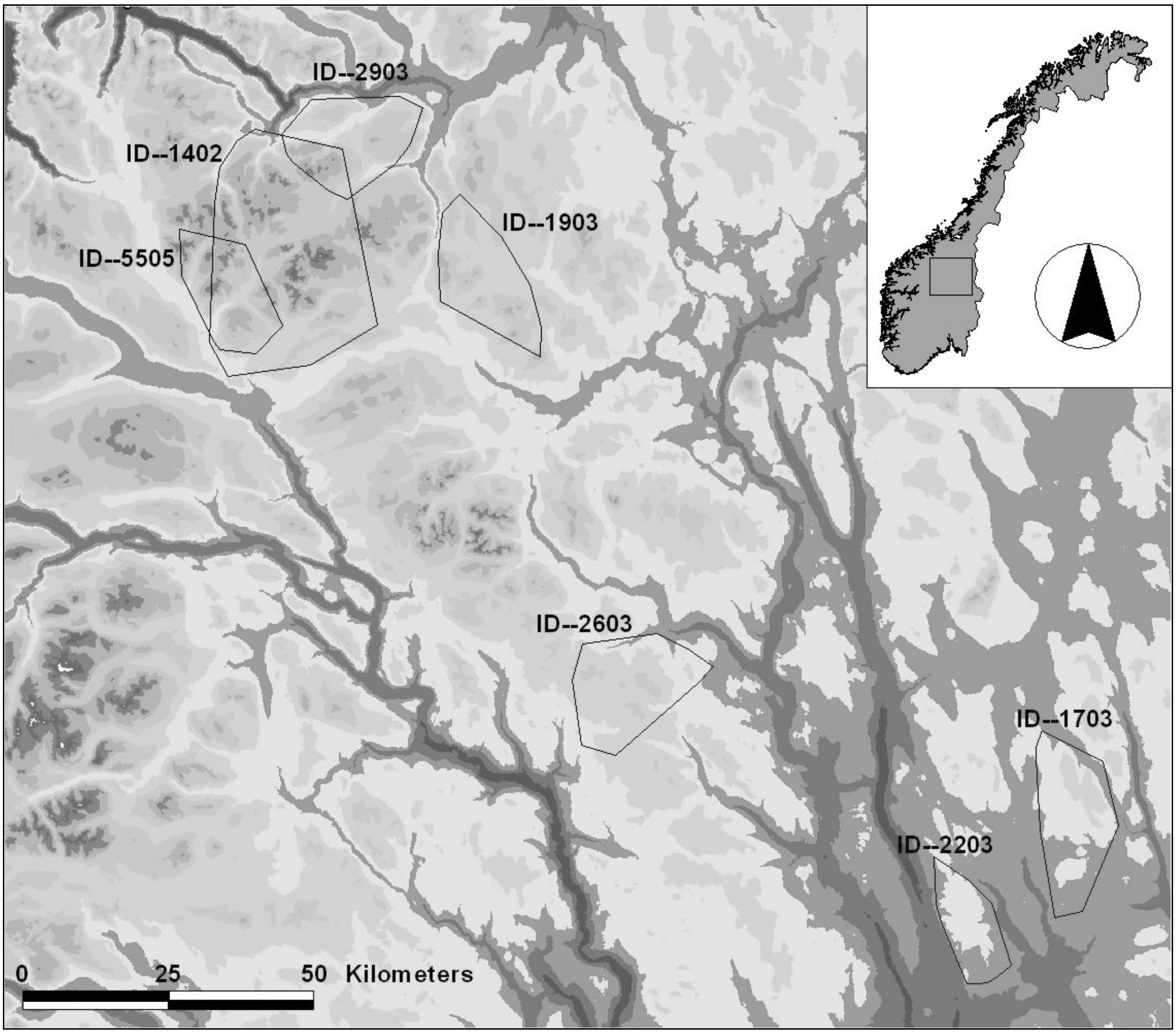
[†] Regional effect is given relative to REGION–mountain.

[‡] Individual effect is given relative to ID–1402.

Figure 1. Placement of the 100% MCP home ranges of the radio-tracked female wolverines in southern Norway, with the approximate location of the study area within Norway as inset. Darkest shadings represent elevations below treeline; lighter shading above.

Figure 2. Proportional distribution of the spatial clustering of radio-tracking locations averaged (+SD) over the seven radio-tracked female wolverines in southern Norway.

Figure 3. Selection strength (y-axis) for elevation (x-axis, in m a.s.l.) at the first of May (PERIOD = 0.33), July (PERIOD = 0.50) and September (PERIOD = 0.67) in the home range periphery (A., SPACE = 0.0), home range centre (C., SPACE = 1.0), and in-between (B., SPACE = 0.5), given for midday (solid line, TIME = 0.0), morning/evening (dashed line, TIME = 0.5) and midnight (dotted line, TIME = 1.0). Values above 1 on the y-axis indicate selection for higher elevations, whereas below 1 indicate selection for lower elevations. The graphs are based on model I given in Table 5.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ID--1402
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25
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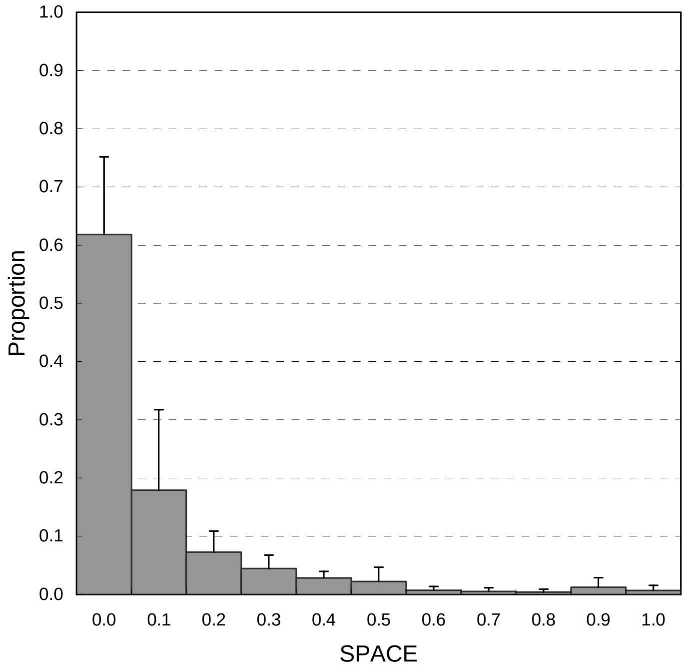
Fig. 1.


1.0
0.9
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Proportion
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1.0
SPACE

Fig. 2.

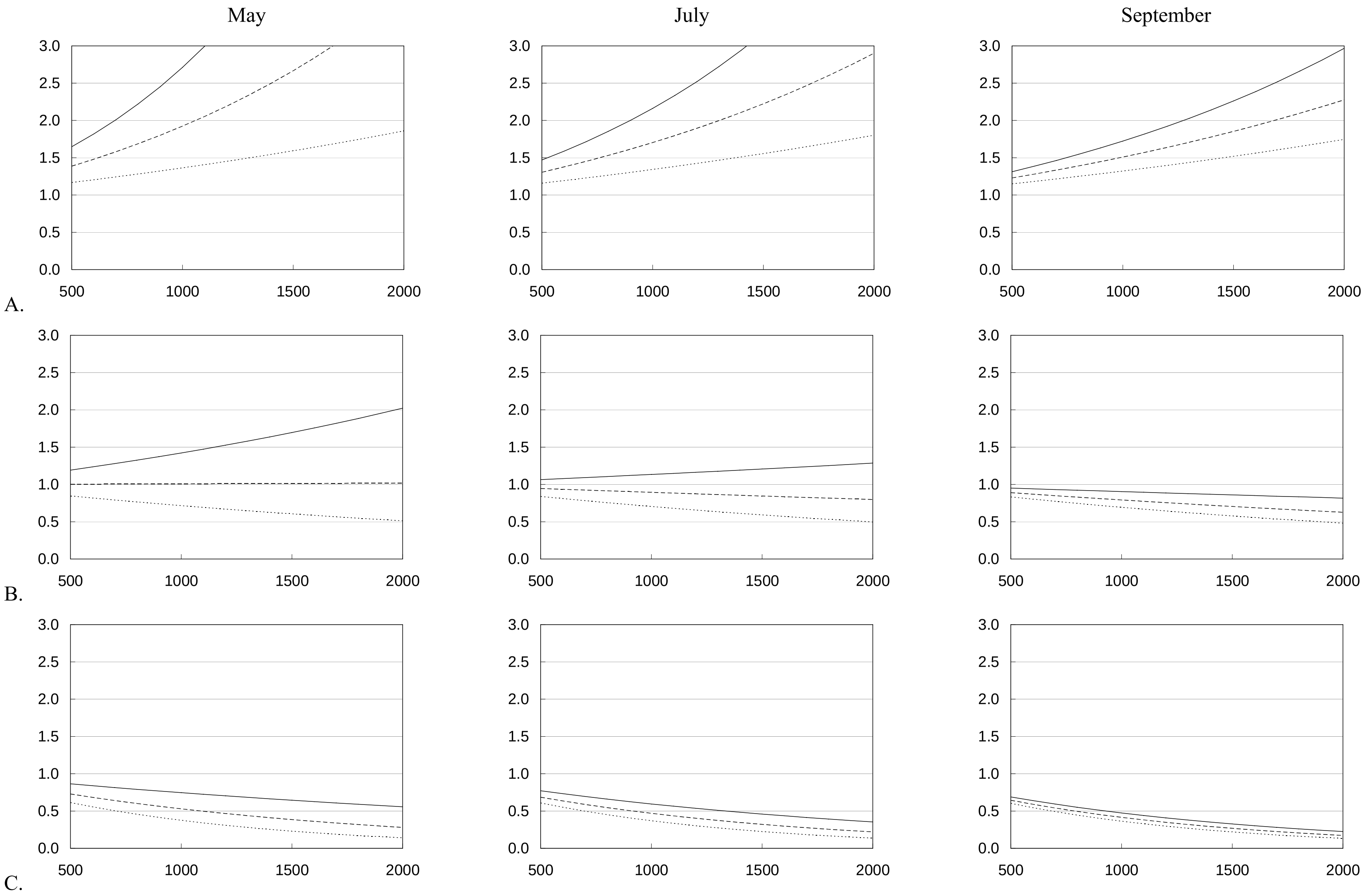

Fig. 3.

Paper IV

Maternal care in wolverines: activity patterns from the den to cub independence

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Running title: Maternal care in wolverines

Abstract

The solitary wolverine *Gulo gulo* is the only non-hibernating large carnivore in the northern hemisphere that gives birth during early spring (February - March). We recorded activity patterns and food caching habits of wolverine family groups through carcass trials and intensive radio-tracking. In the parturition and weaning period, female wolverines apparently rely on food caches and spend most of the time together with their cubs. Activity patterns of females over the denning period correlated with cub growth and presumably consumption of food caches. Over the rearing period, the mother-cub distances increased significantly and by early September, cubs were nearly full-grown and independent from their mother. This implies almost a seven month rearing period which is almost twice as long as for social canids within the same guild (wolf *Canis lupus*, red fox *Vulpes vulpes*, arctic fox *Alopex lagopus*). In general, timing of reproductive seasons is determined by availability of food as well as offspring growth and survival. Being solitary, theoretically is disadvantageous and strongly affects the ability to provide food and simultaneously offer protection for their offspring. However, wolverines seem to have counteracted such constraints by having food caches, early birth in den sites when cubs are small and altricial, and prolonged maternal care until cubs are full-grown and independent before the onset of winter.

Keywords: *Gulo gulo*, activity patterns, cub growth, family groups, early parturition, food hoarding, reproduction

Introduction

The behaviour and timing of parturition in most animals is determined by phylogenetic as well as environmental constraints. The ultimate causes for the timing of reproductive seasons are availability of food and the need to ensure that cubs are born at the most optimal time for their growth and survival (Ferguson et al. 2006; Vander Wall 1990).

The wolverine *Gulo gulo* is the only non-hibernating large carnivore in the northern hemisphere that gives birth during late winter/early spring. Females of this solitary species give birth from mid February to early April (Landa et al. 2000; Banci & Harestad 1988). This time of year may be an inhospitable time to give birth. Such early parturition and subsequent maternal care means that the solitary female will face a trade-off between providing protection for the altricial cubs and being away searching for food. Ungulate carrion however, may be more plentiful in early spring, which may favour parturition at this time in wolverines (Persson 2003; Banci 1994). Parturition in Norway was also shown to correspond closely with the period when reindeer were most vulnerable to predation (Bevanger 1992; Haglund 1966). Security cover for cubs may also be enhanced during winter; since snow tunnels or snow caves are characteristic natal and maternal dens for wolverine in many areas (Haglund 1966; Pulliainen 1968; Myrberget 1968; Banci 1994; Magoun & Copeland 1998).

Normally, wolverines utilize vast home ranges and occur at low densities (Hornocker & Hash 1981; Whitman et al. 1986; Landa et al. 1998). They are known as typical food hoarders and larger prey is dismembered and hidden in caches for later use (Haglund 1966; Landa et al. 1997). This implies that they are adapted to utilize leftovers over a large surface area in highly stochastic environments. However, animals that store sufficient quantities of food are able to relax the constraint imposed upon them by seasonal cycles in food availability (Vander Wall 1990).

In mammals with few offspring, life history traits and cub rearing should be adjusted to allow for the highest possible survival. For example, mustelids of high latitude seasonal environments have delayed implantation, which decouples the timing of mating and parturition allowing both to occur during the optimal, but short summer season (Ferguson et al. 2006). For a medium-sized carnivore like the wolverine, with an average of 1.9 cubs per litter (Persson et al. 2006), cub growth should be adjusted to enable cubs to reach nutritional independence before the onset of winter.

In many northern social living canid species *Canidae,* where two or more individuals provide food for the offspring (Moehlman 1989), young are born in late spring and still full-grown during autumn. For a female that raises young without the help of a male or other congeners, demands of lactation presumably place high energetic demands on the mother's nutritional status (Banci 1994; Persson et al. 2006). A strategy of stored food caches at, or close to the den site will shorten the time the female must be away from the den while the cubs are small, immobile, and vulnerable to predation. It is also likely that declining food stores in the proximity of the den site will require the female to spend time further away from the den at the increased risk of cubs being killed by other predators or conspecifics. Intra-guild predation on wolverines has been documented (Magoun & Copeland 1998; Copeland 1996; Banci 1994; Hornocker & Hash 1981; Boles 1977; Burkholder 1962), and Persson et al. (2003) suggested that intra-specific predation on juveniles (i.e., infanticide) plays a substantial role in wolverine population dynamics. The importance of den sites and food caches in the biology of wolverines, therefore, likely lies not only in the provision of shelter for the cubs from the elements but also enabling the mother to provide protection from predators during the infant period (Magoun & Copeland 1998).

Inhabiting a highly stochastic and unproductive environment places severe constraints on the reproduction in a solitary breeder like the wolverine. In coping with these constraints, wolverines adopt a denning strategy and cache food for later use. Bringing forth cubs early in the spring using den sites dug out of the snow enhances the predictability with regard to previously cached food and enables a prolonged parturition in order to optimize cub growth and survival. Based on this, we hypothesized that cubs have a relatively fast growth until weaning, and that the female's activity outside the denning area is limited during this period. When cubs become larger and food stored around the den site is likely to become depleted, the females are expected to become more active and will be away from the natal den for longer time periods. After the family group has left their natal den and denning area, we predict that activity patterns of wolverine family groups will be characteristic of non-social mammals (i.e. nomadic lifestyle within their joint home range) where family members stay close together early in the summer and demonstrate diminishing group association over the summer (Linn 1984; Sandell 1989). Finally, cubs should be expected to be almost full-grown and nutritional independent before the onset of winter.

Study area

The study area was situated in Troms County in northern Norway (68°N 19°E). Additional data on denning activity was collected in south-central Norway (62°N 9°E) and Sarek, northern Sweden (67°N 17°E).The landscape of inner Troms and Sarek consists of high alpine plateaus with peaks above 2,000 m above sea level, separated by steep valleys. The treeline lies between 600 and 700 m above sea level. Mountain birch *Betula pubescens* woodlands form a band between the alpine habitats and the boreal forests dominated by Scots pine *Pinus sylvestris* and Norwegian spruce *Picea abies* at the lowest altitudes. Human development is mainly concentrated in the valley bottoms. The main human activities are hiking, cross-country skiing and hunting. Semi-domestic reindeer *Rangifer tarandus* are herded throughout both regions by Sámi herders and few domestic sheep *Ovis aries* are grazed in inner Troms, but not in Sarek. Moose *Alces alces* are present in the forested habitats in both areas. In addition, Eurasian lynx *Lynx lynx*, which is a major predator of semi-domestic reindeer (Pedersen et al. 1999), and brown bear, which can occasionally kill moose and reindeer, are both present in these northern regions, but occur at higher densities in Sarek (Swenson et al. 2000). Further details of the ecology of the study area are provided in Vangen et al. (2001).

The landscape, habitats, and climate of south-central Norway are broadly similar to the northern areas, except that the treeline is higher (800 – 1,000 m) and the climate is less continental. Wild mountain reindeer are found throughout alpine habitats. Relatively high densities of free-ranging sheep are grazed during the summer (June – September). Moose, red deer *Cervus elaphus*, and roe deer *Capreolus capreolus* are found in lower altitude forest regions. Lynx are present around the fringes of the study area but seldom venture into the alpine habitats occupied by wolverines and there are no other ungulate predators in the area. Further details are provided in Landa et al. (1997; 1998).

Material and methods

During a 5-year period from 1996 through 2000, 29 wolverine cubs (8 males; 21 females) were captured from 16 litters. Thirteen different females produced these 16 litters, and 12 of these 13 females were radio marked along with all 29 cubs. All cubs and 11 females were captured at secondary dens in the beginning of May. Two cubs died within the first three months after they were captured presumably killed by another wolverine. Adult females were equipped with Telonics® implant transmitters (IMP/400/L) or collars (mod. 315) with an expected operating life of 24 to 36 months. All cubs were equipped with Telonics® implant transmitters (IMP/300/L or IMP/210/L) with an expected operating life of 9 to 13 months. Capturing and handling of animals was done according to national regulations. Radio tracking of these animals was carried out by fixed-wing aircraft (Cessna C-172 and Piper cub), helicopter (Eucoril and Bell Jet Ranger), car, snowmobile, and by foot. Positions of animals tracked from the ground were determined by triangulation in most cases, and a position quality assessment was given by assigning a radius (in meters) surrounding the position. All positions used within this study had a precision of ≤ 1,000 m.

Hoarding activity

Systematic notes on minimum number of reindeer (by counting unique body part remains) found inside primary dens were obtained by visiting den sites in early summer after den abandonment. Hoarding behaviour was obtained by systematic trials. One adult female reindeer carcass was embedded in snow close to a wolverine den and followed by direct observation using night binoculars in the south-central study area. In the Troms study area, small radio transmitters (Televilt®) were attached by wire on body parts of domestic reindeer carcasses killed by lynx (legs, head, neck and spine/thorax). These carcasses were revisited regularly (once a week) and tracked using radio-tracking equipment (see description above) to record the distance over which the different body parts were moved. Furthermore, several random observations obtained during field work on hoarding behaviour have been recorded.

Denning activity

Activity data in denning areas was collected for six female wolverines in Norway (3 and 2 in northern and south-central Norway respectively) and 1 female in Sweden (Table 1). Five of these females were radio marked with an activity collar or implant (Telonics®), which gave a signal with a high pulse rate (circa 1.5/second) when the animal was active and a low pulse rate (circa 1.0 /second) when the animal was passive, thereby allowing us to monitor activity periods of the females within the denning area. The sixth female was marked with a standard VHF radio collar (Televilt®) for which only the strength of the signal was known. We recorded activity in the denning areas in the spring (mid March - mid May of 1993-1998).

Activity signals were recorded with automatic data loggers (Televilt RX 900) that were placed at the valley bottom, approximately 1.5 km from the natal den site and monitored using two directional VHF antennas (Sirtrack®) pointed at each side of the natal den, thus covering 500 – 1000 meters at each side pending on local topography and movement by the female tracked. The data loggers were powered by solar cells and a battery. Antenna number, date, time, and signal strength and pulse rate were recorded, as well as the transmitter frequency of the monitored female in question. The data loggers were checked and data downloaded once a week on a laptop. Because of the local topography and the location of den sites, a denning area was defined as the area covered by the data logger.

Two methods were used to estimate the time the female was inside or outside the denning area. In Troms, and in Sarek, the data loggers also registered ‘dummy’ frequencies next to the female’s frequency. The strength of the ‘dummy’ signals allowed us to rule out disturbance on the actual VHF frequencies. The data loggers in south-central Norway searched for the female’s frequency every 15 minutes. The time spent outside the denning area was therefore registered as being the time between the last registered signal and the first new registration.

For the females with an activity collar, the data was put in a matrix where the activity, rounded in periods of 15 minutes over the day, was noted. We assumed that wolverines were most active at night (Zielinski 1988), so we analyzed activity from 1200 hr to 1200 hr the next day. For all females we noted the time when she moved out of the range of the data logger (outside denning area) and when she returned (inside denning area), rounded to the nearest 15 minutes.

Cub independence and body growth

Cub independence was determined for 16 family groups in Troms between 1996 and 2000. For each family group of wolverines, each position for each cub was assessed according to whether it was tracked together with or separated from its mother. For all individuals, a maximum of one position a day was used in the evaluation to achieve biologically independent positions. We considered individuals in a family group as being together when their signals coincided on the same date at the same time, plus or minus 15 minutes. We used all positions of the adult females and cubs until the cubs reached one year of age. Because wolverines generally give birth in late February to early March in the study area (Landa et al. 2000), a year was calculated from March 1st to March 1st the following year. To determine the length of period the cubs were dependent on their mother, we calculated the period when cubs and mothers were together or alone. We pooled all cubs together and grouped them in 7-days (week) intervals from March 1. We defined independence (splitting up of family groups) as the time of year when the proportion of cases for which the cubs were alone exceeded the time spent with their mother and/or together with their siblings. We compared the proportion of independence in cubs to profile length and weight (Landa & Skogland 1995), which we used to represent cub growth in wolverines. We obtained this information from long-term data collection from shot and marked individuals throughout Norway.

Statistics

To identify differences in activity patterns in denning areas, Wilcoxon signed rank tests were used. Trends in monthly changes in activity patterns were analyzed with linear regression (ANOVA), whereas, trends in daily activity patterns were investigated using quadratic regression. The time cubs spent with or separated from their mother was investigated with the use of sigmoid regression. Timing of independence of cubs was calculated as the 7-day period when the trend line of the proportion of time females spent together with their cubs drops below 50%. We analyzed possible variation in independence caused by growth parameters, i.e., profile, length, and weight measured during catching and marking the cubs using a linear univariate (ANOVA) model. Trends in average distances between females and her cubs were analyzed using linear regression. Differences in average distances before and after independence were tested with a Mann-Whitney U-test. Statistics were performed in SPSS for Windows version 11.0.1 (SPSS Inc.). Non-linear multivariate regressions were performed in SigmaPlot 2000 (SPSS Inc.).

Results

Denning activities

In the altricial parturition and weaning period (March – April), female wolverines spent significantly more time, more than two-fold, inside than outside the denning area (16.4 and 7.3 hours, respectively; $Z = -7.264$, $p < 0.001$) (Table 2). Inside the denning area females spent more time, nearly four-fold, being passive than active (13.0 and 3.4 hours respectively;

$Z = -5.555$, $p < 0.001$). The total passive time also exceeded the time spent active ($Z = -2.364$, $p = 0.018$).

The total time spent outside the denning area increased over weekly periods ($F_{1,111} = 50.016$, $r^2 = 0.311$, $p < 0.001$). Although we found little variation in the activity of female wolverines inside the denning area over weekly periods ($F_{1,111} = 7.591$, $r^2 = 0.064$, $p = 0.007$), they did spend less and less passive time inside the denning area ($F_{1,111} = 30.091$, $r^2 = 0.213$, $p < 0.001$). In March (week 2 through 4), the time spent outside the denning area was less than or equal to the time spent active inside the denning area, but in May (weeks 9 through 11), the total time spent outside the denning area was higher than or equal to the time spent passive within the denning area (Figure 1).

The female wolverines showed a strong trend (Figure 2) in the timing of daily activities inside and outside the denning areas (quadratic regression: outside $F_{2,93} = 346.335$, $r^2 = 0.882$, $p < 0.001$; active inside $F_{2,93} = 9.824$, $r^2 = 0.174$, $p < 0.001$; passive inside $F_{2,93} = 398.295$, $r^2 = 0.895$, $p < 0.001$). Time spent outside the denning area increased during the evening and peaked around midnight. Passive time inside the denning area peaked around midday. Activity inside the denning area showed a minimal response to time of day as seen from the low variability explained (17 %).

Food caching behaviour

In the period 1996 to and including 2000, the minimum number of reindeer individuals cached at wolverine primary den sites during spring, counted by body part remains, ranged from 0 – 7 different carcasses (mean: 1.87 + 0.5 SE, range: 0-7).

Several random observations during late winter/early spring have shown whole reindeer carcasses being divided and cached by wolverines within few nights. The observations at a reindeer carcass embedded in the snow close to a den showed that it was parcelled and cached by the denning female within two nights. The systematic trial, by attaching transmitters to body parts of ten carcasses of domestic reindeer killed by lynx, showed that these for a great part were utilized by wolverines that removed and caching body parts to different locations (Table 3).

Den abandonment

For the 16 family groups we studied, den abandonment was established via radio tracking. After 10 weeks from March 1st (10.31 ± 0.44 SE), all family groups had left the denning area, after which, we located them at daybeds (rendezvous sites) or active within their joint territory.

Cub independence

Over the subsequent rearing period (mid May to independence), the proportion of time females spent together with their cubs decreased significantly ($F_{2,45} = 157.421$, $R^2 = 0.880$, $P < 0.0001$). Independence occurred at the beginning of September, on average 26 weeks (or: 182-188 days) after March 1st (Figure 3, solid line). Break-up of the family groups gradually took place over the period between week 12 and 44. The proportion of time siblings were together without the mother versus separated from each other changed significantly over time ($F_{2,37} = 98.368$, $R^2 = 0.849$, $P < 0.001$). Sibling pairs separated at the end of September, on average 30 weeks (210-216 days) after March 1st (Figure 3, dashed line). Break-up of sibling pairs took place over the period between week 23 and 35. Separation of male and female cubs from the mother showed a clear relationship to weekly period from March 1st (females: $F_{2,44} =$

127.375, $R^2 = 0.858$, $P < 0.001$, independence after 26 weeks; males: $F_{2,25} = 21.583$, $R^2 = 0.652$, $P < 0.001$, independence after 25 weeks). Comparison of male cubs versus female cub's independence from mother showed a higher proportion of independence in male relative to female cubs (exponential curve, $F_{2,22} = 30.603$, $P < 0.001$, Figure 4). Over the entire year, the log-transformed distance between mother and cub increased significantly over the weekly periods (Figure 5; $F_{1,43} = 144.009$, $R^2 = 0.770$, $P < 0.001$). The average distance (± SE) between mother and cubs over the entire year was 4,961 ± 302 meters when separated. Before sibling break up, the correlation between age of offspring and mother – cub distance was strong ($F_{1,23} = 50.098$, $R^2 = 0.685$, $P < 0.001$; 3,295 m ± 361 SE), but was absent thereafter ($F_{1,19} = 0.007$, $R^2 < 0.001$, $P = 0.933$; 5,801 m ± 397 SE). We found no significant sex-specific difference in mother – cub distances. Although we did not define or measure dispersal in this study, two distances, recorded after independence, were exceptionally large (34,942 and 43,463 meters). These two distances were excluded from the analyses as outliers.

Profile length in wolverine cubs followed an exponential curve ($F_{1,40} = 633.019$, $R^2 = 0.970$, $P < 0.001$) until it reaches an average length of 156.64 mm (Figure 6). Cubs reach 95% of their first-year's profile length at 25 weeks after March 1st (birth date). Nearly 75% of the profile growth occurs in the first 10 weeks of life. Weight development in wolverine cubs followed a sigmoid curve ($F_{3,39} = 68.823$, $R^2 = 0.841$, $P < 0.001$) until it reaches an average weight of 12.04 kg (Figure 6). Cubs attain 95% of the first-year's weight at 39 weeks after March 1st. In the first 10-15 weeks, weight strictly follows the sigmoid curve, afterwards becoming more scattered.

As expected, weight and profile length were closely correlated with each other (Spearman's $R^2 = 0.859$, $P < 0.001$). An ANOVA model, with independence as a dependent variable and profile length and weight as covariates, showed that independence was significantly influenced by weight ($F_{1,34} = 5.918$, $P = 0.020$), but not by profile length ($F_{1,34} = 0.918$, $P = 0.345$). Weight therefore explained more variation (partial $R^2 = 0.385$) in independence than did profile length (partial $R^2 = 0.162$). Both parameters together explained 67% of the variation in independence ($F_{2,34} = 33.893$, $P < 0.001$). For female cubs, independence tended to be explained more by weight ($F_{1,21} = 3.458$, $P = 0.077$, partial $R^2 = 0.376$) than profile length ($F_{1,21} = 0.282$, $P = 0.601$, partial $R^2 = 0.115$) with 67% of the variation in independence in female cubs explained by both parameters together ($F_{2,21} = 21.284$, $P < 0.001$). For male cubs, both parameters together explained 52% of the variation in independence ($F_{2,12} = 6.563$, $P = 0.012$); neither weight ($F_{1,12} = 0.209$, $P = 0.656$, partial $R^2 = 0.131$) nor profile length ($F_{1,12} = 0.066$, $P = 0.802$, partial $R^2 = 0.074$) could explain any variation separately.

Discussion

Denning activity

Although different aspects of denning in reproductive wolverines have been described previously (Magoun 1985; Myrberget & Sørumgård 1979; Myhre & Myrberget 1975; McCracken 1985), our study is the first systematically collected documentation of female activity patterns when cubs are altricial. Our findings show that reproductive females spent most time passively, assumingly with, or in close vicinity, of their offspring while inside the denning area. However, rapid growth of cubs and demands of lactation place increased energetic demands on the mother. We assume the female is forced to increase her foraging time to continuously provide enough food for her offspring. During the parturition and weaning period (mid April – May), we found that the total time spent outside the denning area increased over time and the female spent less time passively inside the denning area. By nine weeks, the time spent outside the denning area exceeded the time spent passively inside the denning area. Cubs are weaned for nine to ten weeks (Iversen 1972; Krott 1960) and in the first weeks of May the natal den is abandoned (Magoun 1985; Myhre & Myrberget 1975). Our results showed that denning females in our study area had a nocturnal daily activity pattern. The peak in their activity outside the denning area was recorded around midnight. Between 0600 and 1500 there was little activity outside the denning areas. This nocturnal activity pattern was similar for fishers *Martes pennanti* (Paragi et al. 1994), but contrary to north-western Alaska, where wolverines left their dens at midday to forage when ground squirrels were active (Magoun 1985).

Foraging and anti-predator strategy

Diet studies of wolverine females have shown that large herbivores, mainly reindeer, are prevalent in the diet during the denning period (Landa et al. 1997). According to Sandell (1989), reproductive success of females that must rear young alone closely correlates with the amount of energy they can allocate to reproduction. For wolverines this amount of energy is in turn determined by the combined effect of the preceding year's reproductive effort and winter food availability (Persson 2003). Raising altricial cubs to weaning dictates brief foraging trips for the female during the denning period and is consistent with Haglund (1966), who suggested that food caching is especially important in the vicinity of parturition dens to reduce the time spent foraging. Subsequent consumption of this food may be an important determinant for the female wolverine's condition at the time of pregnancy and early lactation (Persson 2003) and may supplement the diet of growing young (Pasitschniak-Arts & Larivière 1995; Vander Wall 1990).

Time spent in the den together with their cubs is likely related to thermoregulation requirements of the cubs, and/or protection before the cubs have grown enough to be able to engage in escape behaviour (Magoun & Copeland 1998). Juveniles are likely to be more vulnerable to predation during the period when they are left unattended in the den (March-April), when they have just left the den site in early May (Landa et al. 1997; Magoun 1985), and when becoming independent in August – September (Vangen et al. 2001). Although wolves *Canis lupus,* black bears *Ursus americaus*, brown bears *Ursus arctos*, cougars *Felis concolor*, and golden eagle *Aquila chrysaetos* are capable of or known to kill young wolverines (e.g., Hornocker & Hash 1981; Boles 1977; Burkholder 1962), Persson et al. (2003) showed that intra-specific predation was the most important cause of juvenile mortality in Sarek and Troms. They suggested that intra-specific predation mainly occurs in May to early June and in August-September. When the risk of (intra-specific) predation is high for cubs which are left unattended at the den, the choice of the female to stay away for longer periods might be driven by food depletion. The recorded hoarding behaviour likely enables the female cope with for the high energetic costs of raising cubs and to spend as much time as possible in the vicinity of the den (Oftedal & Gittleman 1989; Sadleir 1984) when cubs are still too small to accompany their mother and are vulnerable to predation. Female wolverines with altricial cubs therefore face a trade-off between a limited food source (i.e., cached food) and a limited activity radius in order to minimize predation risk. This is consistent with our prediction that the female's activity outside the denning area is limited at first, but that she leaves the cubs unattended in the den more often and for longer periods when the cubs grow larger, and food sources at the den site are likely to become depleted.

Female wolverines were only away from the denning area for less than one hour in the beginning of March; this time increased to over half a day at the end of May. Our finding that family groups left the denning area after circa 10 weeks (between 4th and 10th of May) is consistent with what Myrberget (1968) found that dens are deserted after the first week of

May. After natal dens are abandoned, the cubs are still too young to follow the mother very far, so she moves them to rendezvous sites (Magoun & Copeland 1998), where they are left while the female hunts. The time spent at rendezvous sites likely decreases gradually as the cubs get older until they no longer use them, but are able to follow the mother for extended periods (Magoun 1985). This may explain the dip in Figure 5 at the second half of June (week 16-17). The cubs' ability to accompany the mother after weaning puts less energetic costs on the mother, and accompanying the mother optimizes growth, foraging skills, and independence in the cubs.

Period of cub development and independence

The proportion of time females spent with cubs decreased significantly over time. Magoun (1985) found that young wolverines grow quickly after weaning and by seven months of age have achieved adult size in body weight; however, other measures of development probably related to intra-specific abilities (i.e., fighting abilities) such as scull development and appurtenant musculature (especially in the sexually-selected males) continues to grow (Landa & Skogland 1995). In our study independence occurred after 25 weeks (between August 19 - 25) for male cubs and after 26 weeks (between August 26 and September 1) for female cubs. This is in accordance with Magoun (1985) and Vangen et al. (2001), who suggested that wolverine juveniles are nutritionally independent in August-September. Siblings stayed together until after 30 weeks (between September 27 and October 3), indicating a strong sibling bond. However, cubs may become nutritionally independent as early as 23 weeks (between August 9-15), when sibling pairs start breaking up. Cub independence, as estimated in this study, is not equal to dispersal, which in our study area took place between 7 and 18 months of age among dispersing male juveniles and between 7 and 26 months among dispersing females (Vangen et al. 2001). The mean mother – cub distances increased linearly over the rearing period. Only after 30 weeks did these intervening distances show a random pattern over time, indicating that females had now left their offspring altogether and the cubs were nutritionally independent. From this time onwards, the cubs may start dispersing from their mother's home range (Vangen et al. 2001).

Autumn is the time of nutrimental independence for offspring in many other northern carnivores, birds and mammals. The needed time window to raise cubs is likely dependent on many different factors such as number of cubs, being solitary versus social, food habits, being specialist versus generalist, body size, phyliogenetic constraints, etc. Within the northern generalist carnivore guild, all the canids (arctic fox *Alopex lagopus*, red fox *Vulpes vulpes* and wolf) produce a higher number of cubs at a much narrower time window than the solitary wolverine (Moehlman 1989). However, the constraints faced by wolverine females solitary raising cubs within relatively oligotrophic environments seems to be counteracted by early birth in den sites when cubs are small and altricial, and prolonged maternal care until cubs are full-grown and independent before the onset of winter.

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References

BANCI, V. 1994. Wolverine, Pp. 99-123 in The scientific basis for conserving forest carnivores, american marten, fisher, lynx and wolverine (L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon and W. J. Zielinski, eds.). USDA Forest Service General Technical Report RM-254.

BANCI, V., AND A. S. HARESTAD. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. Annales Zoologici Fennici 25**:**265-270.

BEVANGER, K. 1992. Report on the Norwegian wolverine (*Gulo gulo* L.). Small Carnivore Conservation 6**:**8-10.

BOLES, B. K. 1977. Predation by wolves on wolverines. Canadian Field Naturalist 19**:**68-69.

BURKHOLDER, B. L. 1962. Observations concerning wolverine. Journal of Mammalogy 43**:**263-264.

COPELAND, J. P. 1996. Biology of the wolverine in central Idaho. MSc Thesis, University of Idaho.

FERGUSON, S. H., J. W. HIGDON, AND S. LARIVIÈRE. 2006. Does seasonality explain the evolution and maintenance of delayed implantation in the family Mustelidae (Mammalia: Carnivora)? Oikos 114**:**249-256.

HAGLUND, B. 1966. De stora rovdjurens vintervanor. Viltrevy 4**:**1-311.

HORNOCKER, M. G., AND H. S. HASH. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59**:**1286-1301.

IVERSEN, J. A. 1972. Basal metabolic rate of wolverines during growth. Norwegian Journal of Zoology 20**:**317-322.

KROTT, P. 1960. Ways of the wolverine. Natural History 69**:**132-133.

LANDA, A., K. GUDVANGEN, J. E. SWENSON, AND E. RØSKAFT. 1999. Factors associated with wolverine *Gulo gulo* predation on domestic sheep. Journal of Applied Ecology 36**:**963-973.

LANDA, A., M. LINDÉN, AND I. KOJOLA. 2000. Action plan for the conservation of wolverines (*Gulo gulo*) in Europe. Council of Europe Press: 1-45.

LANDA, A., AND T. SKOGLAND. 1995. The relationship between population density and body size of wolverines *Gulo gulo* in Scandinavia. Wildlife Biology 1**:**165-175.

LANDA, A., O. STRAND, J. D. C. LINNELL, AND T. SKOGLAND. 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. Canadian Journal of Zoology 76**:**448-457.

LANDA, A., O. STRAND, J. E. SWENSON, AND T. SKOGLAND. 1997. Wolverines and their prey in southern Norway. Canadian Journal of Zoology 75**:**1292-1299.

LINN, I. 1984. Home ranges and social systems in solitary mammals. Acta Zoologica Fennica 171**:**245-249.

MAGOUN, A. J. 1985. Population characteristics, ecology and management of wolverines in northwest Alaska. PhD Thesis, University of Alaska, Fairbanks, Fairbanks, Alaska.

MAGOUN, A. J., AND J. P. COPELAND. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62**:**1313-1320.

MCCRACKEN, H. 1985. Skunk bear. Wyoming Wildlife 49**:**30-33.

MOEHLMAN, P. D. 1989. Intraspecific variation in canid social systems. In: Carnivore behaviour, ecology and evolution. ed J. L. Gittleman. Cornell University Press, Ithaca, New York**:**143-163.

MYHRE, R., AND S. MYRBERGET. 1975. Diet of wolverine (*Gulo gulo*) in Norway. Journal of Mammalogy 56**:**752-757.

MYRBERGET, S. 1968. Jervens ynglehi. Fauna 21**:**108-115.

MYRBERGET, S., AND R. SØRUMGÅRD. 1979. Fødselstidspunkt og kullstørrelse hos jerv. Fauna 32:9-13.

OFTEDAL, O. T., AND J. L. GITTLEMAN. 1989. Patterns of energy output during reproduction in carnivores, Pp. 355-377 in Carnivore behaviour, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, New York.

PARAGI, T. F., S. M. ARTHUR, AND W. B. KROHN. 1994. Seasonal and circadian activity patterns of female fishers, *Martes pennanti*, with kits. Canadian Field-Naturalist 108:52-57.

PASITSCHNIAK-ARTS, M., AND S. LARIVIÈRE. 1995. *Gulo gulo*. Mammalian Species 499:1-10.

PEDERSEN, V. A., J. D. C. LINNELL, R. ANDERSEN, H. ANDRÉN, M. LINDÉN, AND P. SEGERSTRÖM. 1999. Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. Wildlife Biology 5:203-211.

PERSSON, J. 2003.Population Ecology of Scandinavian Wolverines. PhD, Swedish University of Agricultural Sciences, UMEÅ.

PERSSON, J., A. LANDA, R. ANDERSEN, AND P. SEGERSTRÖM. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. Journal of Mammalogy 87:75-79.

PERSSON, J., T. WILLEBRAND, A. LANDA, R. ANDERSEN, AND P. SEGERSTRÖM. 2003. The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. Wildlife Biology 9:89-90.

SADLEIR, R. M. F. S. 1984. Ecological consequences of lactation. Acta Zoologica Fennica 171: 179-182.

SANDELL, M. 1989. The mating tactics and spacing behaviour of solitary carnivores, Pp. 164-182 in Carnivore behaviour, ecology and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.

SWENSON, J. E., N. GERSTL, B. DAHLE, AND A. ZEDROSSER. 2000. Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe, Research Paper T-PVS (2000) 24: 1-68.

VANDER WALL, S. B. 1990. Food hoarding in animals. University of Chicago Press, London.

VANGEN, K. M., J. PERSSON, A. LANDA, R. ANDERSEN, AND P. SEGERSTRÖM. 2001. Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79**:**1641-1649.

WHITMAN, J. S., W. B. BALLARD, AND C. L. GARDNER. 1986. Home range and habitat use by wolverines in southcentral Alaska. Journal of Wildlife Management 50**:**450-463.

ZIELINSKI, W. J. 1988. The influence of daily variation in foraging cost on the activity of small carnivores. Animal Behaviour 36**:**239-249.

Figure legends:

Figure 1. Average time (+ SE) female wolverines spent around the denning area. Black bars indicate time spent outside the denning area. Grey and white bars indicate time spent active and passive inside the denning are, respectively.

Figure 2. Trends of daily activities of female wolverines around the denning area. Time spent outside the denning area is indicated with black triangles. Active and passive time spent inside the denning area is indicated with plusses and white squares, respectively.

Figure 3. Observed proportion of females together with their cubs (black triangles) and cubs together among themselves (white triangles) over weeks, as calculated from 1st of March. The two lines indicate the sigmoid trend lines for females and cubs (solid line) and among cubs (dashed line).

Figure 4. Observed relationship between the proportions of female and male cubs separated from their mother.

Figure 5. Trend of increasing log-transformed distance between female wolverines and their cubs over weeks, as calculated from the 1st of March.

Figure 6. Trend of growth development in wolverine cubs over weeks, as calculated from the 1st of March. White circles and solid line represent weight, whereas black triangles and dotted line give the profile length.

Table 1. Overview of the wolverine females used within the activity assessments, registration periods, collar type and study area.

Name	*ID*	*Registration period*	*Type of collar*	*Study area*
Skrubba	J-02/96	Spring 1997	Activity collar	Troms, Norway
Diva	J-17/97	Spring 1998	Activity collar	Troms, Norway
May	J-16/96	Spring 1997	Activity collar	Troms, Norway
Jonsi	S08-94	Spring 1995	Activity collar	Snøhetta, Norway
Eli	S04-93	Spring 1993	VHF collar	Snøhetta, Norway
Låptå	xxxxx	Spring 1996	Activity collar	Sarek, Sweden

Table 2. Statistics of daily activities of female wolverines.

Daily activities (time in quarter-hours)	Mean	SE
Total (active) time outside denning area	29.10	1.95
number of trips outside denning area	1.04	0.06
trip time outside denning area	26.21	1.64
departure from denning area	22:31	00:37
return to denning area	03:11	00:30
Total time inside denning area	65.52	2.01
active time inside	13.59	0.78
passive time inside	51.93	1.88
Time unaccounted for	1.38	0.72

Table 3. Wolverine hoarding behaviour on radio marked body parts of nine domestic reindeer carcasses killed by lynx in Troms, northern Norway.

	Proportion moved	**Distance moved (m)**		
		mean	**SE**	**n (of N)**
Body parts:				
front legs	0.77	866	186	10 (13)
hind legs	0.77	513	205	10 (13)
other body parts[†]	0.47	128	54	7 (17)
Moved by:				
certain wolverine	0.33	457	148	9
assumed/certain wolverine	0.44	448	117	12
uncertain	0.56	620	186	15
Total moved	0.63	544	115	27
Not moved	0.33	0	NA	14
Unknown fate	0.05	NA	NA	2

[†] Head, neck, back, spine or ribcage

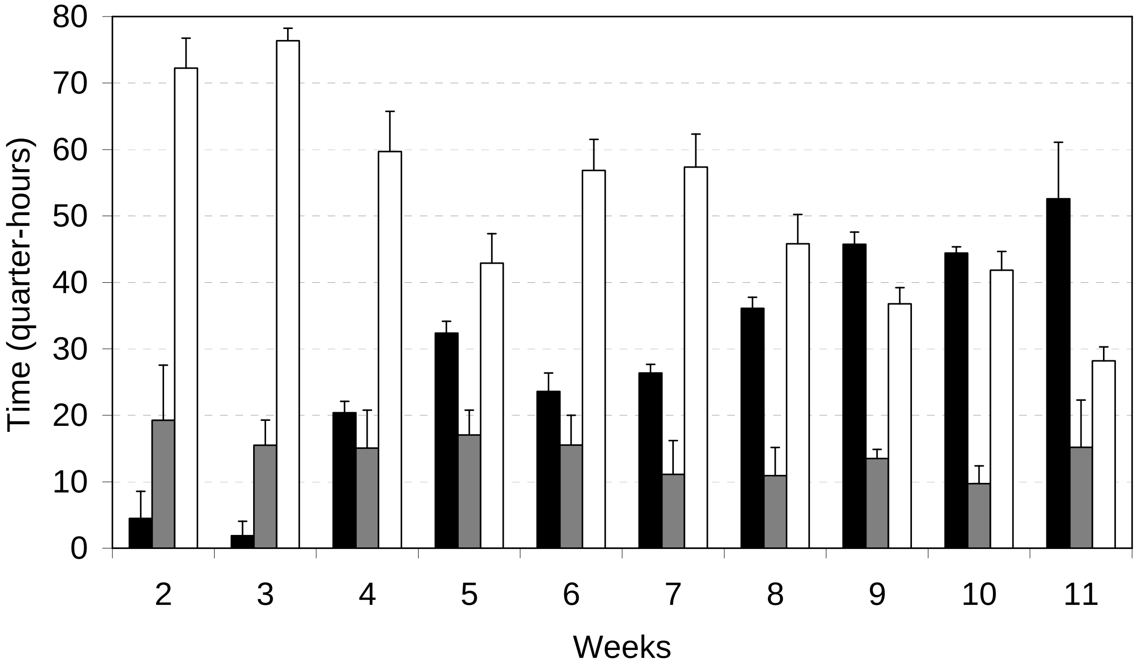
80
70
60
50
40
30
20
10
0
Time (quarter-hours)
2
3
4
5
6
7
8
9
10
11
Weeks

Figure 1.

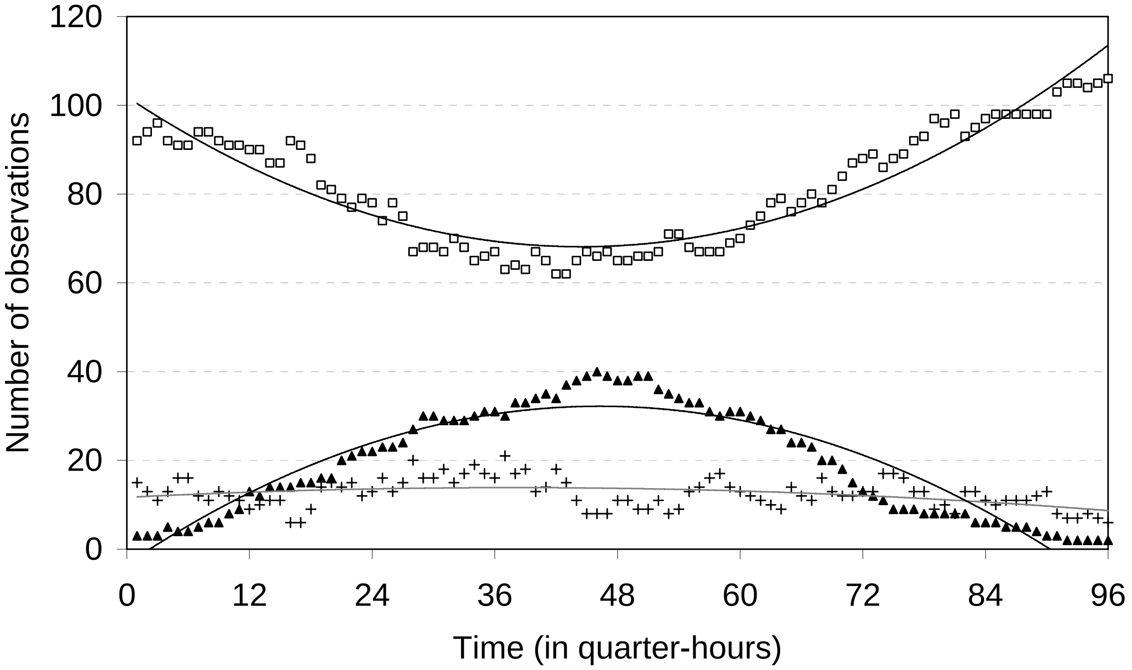
Number of observations
0
20
40
60
80
100
120
0
12
24
36
48
60
72
84
96
Time (in quarter-hours)

Figure 2.

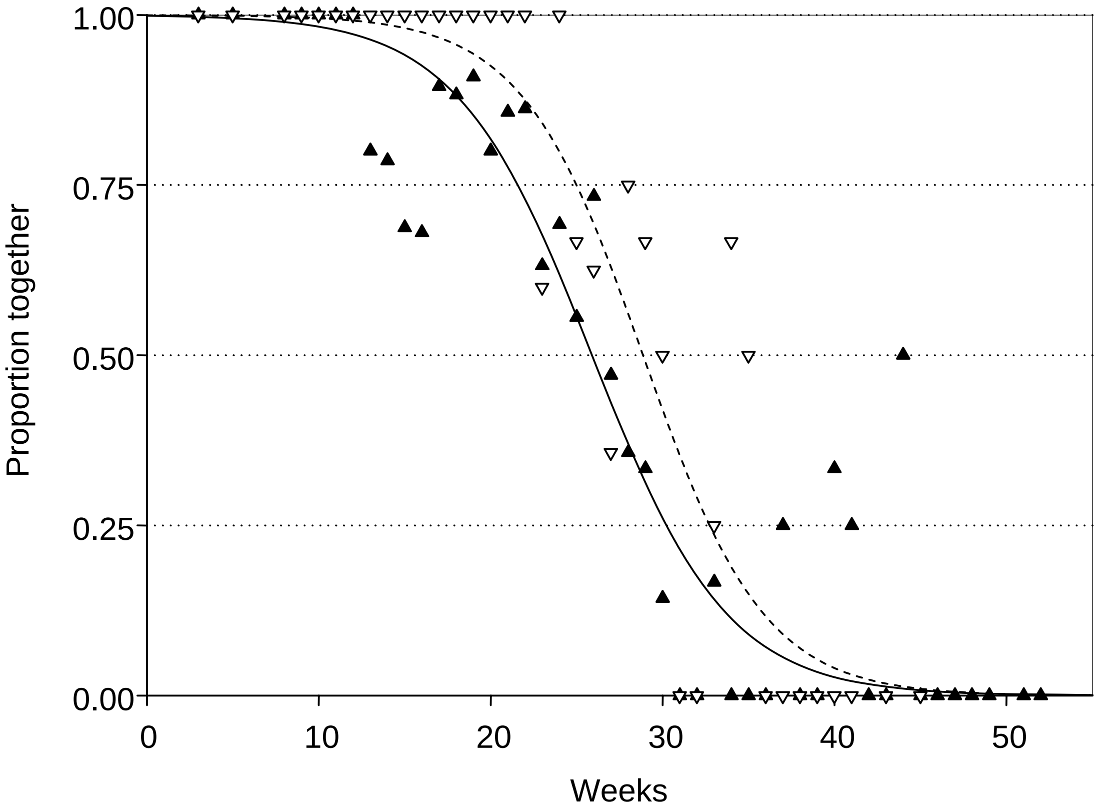

Figure 3.

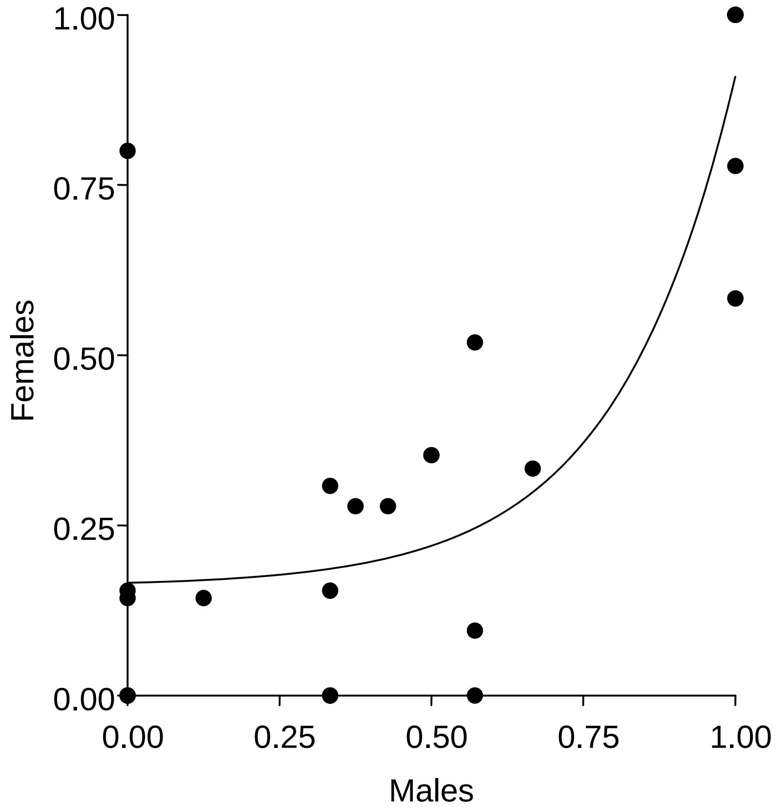

Figure 4.

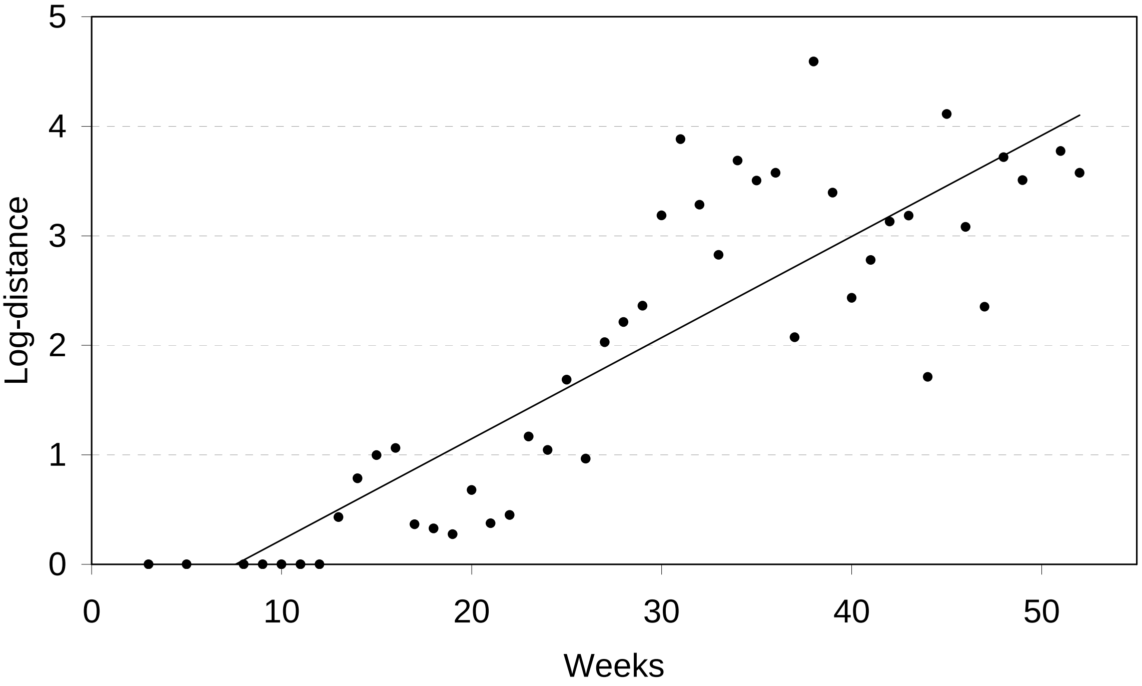

Figure 5.

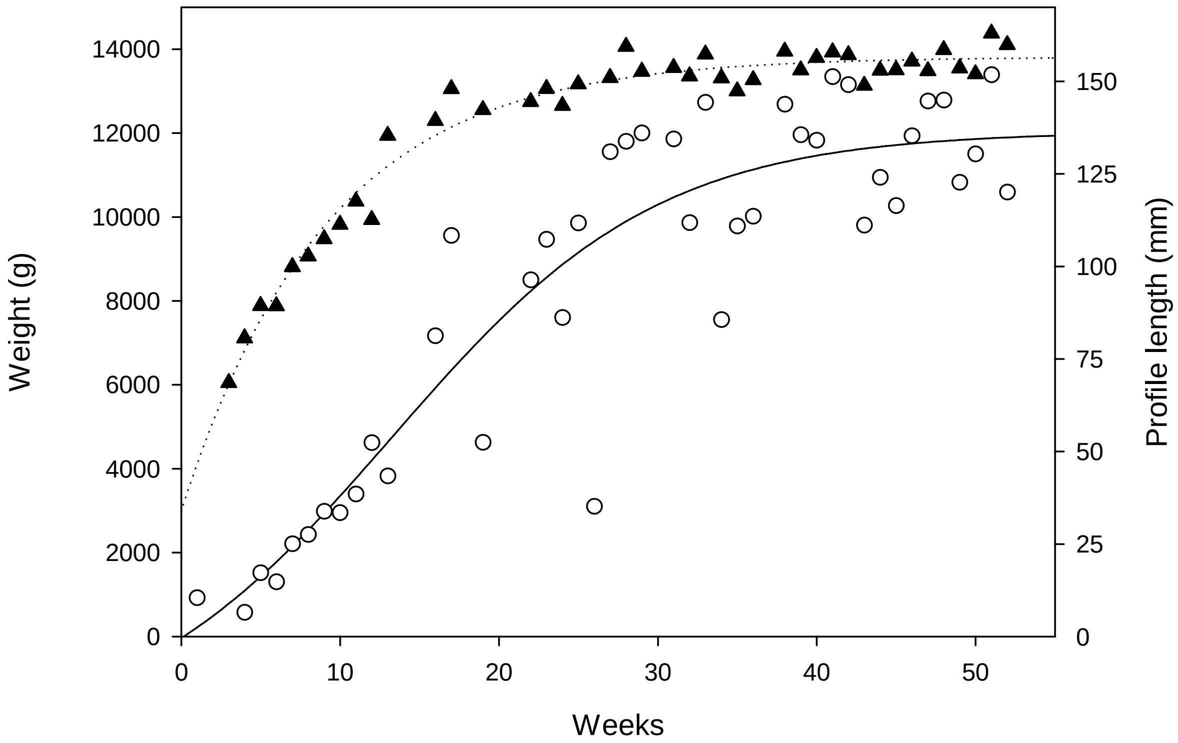
Weight (g)
0
2000
4000
6000
8000
10000
12000
14000
Profile length (mm)
0
25
50
75
100
125
150
Weeks
0
10
20
30
40
50

Figure 6.

Paper V

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Reproductive den site selection in Norwegian wolverines at different spatial scales

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Abstract: Compared to other northern large carnivores, wolverines (*Gulo gulo*) are thought to be more selective about habitat quality and particularly sensitive to human disturbance during the natal denning period for reproductive females. Successful reproduction, and thereby population viability, is likely to be enhanced by the choice of suitable den sites. We investigated which topographic features were selected for den sites, at two spatial scales using discrete choice models and multinomial logistic regression. This was based on 50 natal den sites from southern Norway (2000-2005). We further assessed reproductive frequency, based on denning localities registered in 1992-2005, and related it to topographic features. At the site-specific scale, den sites were associated with steep, rugged terrain with bare rock and shrub vegetation, at distance from private roads. At the landscape scale, den sites were placed in rugged terrain, facing northwest at 1,000 meters above sea level and away from infrastructure. Reproductive frequency was 0.56 ± 0.04 (SE). Re-use of den sites was higher in denning localities found on higher-lying steeper slopes away from public roads. Our results are associated with characteristic wolverine den sites dug out in deep snow, but also indicate an avoidance of infrastructure. Reproductive frequency was influenced by topographic features of den sites, indicating that den site distribution, and possibly successful reproduction, may be partly influenced by human disturbance. Recurrent use of specific topographic features may provide valuable information for directing monitoring efforts, protecting denning localities from unnecessary human disturbance and augmenting recovery of endangered wolverine populations.

Key words: den site selection, discrete choice models, *Gulo gulo*, habitat preferences, human infrastructure, reproductive frequency, site-specific and landscape scale, southern Norway, terrain ruggedness.

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Successful reproduction is essential for population viability. In exploited and controlled carnivore populations, as in Norway, decrease in population densities can reduce reproductive rates, increase infanticide and influence dispersal (Frank and Woodroffe 2001; Swenson *et al.* 1997a). Therefore knowledge on the reproductive biology of carnivores is of the utmost importance. Research throughout Europe and North America in the last 30 years has accumulated a large amount of knowledge about the biology of brown bears (*Ursus arctos*) (e.g., Swenson *et al.* 2000; Swenson *et al.* 1997b), wolves (*Canis lupus*) (e.g., Mech and Boitani 2003; Boitani 2000; Ballard *et al.* 1991; Fuller 1989) and lynx (*Lynx lynx*) (e.g., Breitenmoser *et al.* 2000). In contrast, there is a far poorer knowledge on which to base sustainable management for the wolverine (*Gulo gulo*) (Landa *et al.* 2000). The data that do exist however indicate that wolverines have small litter sizes and usually do not breed every year, and therefore have slower population growth rates and a relatively low resilience (Landa *et al.* 2000). Also, wolverines are thought to be most selective about habitat quality and particularly sensitive to human disturbance (May *et al.* 2006), especially during the natal denning period (February-May) for reproductive females (Heinemeyer *et al.* 2001; Magoun and Copeland 1998). During this period, females with newborn young employ central place strategies constraining their movements to areas close to the den. Otherwise, wolverines do not use any central place structure (Landa *et al.* 1998a). The importance of den sites in the biology of wolverines not only lies in the provision of shelter for cubs from the elements, but also safety from predators during the infant period. It is therefore imperative to improve our knowledge on factors relevant to successful reproduction, such as reproductive frequency and den site preferences during the natal denning period. This will provide important information on which to base management and conservation efforts especially in threatened or recovering populations.

Earlier, Landa et al. (1997) hypothesized that the differences in reproductive frequency could be due to differences in habitat quality of the various den sites and/or their immediate surroundings. However, at present there is little information available on the factors that characterize good denning habitat. Magoun and Copeland (1998) found that wolverine reproductive den sites were primarily found above treeline in deep snow, where snow tunnels led to fallen trees, large rocks or boulder scree. Several factors may be associated with selection of suitable den sites, each associated with different spatial scales (Magoun and Copeland 1998). Whereas thermoregulatory advantages and suitability of the site during snow melt in spring can be provided on a relatively small spatial scale (i.e., site-specific or micro-scale), protection from predators and humans, and vicinity of rearing habitat encompass a larger spatial scale (i.e., landscape or macro-scale). Wolverines are therefore expected to face hierarchical, multi-scalar decisions in choosing the most suitable den site. However, based on existing knowledge it is likely that there are three aspects that can potentially increase the suitability of an area for denning: (1) structures or topographic elements suitable for dens, (2) inaccessibility to humans (disturbance, legal and illegal hunting) and predators, and (3) the availability of rearing habitat. Based on data collected during regular monitoring and/or research activity in Norway this paper aims to evaluate habitat quality of wolverine den sites. First, we aim to identify which topographic elements were associated with suitability of den sites, and at which spatial scales these elements were selected. We thereafter aim to estimate the reproductive frequency from different denning localities, and relate variation in reproductive frequency to habitat characteristics in the vicinity of the natal den sites.

Study area

This study was executed in south-central Norway (Figure 1). This area encloses many different ecological conditions, from remote mountainous areas in the west and centre where high densities of unattended free-ranging sheep grazed in their summer pastures (June-September) to more accessible forest areas in the east where wolverine co-existed with wolf, lynx and brown bear. In the mountainous regions in the west the largest European populations of wild reindeer were found. In the north-eastern part, semi-domestic reindeer was found. Moose (*Alces alces*), roe deer (*Capreolus Capreolus*), mountain hare (*Lepus timidus*), grouse (*Lagopus* spp.), lemming (*Lemmus lemmus*) and various rodents (*Microtus* spp. and *Clethrionomys* spp.) and insectivores formed possible sources of food for the wolverine; either as prey or through scavenging. The habitat in the mountain ranges consisted of mountain plateaus with peaks up to 2,000 m with bare rock, which gave way to alpine tundra with heath (e.g., heather (*Caluna* spp.), crowberry (*Empetrum* spp.)) and lichen (*Cladonia* spp.) vegetations. At lower elevations, alpine shrubland (e.g., willow (*Salix* spp.), dwarf birch (*Betula nana*)) was found down towards the treeline at circa 1,000 m a.s.l. From the treeline downwards, forests were comprised of mountain birch (*Betula pubescens*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with a varied undercover (e.g., blueberry (*Vaccinium* spp.), grasses (*Molina* spp./*Deschampsia* spp.), mosses (*Sphagnum* spp.)). The mountain ranges are divided by steep valleys. The forest region is mostly characterized by hills or lower mountains and wider valleys. The vegetation here was comprised of mixed forests of birch, spruce and pine, interspersed with open bogs, and some agricultural lands. In the study area, snow was present from October/November until May/June depending on elevation. Human infrastructure was mainly concentrated at lower elevations in the valley bottoms. Recreational cabins were found at higher elevations as well. Human activities consisted of hunting, hiking and camping, and cross-country skiing.

Methods

Locating wolverine natal dens and monitoring. Throughout Norway, systematic monitoring of den sites has been a standard monitoring tool for wolverines during the last 15 years. Den sites are systematically localized by personnel of the Norwegian State Nature Inspectorate and other wildlife management authorities. Standard criteria, derived from studies of radio-collared individuals, are used to identify if a given den is a natal den or not. Based on the number of den sites with reproduction a yearly estimate is made of the population size of wolverines in Norway (Landa *et al.* 1998b). We attempted to use a consistent terminology throughout. A “den site” refers to the specific location of a primary natal den in a given year. Radio-telemetry data indicate that individual females tend to den within a limited area, and even when females are replaced the same locations tend to be used again. Within the monitoring program, each den site receives a “locality” code clustering proximate den sites among years, as they likely represent the den sites used within a single home range. In some cases reproduction was identified within a given locality even if no den was located, by visual observation of a female with cubs during the spring or summer. This induced a certain non-systematic element into the data, but could not be controlled for because of the nature of the data received from the authorities. However, in practice this does mean that all reproductions are likely to have been recorded. Because of the nature of the reproductive data we cannot consider the number or survival of cubs as was done by Landa et al. (1997), therefore we simply consider reproduction or no reproduction for each denning locality.

Reproductive frequency. We estimated “reproductive frequency” as the number of reproductions per denning locality divided by number of years between the first and last recorded reproduction. Although reproductive frequency is usually calculated per individual, our “pseudo-frequency” represents a measure for the frequency of re-use of denning localities. The various denning localities were all monitored for different lengths of time, up to 14 years, covering the period 1992 up to, and including, 2005. To minimize any bias which originated from this, we only included denning localities monitored for more than 2 successive years above which we found no significant correlation between reproductive frequency and the number of years monitored (Spearman’s *rho* = -0.231, $P = 0.255$, $N = 26$). Also, denning localities close to the Swedish border (i.e., within 10 km) were excluded as to avoid any bias resulting from unrecorded reproductions east of the border.

Den site selection. Den site selection was determined based on 50 wolverine natal dens we visited in the field, and which were recorded to have been used for reproduction in the period 2000-2005. We visited these sites from the end of June to the beginning of September 2005. We characterized each den site by recording the type of substrate and estimating the den size (m^2) considering the area delimited by prey remains, faeces and hair. The placement on the immediate hillside was given as the proportion between 0 (bottom) and 1 (top of the hillside) based on what was visible. Using 1:50,000 topographic maps (Norwegian Mapping Authority), we estimated the total surface area (km^2) visible from the den site. The general aspect (with a compass) and slope (estimated to the nearest 5°) of the hillside on which the den site was located were also recorded.

In order to analyze wolverine den site selection at a site-specific scale, we compared data at each den site with data collected in the field at four alternative locations at respectively 50 m, 100 m, 250 m and 500 m distance in a random direction from the den site. The control sites were placed at these distances as to give an indication at which scale (i.e., grain) different topographic features were available to the animal at a local scale. Information was recorded in a 10 m radius surrounding each location. At the landscape scale, data calculated from GIS-based digital maps was compared between the den site and four alternative locations at respective distances of 500 m, 1 km, 2.5 km and 5 km in a random direction from the den site. These distances were chosen to represent different scales of selection in reproducing wolverines. Radio-telemetry data indicate that individual females tend to den within a limited denning area (approximately within 1 km radius), and even when females are replaced the same localities tend to be used again. A 5 km radius corresponds to an area of 78 km^2, approximately the same as a reproducing female's home range size (Vangen *et al.* 2001; Landa *et al.* 1998a). The remaining two distances represented intermediate scales of selection, and provided connection (i.e., 500 m) to the site-specific scale. Explanatory covariates were calculated for each den site and the four corresponding alternative locations at both scales.

Explanatory covariates. An overview of the topographic features used as explanatory covariates in the analyses are given in Table 1, with a description of collection methods at both scales and their acronyms used throughout the remainder of this paper. All covariates were expected to possibly influence wolverine den site selection (see for references in the Introduction). Vegetation, and especially rock, shrub and trees, may provide for good hiding places or substrate at the den site and may increase the overall ruggedness of the terrain. However, because different vegetations may affect choices differently, we included all categories as possible covariates. At the landscape scale, elevation represented the spatial configuration of vegetation zones (and placement of the treeline). Previous studies have indicated that den sites are generally associated with the treeline. Terrain ruggedness, slope and aspect affect the snow depth, and therefore possibilities for digging tunnels, both at the site-specific and landscape scale. Roads increase the accessibility of humans to wolverine habitat at both scales. We considered the division in two road categories (i.e., public and private roads) useful because of the different levels of disturbance caused by the two categories. Many private roads are closed during winter and early spring, due to the abundant snow, whereas main public roads are kept open throughout the year. However, private roads are found further in natural areas than public roads.

Statistical analyses. Prior to the analyses we assessed possible collinearity between covariates using a correlation and collinearity analysis, performed in the statistical software program R 2.4.1 (R Development Core Team 2006) using the perturb package. For the inter-correlated pairs ($r > |0.6|$) given in Table 2 we entered only one covariate at a time in our modeling efforts. Although no strong collinearity was found between ruggedness and slope at the site-specific scale ($r = 0.422$), we suspected a possible interaction (i.e., on steeper slopes ruggedness becomes less important, and vice versa). Visual assessment of the data suggested possible non-linear effects for elevation, ruggedness, aspect, and slope. Restricted cubic splines with 3 knots were used to model these non-linear relationships (Harrell 2001). Here, X represents the effect for the covariate below and X' above the central knot.

We assessed whether reproductive frequency of the denning localities was affected by landscape scale habitat variables using a general linear model with a binomial distribution. The covariates for each denning locality were derived by averaging the point values over all natal den sites within the denning locality. Because reproductive frequency was based on all den sites in the period 1992-2005, which were not all visited, we could not assess whether site-specific topographic features affected reproductive frequency of the denning localities.

Analysis of den site selection, both at the landscape and site-specific scale, was done using discrete choice models. Discrete choice models are based on the assumption that the probability for an animal to choose a j^{th} resource unit among all the available ones (defined by the p variables $X_1, X_2 \ldots X_p$ of values $x_1, x_2 \ldots x_p$) at the i^{th} choice is “proportional to an exponential function of a linear combination of the X variables” (Manly *et al.* 2002). Comparing the values of the variables among the chosen units (den sites) and the not chosen units (alternative locations), this method is able to construct models indicating which variables are most important for the animal to select a specific site. For both scales, we produced models reflecting den site selection of wolverines. Statistics were performed in the statistical software program R using a ‘tricked’ stratified Cox proportional hazards model, wherein the lifetime of the selected resource unit is set to 1 and all other units in the choice set is set to 2 (c.f., Manly *et al.* 2002). For this we used the cph function of the Design library. Robust variance estimates of the standard errors were obtained based on the Huber-White method to correct for heteroscedasticity and for correlated responses of clustered den site localities using the robcov option. The model that could not be simplified any more without dropping a significant effect or violating the hierarchy principle (i.e., non-significant lower-order effects cannot be removed if a significant higher-order interaction of the same factors is present) was selected as the final one (c.f., Wu and Hamada 2000). The most parsimonious model was validated using a clustered bootstrap model validation (B = 1,000) to obtain unbiased estimates of model performance (Harrell 2001). Based on the most parsimonious model, we further checked for possible regional differences between the mountainous region in the west and the forested region in the east (40 and 10 den sites, respectively) by including a regional interaction term in the model.

In choosing the models best describing reproductive frequency and den site selection at both spatial scales, we followed the information theoretic approach of Burnham and Anderson (2002) and Anderson et al. (2000). Model selection was determined using a stepwise procedure, where all possible candidate models were considered (383, 592 and 103,424 models for the reproductive frequency, landscape scale and site-specific selection, respectively). The most parsimonious model corresponded to the model with the lowest corrected Akaike Information Criterion (AIC_c) score (Burnham and Anderson 2002). Models with ΔAIC_c scores lower than 2 from the most parsimonious model (i.e., model with the lowest AIC_c score) were included as possible alternative models (Burnham and Anderson 2002). The AIC_c weights of those models (ΔAIC_c <2) subsequently give the probability how well model *i* fits the data (Burnham and Anderson 2002).

The spatial selection scale of each variable within the most parsimonious den site selection models (i.e., models with $\Delta AIC_c < 2$) for both the site-specific and the landscape scale were further analyzed using multinomial logistic regression, using the multinom package in R. Here, the distance from the den site (respectively: 0 m, 50 m, 100 m, 250 m, and 500 m; 0 m, 500 m, 1 km, 2.5 km, and 5 km) were used as the dependent categorical variable with 0 m as reference category. The Wald test results allowed us to detect significant departure from the den site at the different distance classes for each of the explanatory covariates.

Results

Wolverine den site characteristics. The 50 wolverine natal den sites which were visited in southern Norway in 2005 were described for various characteristics (Table 3). The average aspect of the hillside on which the den sites were placed had a circular mean aspect of 2° ± 7 (SE), and tended to be north-facing (Rayleigh test of uniformity: $\overline{R} = 0.210$; $P = 0.109$). However, for the aspect at the den site, which had a circular mean of 348° ± 8 (SE), no preferred direction was detected (Rayleigh test of uniformity: $\overline{R} = 0.111$; $P = 0.543$).

Site-specific den site selection. In all, six models could explain site-specific den site selection in wolverines. The most parsimonious model included SLOPE, RUGGEDNESS, PRIVATE ROAD, SHRUB, ROCK, and SLOPE*RUGGEDNESS (Table 5). This model rendered, after bootstrap validation, a Nagelkerke R^2 of 0.764. Model 3 represents the minimal model with the most important covariates, which are part of all models. With decreasing relative importance (measured as the sum of the AIC_c weights for each covariate), SHRUB (0.685), PRIVATE ROAD (0.438) and TREES (0.251) also explained part of the variation in den site placement. Inclusion of possible regional differentiation slightly increased the parsimony of the best model ($AIC_c = 58.825$), and included one nearly significant negative regional interaction term (ROCK*REGION: $\chi^2 = 1.93$, $P = 0.053$). The multinomial logistic regression showed that all variables were selected at the 50 m category (Table 6).

Landscape scale den site selection. The non-linear term of ASPECT (i.e., ASPECT'), which was first entered in the model, was not significant (Wald test: $\chi^2 = 0.097$, $P = 0.923$); we thereafter only included the linear term of ASPECT. The most parsimonious model included RUGGEDNESS, RUGGEDNESS', ELEVATION, ELEVATION', PRIVATE ROAD, PUBLIC ROAD and ASPECT (Table 5). This model rendered, after bootstrap validation, a Nagelkerke R^2 of 0.503. Both the use of SLOPE instead of RUGGEDNESS and TREELINE instead of ELEVATION resulted in less parsimonious models ($AIC_c = 107.977$ and $AIC_c = 112.433$, respectively). Inclusion of possible regional differentiation slightly decreased the parsimony of the best model ($AIC_c = 107.347$), and included a positive regional interaction term for RUGGEDNESS (Wald test: $\chi^2 = 1.11$, $P = 0.270$). The multinomial logistic regression showed that RUGGEDNESS and RUGGEDNESS' were selected at the finest scale of 500 m. ELEVATION was also selected for at the 500 m meter scale, however no clear effect was found in ELEVATION'. We found no clear scale selection for PUBLIC ROAD, PRIVATE ROAD and ASPECT, although PUBLIC ROAD was nearly significant at 5,000 m ($P = 0.101$; Table 6).

Reproductive frequency. On average, denning localities in southern Norway had a reproductive frequency of 0.56 ± 0.04 (SE), which represented a total of 145 reproductive events at 26 denning localities. Still, there were considerable differences in the number of reproductive events in the different denning localities, with some having only one documented reproduction, and others being used for reproduction virtually each year.

Reproductive frequency increased when denning localities were placed on gentle slopes at higher elevations and at a distance from public roads (Table 4). Because of their high collinearity (Table 2), slope could be replaced with terrain ruggedness (i.e., less rugged) to explain part of the variation in reproductive frequency.

Discussion

Den site placement and characteristics. Considering that wolverine cubs are born in an altricial state in mid winter (January to March, Myrberget and Sørumgård 1979; Pulliainen 1968) it is obvious that they depend on some form of den to protect them from temperature extremes, intra-guild predation and cannibalism. As in most previous studies of northern wolverines (Magoun and Copeland 1998; Banci 1994; Myrberget 1968; Pulliainen 1968), all the dens in our study consisted of snow tunnels dug into deep snowdrifts. Although once a fallen tree was used as substrate, most of the tunnel systems reached down to boulder fields, talus slopes or cracks in the rock that were large enough to allow cubs to crawl around them. At the site-specific scale, den sites were selected on steep slopes in rugged terrain. The presence of rocks both indicates the preference for rugged terrain and the opportunity to seek dry and safe shelter among and beneath them. Shrubs in combination with rocks will likely further increase the overall ruggedness of the terrain on such a fine scale that it could not be picked up by the ruggedness parameter itself. In such rugged places snowdrifts tend to be formed, like in gullies or under small overhangs. In all, wolverines are thus provided with den sites in snowdrifts with dry and safe cavities. The topographic features associated with den sites, explained over 75% of all variation in den site placement. Overall our results support Magoun and Copeland's (1998) claim that the most important requirement for den site selection on a site-specific scale appears to be the existence of a deep snow bank that provides stable snow conditions for the winter and spring. Even though our study area encompassed not only high alpine areas but also boreal forests with low mountain ranges, wolverines preferred similar topographic features. These features are also thought to be preferred for the placement of den sites in the boreal forests of Finland (I. Kojola, Finnish Game and Fisheries Research Institute, personal communication). The only regional differentiation we found was a lower selection for rocky substrate in the forest region. Our result showed that at a site-specific scale den sites were selected farther from private roads. This is corroborated by previous authors who have expressed their concern that wolverines may be especially sensitive to disturbance during the natal denning period (COSEWIC 2003; Heinemeyer *et al.* 2001; Magoun and Copeland 1998; Weaver *et al.* 1996). The preferences detected were all selected for at a very fine scale (50 m), indicating that the local requirements for a suitable den site are very stringent.

Denning in a landscape perspective. At the landscape scale, den sites were found in rugged, or steep, terrain with a north to north-westerly aspect around the treeline (i.e., around 1,120 m a.s.l.) and far from public and private roads. Over 50% of all variation in den site placement could be explained by these topographic features. Even at a landscape scale, the overall ruggedness or steepness of the terrain appeared to be an important feature for den sites. This would be consistent with selection for suitable snow drifts as these are often associated with steep and rugged terrain. It is also possible that steep and rugged terrain, especially when placed farther from human infrastructure, is perceived as providing security from humans or other potentially dangerous carnivores. This appears to be a general pattern for wolverines to prefer steep slopes, ravines or boulder fields (Magoun and Copeland 1998; Banci 1994; Pulliainen 1968). Den sites were further selected on elevations slightly over 1,000 m, which corresponds well with the treeline in southern Norway. In the forest region, wolverines preferred to place their den sites in more rugged areas. Our results are consistent with earlier Scandinavian studies (Myrberget 1968; Pulliainen 1968). As expected from the site-specific analysis, ruggedness was selected at a fine scale (500 m), as was elevation. The existence of aspect selection varies between studies (Löfstrand 2000; Myrberget 1968; Pulliainen 1968) (Löfstrand 2000; Myrberget 1968; Pulliainen 1968)but appears more likely to reflect local differences in topography, wind direction, and snowdrift rather than selection for a specific aspect *per se*. Overall, dens were generally located relatively far from human infrastructure (on average over 7.5 km from public roads and 3 km from private roads), which is difficult considering the almost complete lack of true wilderness areas in modern Norway. However, it is quite possible that linear distance is too simple a measurement of disturbance potential, as the vertical difference and topographical complexity will greatly modulate the disturbance potential at given distances (Linnell *et al.* 2000).

Reproduction and re-use of den sites. Wolverines are known to have low reproductive rates as compared to similar sized carnivore species. While a high proportion of carcasses examined carry fetuses or show signs of ovulation, this appears to not always translate into high rates of cubs actually being born or raised (Banci 1994). Our estimate of "reproductive frequency" from monitoring of denning localities (0.56) was similar to reproductive rates of radio-collared wolverines in Scandinavia (0.53 (95% CI: 0.43 - 0.63), Persson *et al.* 2006). Although we did not measure reproductive rates directly, clusters of den sites are generally associated with the certain home range, often of one and the same individual. Therefore, our frequency of reproduction does form an indication of reproductive rates in space and time. As Landa et al. (1997) hypothesized, differences in reproductive frequency are likely to be due to differences in habitat quality of the various denning localities. It is important to bare in mind that in this analysis we have only examined areas that wolverines have used for reproduction at least once, indicating that all of them are suitable to some degree. There are clearly many areas that are not suitable for wolverines and where wolverines have never settled. However, those areas where wolverine did settle, we found that their reproductive frequency was positively influenced by placement at higher elevation, on gentler slopes and farther from humans (i.e., public roads). This indicates that the distribution of den sites, and possibly successful reproduction, may be partly influenced by direct disturbance or a higher risk of human-caused mortality associated with infrastructure (Landa *et al.* 2000; Thurber *et al.* 1994).

Management implications

Wolverine den sites can be described as being located in steep, rugged and rocky terrain, facing north to north-west, relatively far from human activity, and just above the treeline. However, once a general area is used it appears to be re-used in subsequent years (Magoun and Copeland 1998; Lee and Niptanatiak 1996), indicating that there is something about these areas that is consistently preferred. Given this recurrent use of denning localities and topographic characteristics of den sites it would appear to be best to base management around areas that wolverines have demonstrated as being suitable by selecting them themselves. The importance of identifying and protecting den sites had often been emphasized by previous authors (COSEWIC 2003; Magoun and Copeland 1998). The results from our study may direct monitoring efforts which are based on localizing den sites (Landa *et al.* 1998b). Also, this study may provide valuable information for protecting known denning localities from unnecessary disturbance by minimizing human activities during the natal denning period close to such areas. Also, identification of “typical” den sites within potentially suitable wolverine habitat may augment the chances for successful recovery or reintroduction of wolverines to previously inhabited landscapes (e.g., Fortin *et al.* 2005) by establishing recovery zones or delineating reintroduction sites.

Acknowledgments

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Literature cited

Anderson, D.R., Burnham, K.P. and Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64(4):912-923.

Ballard, W.B., Ayres, L.A., Gardner, C.L. and Foster, J.W. 1991. Den site activity patterns of gray wolves, Canis lupus, in southcentral Alaska. Canadian Field-Naturalist 105:497-504.

Banci, V. 1994. Wolverine. In: Ruggiero LF, Aubry KB, Buskirk SW, Lyon LJ, Zielinski WJ, editors. The scientific basis for conserving forest carnivores, american marten, fisher, lynx and wolverine. General Technical Report RM-254. Fort Collins, Colorado: United States Department of Agriculture, Forest Service,Rocky Mountain Forest and Range Experiment Station. p 99-123.

Boitani, L. 2000. Action plan for the conservation of wolves in Europe (Canis lupus). Nature and environment 113:74.

Breitenmoser, U., Breitenmoser-Würsten, C., Okarma, H., Kaphegyi, T., Kaphegyi-Wallmann, U. and Müller, U.M. 2000. Action plan for the conservation of the Eurasian lynx in Europe (Lynx lynx). Council of Europe Nature and Environment 112:1-69.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: a practical informtaion-theoretic approach. 2nd edition. New York, New York, USA: Springer-Verlag. 488 p.

COSEWIC. 2003. COSEWIC assessment and updat status report on the wolverine Gulo gulo in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. vi + 41 p.

Fortin, C., Banci, V., Brazil, J., Crête, M., Huot, J., Huot, M., Lafond, R., Paré, P., Shaefer, J. and Vandal, D. 2005. National Recovery Plan for the Wolverine (*Gulo gulo*) [Eastern Population]. National Recovery Plan No. 26. Recovery of Nationally Endangered Wildlife. Ottawa, Ontario. 33 p.

Frank, L.G. and Woodroffe, R. 2001. Behaviour of carnivores in exploited and controlled populations. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK, editors. Carnivore conservation. Cambridge: Cambridge University Press. p 419-442.

Fuller, T.K. 1989. Denning behavior of wolves in north-central Minnesota. American Midland Naturalist 121:184-188.

Harrell, F.E. 2001. Regression Modelling Strategies with Applications to Linear Models, Logistic Regression, and Survival Analysis. New York, New York, USA: Springer-Verlag.

Heinemeyer, K.S., Aber, B.C. and Doak, D.F. 2001. Aerial surveys for wolverine presence and potential winter recreation impacts to predicted wolverine denning habitats in the southwestern Yellowstone ecosystem. 21 p.

Landa, A., Strand, O., Swenson, J.E. and Skogland, T. 1997. Wolverines and their prey in southern Norway. Canadian Journal of Zoology 75:1292-1299.

Landa, A., Strand, O., Linnell, J.D.C. and Skogland, T. 1998a. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. Canadian Journal of Zoology 76(3):448-457.

Landa, A., Tufto, J., Franzén, R., Bø, T., Lindén, M. and Swenson, J.E. 1998b. Active wolverine dens as a minimum population estimator in Scandinavia. Wildlife Biology 4:159-168.

Landa, A., Lindén, M. and Kojola, I. 2000. Action plan for the conservation of wolverines (*Gulo gulo*) in Europe. Strasbourg: Council of Europe Press. 1-45 p.

Lee, J. and Niptanatiak, A. 1996. Observation of repeated use of a wolverine, Gulo gulo, den on the tundra of the Northwest Territories. Canadian field-naturalist 110(2):349-350.

Linnell, J.D.C., Barnes, B., Swenson, J.E. and Andersen, R. 2000. How vulnerable are denning bears to disturbance ? Wildlife Society Bulletin 28(2):400-413.

Löfstrand, R. 2000. Wolverine habitat selection. A GIS approach [Examensarbete i ämnet skoglig zooekologi]. Umeå: Sveriges Landbruks Universitet. 30 p.

Magoun, A.J. and Copeland, J.P. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62(4):1313-1320.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. and Erickson, W.P. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second edition. New York, New York, USA: Kluwer Press.

May, R., Landa, A., Dijk, J., van and Andersen, R. 2006. Impact of infrastructure on habitat selection of wolverines. Wildlife Biology 12(3):285-295.

Mech, L.D. and Boitani, L., editors. 2003. Wolves: Behavior, Ecology, and Conservation. Chicago: University of Chicago Press. 465 p.

Myrberget, S. 1968. Jervens ynglehi. Fauna 21:108-115.

Myrberget, S. and Sørumgård, R. 1979. Fødselstidspunkt og kullstørrelse hos jerv. Fauna 32:9-13.

Persson, J., Landa, A., Andersen, R. and Segerström, P. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. Journal of Mammalogy 87(1):75-79.

Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. Helsinki: Department of Agricultural and Forest Zoology. 338-344 p.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riley, S.J., DeGloria, S.D. and Elliot, R. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5(1-4):23-27.

Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. and Wabakken, P. 1997a. Infanticide caused by hunting of male bears. Nature 386:450-451.

Swenson, J.E., Sandegren, F., Wabakken, P., Bjärvall, A., Franzén, R. and Söderberg, A. 1997b. Winter den abandonment by brown bears, Ursus acrtos: causes and consequencies. Wildlife Biology 3(1):35-38.

Swenson, J.E., Gerstl, N., Dahle, B. and Zedrosser, A. 2000. Action plan for the conservation of the brown bear (Ursus arctos) in Europe. Report nr T-PVS (2000) 24. 1-68 p.

Thurber, J.M., Peterson, R., Drummer, T.D. and Thomasma, S.A. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin 22:61-68.

Vangen, K.M., Persson, J., Landa, A., Andersen, R. and Segerström, P. 2001. Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79:1641-1649.

Weaver, J.L., Paquet, P.C. and Ruggiero, L.F. 1996. Resilience and conservation of large carnivore conservation in North America. Conservation Biology 10(4):964-976.

Wu, C.F.J. and Hamada, M. 2000. Experiments: Planning, Analysis, and Parameter Design Optimization. New York, New York, USA: John Wiley & Sons, Inc.

Associate editor:

Figure 1. Overview of the location of the denning localities in southern Norway. Black circles depict all denning localities for 1992-2005. The white symbols depict the 50 den sites included in the den site selection analysis; 40 circles and 10 squares for the mountain and forest region, respectively. The grey lines depict public (solid lines) and private roads (fine lines).

Table 1. Overview of the variables, and their acronyms, used in the site-specific scale, and/or landscape scale den site selection models.

Variable	**Site-specific description**	**Landscape scale description**	**Acronym**
Vegetation composition:	for all vegetation categories estimated as percentages in the field within a 10 m radius		
trees			TREES
shrub vegetation			SHRUB
woody dwarf vegetation			HEATH
grasses, forbs and herbs			GRASS
mosses and lichens			MOSS
bare rock			ROCK
water			WATER
Elevation	measured in m a.s.l. using a hand-held 12-channel GPS	derived from a 100 m resolution DEM[a]	ELEVATION
Slope	visually estimated to the nearest 5 degrees in the field	derived from a 100 m resolution DEM[a]	SLOPE
Aspect	estimated in degrees using a hand-held compass	derived from a 100 m resolution DEM[a]	ASPECT
Terrain ruggedness index	given as the sum of the linear distances (L) measured from begin to end of a 10 m rope laid down following the irregularities of the terrain in four directions (uphill and downhill perpendicular	measured by taking the square root of the sum of squared differences in elevation of each pixel in a 100 m DEM to its 8 neighbors[a,b]	RUGGEDNESS

	to hillside, left and right parallel to hillside) relative to the maximum possible distance of 40 m: (40 – L)/40, rendering 0 for non-rugged terrain and approaching 1 with increasing ruggedness		
Distance to treeline/forest edge	visually estimated in m in the field; designated as negative when below treeline	calculated from digital 1:50,000 topographic maps[a]	TREELINE
Distance to nearest:	both distances calculated from digital 1:50,000 topographic maps[a]	both distances calculated from digital 1:50,000 topographic maps[a]	
public road			PUBLIC ROAD
private road			PRIVATE ROAD

Sources:

[a] Norwegian State Mapping Authority

[b] Riley, DeGloria and Elliot 1999

Table 2. Correlation analysis for collinearity of explanatory covariates.

Model	**Pair of covariates**	**Correlation**
reproductive frequency	ruggedness – slope	0.966^{***}
	treeline – private	0.991^{***}
	treeline – public	0.962^{***}
	private – public	0.963^{***}
landscape scale selection	ruggedness – slope	0.958^{***}
	elevation – treeline	0.614^{***}
site-specific selection	elevation – treeline	0.609^{***}

Table 3. Topographic characteristics of 50 natal den sites of wolverines in southern Norway. The numbers for all statistics, but for the first four, indicate SE.

Den site characteristic	**Statistic**
Substrate:	
bare rock	46 (92%)
vegetation	2 (4%)
under fallen tree	1 (2%)
not classified	1 (2%)
Den size	80 m^2 ± 18
Field of view	16.3 km^2 ± 2.1
Slope	49° ± 3
Aspect	348° ± 8
Placement on hillside	0.54 ± 0.03
Hillside:	
slope	41° ± 2
aspect	2° ± 7
Elevation	1,120 m ± 24
Distance to treeline (n = 31)	110 m ± 62
Terrain ruggedness index	0.39 ± 0.01
Distance to nearest:	
public road	7,461 m ± 206
private road	3,058 m ± 120

Table 4. Binomial generalized linear model, indicating effect of environmental covariates on reproductive frequency ($n = 26$) in southern Norway.

Model	**Covariates**	**Coeff**	**SE**	**Wald**	***P***	AIC_c	ΔAIC_c	AIC_cw
model 1	intercept	-4.429	1.422	3.12	0.002	97.219	0.000	0.667
	ELEVATION	$4.0E^{-3}$	$1.1E^{-3}$	3.66	0.000			
	SLOPE	-0.052	0.016	3.36	0.000			
	PUBLIC ROAD	$1.1E^{-4}$	$4.2E^{-5}$	2.61	0.009			
model 2	intercept	-4.508	1.422	3.17	0.002	98.609	1.390	0.333
	ELEVATION	$4.0E^{-3}$	$1.1E^{-3}$	3.60	0.000			
	RUGGEDNESS	$-8.5E^{-3}$	$2.7E^{-3}$	3.17	0.002			
	PUBLIC ROAD	$1.1E^{-4}$	$4.1E^{-5}$	2.57	0.010			

Table 5. Resource selection function models, using discrete choice models, indicating landscape scale and site-specific wolverine den site selection (n = 50) in southern Norway. The Wald statistics represent the partial direct effects and excludes contributions from second-order effects.

Model	**Covariates**	**Coeff**	**SE**	**Wald**	P	AIC_c	ΔAIC_c	$AIC_c w$
Landscape scale, model 1	RUGGEDNESS	0.111	0.023	4.82	0.000	107.155	0.000	0.601
	RUGGEDNESS'	-0.110	0.026	4.27	0.000			
	ELEVATION	$5.2E^{-3}$	$3.7E^{-3}$	1.42	0.155			
	ELEVATION'	$-9.3E^{-3}$	$3.3E^{-3}$	2.83	0.005			
	PRIVATE ROAD	$6.3E^{-4}$	$2.3E^{-4}$	2.79	0.005			
	PUBLIC ROAD	$4.1E^{-4}$	$1.6E^{-4}$	2.64	0.008			
	ASPECT	$3.9E^{-3}$	$2.1E^{-3}$	1.87	0.062			
Landscape scale, model 2	SLOPE	0.496	0.114	4.37	0.000	107.977	1.430	0.399
	SLOPE'	-0.565	0.152	3.72	0.000			
	ELEVATION	$7.7E^{-3}$	$3.7E^{-3}$	2.08	0.037			
	ELEVATION'	$-1.1E^{-2}$	$3.1E^{-3}$	3.56	0.000			
	PRIVATE ROAD	$6.7E^{-4}$	$2.5E^{-4}$	2.65	0.008			
	PUBLIC ROAD	$4.0E^{-4}$	$1.5E^{-4}$	2.71	0.007			
	ASPECT	$5.4E^{-3}$	$2.4E^{-3}$	2.26	0.024			
Site-specific, model 1	SLOPE	0.235	0.054	4.39	0.000	60.900	0.000	0.249
	RUGGEDNESS	43.222	10.244	4.22	0.000			
	PRIVATE ROAD	$4.4E^{-3}$	$2.1E^{-3}$	2.14	0.033			
	SHRUB	3.602	1.566	2.30	0.021			
	ROCK	5.217	2.677	1.95	0.051			
	SLOPE*RUGGEDNESS	-0.585	0.156	3.75	0.000			
Site-specific, model 2	SLOPE	0.207	0.045	4.64	0.000	61.491	0.591	0.185
	RUGGEDNESS	37.538	10.366	3.62	0.000			
	SHRUB	2.847	1.446	1.97	0.049			
	ROCK	4.320	2.334	1.85	0.064			
	SLOPE*RUGGEDNESS	-0.486	0.134	3.62	0.000			
Site-specific,	SLOPE	0.210	0.050	4.21	0.000	61.739	0.839	0.164

model 3	RUGGEDNESS	37.005	10.487	3.53	0.000			
	ROCK	3.591	2.213	1.62	0.105			
	SLOPE* RUGGEDNESS	-0.488	0.148	3.29	0.001			
Site-specific,	SLOPE	0.236	0.063	3.76	0.000	61.898	0.998	0.151
model 4	RUGGEDNESS	41.889	10.511	3.99	0.000			
	PRIVATE	$3.6E^{-3}$	$2.0E^{-3}$	1.80	0.072			
	ROCK	4.086	2.462	1.66	0.097			
	SLOPE* RUGGEDNESS	-0.573	0.176	3.25	0.001			
Site-specific,	SLOPE	0.232	0.062	3.77	0.000	62.087	1.187	0.138
model 5	RUGGEDNESS	42.229	11.396	3.71	0.000			
	PRIVATE ROAD	$4.2E^{-3}$	$2.1E^{-3}$	2.01	0.044			
	TREES	-3.335	2.099	1.59	0.112			
	SHRUB	3.785	1.958	1.93	0.053			
	ROCK	5.150	2.740	1.88	0.060			
	SLOPE* RUGGEDNESS	-0.570	0.177	3.23	0.001			
Site-specific,	SLOPE	0.198	0.053	3.75	0.000	62.477	1.577	0.113
model 6	RUGGEDNESS	35.819	11.713	3.06	0.002			
	TREES	-3.218	1.774	1.81	0.070			
	BUSH	3.276	1.977	1.66	0.098			
	ROCK	4.245	2.429	1.75	0.081			
	SLOPE* RUGGEDNESS	-0.453	0.158	2.88	0.004			

Table 6. Multinomial logistic regression comparing den selection covariates between the den site and each distance class, both for the landscape and site-specific scale. The last four columns give the Wald statistic for each covariate. One, two and three asterisks indicate $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

Model	**Covariates**	**Distance classes (m)**			
Landscape scale		**500**	**1,000**	**2,500**	**5,000**
	RUGGEDNESS	2.55^{*}	3.71^{***}	3.33^{***}	4.65^{***}
	RUGGEDNESS'	2.00^{*}	3.01^{**}	2.10^{*}	3.92^{***}
	ELEVATION	2.53^{*}	3.20^{**}	3.49^{***}	4.27^{***}
	ELEVATION'	0.88	1.74	0.86	1.35
	PRIVATE ROAD	0.26	0.71	1.07	1.33
	PUBLIC ROAD	0.05	0.00	0.33	1.64
	ASPECT	0.89	0.22	0.90	0.65
Site-specific		**50**	**100**	**250**	**500**
	SLOPE	2.75^{**}	2.70^{**}	2.17^{*}	2.11^{*}
	RUGGEDNESS	5598.35^{***}	5893.01^{***}	5948.80^{***}	2347.92^{***}
	PRIVATE ROAD	3.24^{**}	3.48^{***}	3.81^{***}	4.61^{***}
	SHRUB	2340.92^{***}	3386.40^{***}	1030.68^{***}	1605.51^{***}
	ROCK	3100.94^{***}	3779.09^{***}	2289.32^{***}	1537.42^{***}
	RUGGEDNESS*SLOPE	3.87^{***}	4.14^{***}	4.44^{***}	4.91^{***}

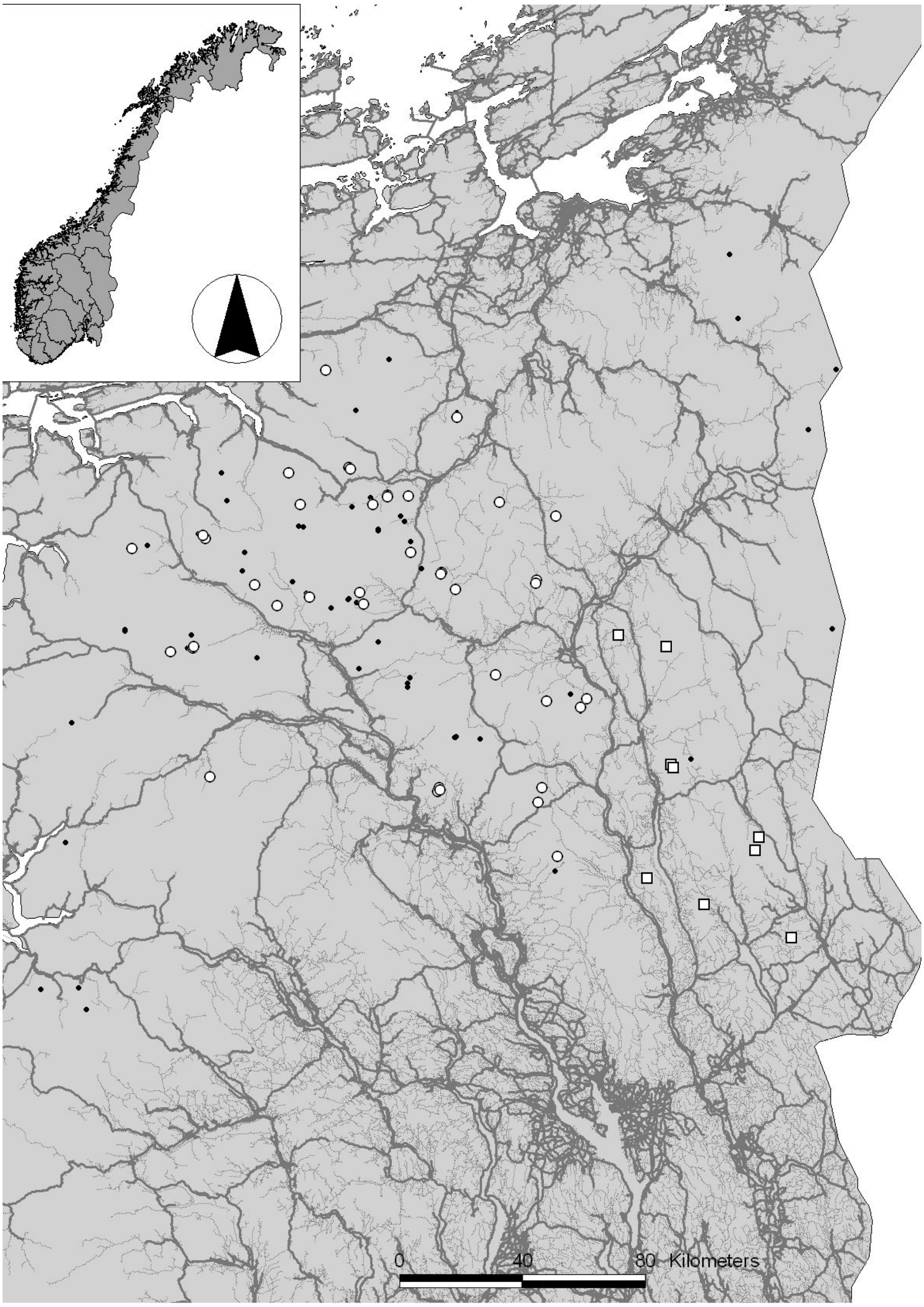

Figure 1.

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos Bothany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.

1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.

1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*

1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size

2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt

2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Ander Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge

2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	Phd Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	phD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	phD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	phD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	phD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	phD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	phD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	phD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	phD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	phD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	phD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	phD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	phD Biology	Spatial and temporal variation in herbivore resources at northern latitudes