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Wolverine foraging strategies in a multiple-use landscape

Thesis for the degree of philosophiae doctor

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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 (Ph.D.). 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 a 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.

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To my family, thanks for having faith in me, as usual, as it has been for over 35 years now. Thanks to Dave Sowards for saying I could do it and for listening to my grumbles, and to Vemund Jaren explaining the Norwegian wolverine management system. I also express my sincere thanks to Harry Reynolds, not only for what he taught me as a professional about how to handle wild animals in the field, the ethical side of doing animal research, and for his scientific contributions and English corrections to my papers, but also for his friendship. Last, but definitely not least, I would like to express my dearest thanks and love to Roel May. Without Roel this thesis would not have been accomplished. It must have been tough for Roel to be both my colleague and my husband at the same time during the last four years. Although our dog Timmy helped us tremendously to see the joy of life at difficult times, Roel deserves and gets my greatest love.

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II. **van Dijk, J.**, Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Broseth, H., Andersen, R., Andersen, R., Steen, H., & Landa, A. (submitted manuscript). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. – *Journal of Animal Ecology*.

III. **van Dijk, J.**, Andersen, T., May, R., Andersen, R., Andersen, R. & Landa, A. (submitted manuscript). Foraging strategies of wolverines within a predator guild. – *Canadian Journal of Zoology*.

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Introduction

Large carnivore guilds in multiple-use landscapes

During recent centuries, human development and urbanization in Europe have changed wilderness areas into fragmented multiple-use landscapes. Although these changes are considered to be the most important threat to biological diversity in terrestrial ecosystems (May et al. 2006; Entwistle & Dunstone 2000), still many wildlife species, including most of the large herbivore species and large carnivore species, are able to survive in multiple-use landscapes. European large carnivore (brown bear *Ursus arctos*, wolf *Canis lupus*, wolverine *Gulo gulo* and lynx *Lynx lynx*) still remain absent from huge parts of their former range, however, most metapopulations are stable or increasing. Because large carnivores require large areas of suitable habitat (Crooks & Soulé 1999; Purvis *et al.* 2000; Sunquist & Sunquist 2001; Cardillo *et al.* 2004), they have to be integrated in multiple-use landscapes in order to be conserved in viable populations. Before such integration can occur, strategies must be developed that allow humans to coexist with large carnivores.

The recent recolonization of wolves and bears to their former range in both Europe and North America is linked to legal protection, reduced hunting, and increased ungulate populations (Massolo & Meriggi 1998; Berger, Swenson & Persson 2001; Kunkel *et al.* 2004; Oakleaf *et al.* 2006). This has sparked great interest into how ecosystem function has changed after the return of these top predators. To date, primary attention has focused on the effects of wolf recolonization on deer populations, and how this in turn affects vegetative cover (Ripple *et al.* 2001; Vucetich & Peterson 2004; Fortin *et al.* 2005; Ripple & Beschta 2006). Surprisingly little attention has been paid to the influence of top predators on scavengers, with a few notable exceptions in North America and Poland (Berger 1999; Wilmers *et al.* 2003; Ripple & Beschta 2004; Wilmers & Post 2006; Selva & Fortuna 2007). As large carnivores play a central role in the maintenance of the biodiversity, stability, and integrity of various communities (Noss *et al.* 1996; Berger 1999), conservation of these species in a community context is a challenge worldwide. However, successful conservation of large carnivore communities is best achieved when knowledge of the factors favouring coexistence among the large carnivore species exists.

Wolverine foraging strategies in multiple-use landscapes

Large carnivores, especially wolverines, are increasingly involved in conflicts with human interests in Norway because of their depredation on semi-domestic reindeer *Rangifer tarandus* throughout the year, and on free-ranging domestic sheep *Ovis aries* during summer. In an attempt to minimize conflict levels, management agencies have initiated licensed hunting, depredation control, and *ex post facto* compensation schemes (Landa, Lindén & Kojola 2000; Swenson & Andrén 2005), as well as regional zoning of large carnivores (Linnell *et al.* 2005). Despite these measures, effective conservation of the Norwegian wolverine populations is still substantially limited by depredation conflicts and the lack of knowledge on the exact nature of wolverine depredation (i.e., why and who) has limited the acceptance for wolverines by local people.

In an intra-guild context, wolverines have evolved as scavengers, utilizing remains left by other, more efficient predators such as lynx and wolf, in addition to carcasses of animals which have died from accidents or diseases (Haglund 1966; Banci 1987; Magoun 1987; Banci 1994; Novikov 1994; Landa & Skogland 1995; Landa *et al.* 1997). On the other hand complex systems of interactions, such as intra-guild competition and predation, exist among mammalian carnivores (Hornocker & Hash 1981; Banci 1994; Caro 1994; Creel & Creel 1996; Palomares & Caro 1999). In their search for food wolverines may well displace lynx from their kills, potentially resulting in an increased kill rate by lynx. On the other hand, wolverines may scavenge the remains of wolf and lynx kills, thus potentially reducing the necessity for wolverines to kill other prey. Given the requirements by wolverines for large and relatively unfragmented habitat, it is important for effective management to know intra-guild relationships between wolverines and other large carnivores in terms of species' depredation rates. For example, if wolverine interactions with other large carnivores would result in decreased wolverine depredation rates, this knowledge would affect predation management strategies. Having a better understanding of wolverine foraging strategies, when in sympatry with other large carnivores, should assist the process of integrating viable wolverine populations into multiple-use landscapes and minimizing conflicts with domestic sheep and semi-domestic reindeer.

Aim of the thesis

The principal objective of the research project *Wolverines in a Changing World* was to gain better insights into the role wolverines have 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 wolverine foraging strategies in a multiple-use landscape, especially in higher alpine habitat where livestock are grazed without human supervision or protection and in the boreal forest where wolverines co-exist with other intra-guild species. This aim was addressed by focusing on the following research questions.

1. Which analytical method is most appropriate to analyze wolverine diet? [Paper I]
2. Do wolverines shift their food habit in areas where they co-exist with wolves? [Paper II]
3. Which foraging strategies do wolverines employ within a predator guild? [Paper III]
4. Is the large carnivore guild differentiated in habitat tolerances and distribution, and what effect does this have on the potential for regional zoning of large carnivores? [Paper IV]

5. Can spatio-temporal variation in lamb depredation rates be explained by local wolverine density and/or predator removal programs, and are certain demographic classes of wolverines responsible for the increased depredation rate during the latter portion of the grazing season? [Paper V]

Methods

Study species

The wolverine is the largest terrestrial member of the family *Mustelidae* with a circumpolar distribution, and primarily inhabits tundra and taiga of northern latitudes (Wilson 1982). Wolverine distribution is almost entirely sympatric with that of wild and semi-domestic reindeer (Landa, Lindén & Kojola 2000). Present populations of wolverines in Scandinavia are found in the central to northern regions of Norway and Sweden, and are primarily found in mountain areas (Landa & Skogland 1995; Landa, Lindén & Kojola 2000). In south-central Norway, during the last decade, the wolverine has extended its distribution eastwards into the boreal forests (Brøseth & Andersen 2004; Flagstad *et al.* 2004a; Flagstad *et al.* 2004b) after wolves recolonized the same region a few years earlier (Wabakken *et al.* 2001). In Norway, the population estimate, based on the average annual minimum number of reproductions during last three years, was set to 354 ± 42 individuals (≥ 1 yr) in 2006 (Andersen & Brøseth 2006). The wolverine is labelled by the IUCN as a vulnerable species (Hilton-Taylor 2000), and is considered to be endangered in Norway (Norwegian National Red List; Kålås, Viken & Bakken 2006).

Wolverines range in size from 10-20 kg, with males being heavier than females. With their broad robust skull, set with 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 or occasionally even moose *Alces alces* (Haglund 1966).

Home ranges vary from 40–100 km^2 for reproducing females to 200–1,500 km^2 for females without cubs and adult males, whereas sub-adults may even roam over several thousand square kilometres (Landa, Lindén & Kojola 2000). Mating occurs during the summer but, due to delayed implantation, wolverines don't give birth before early spring (Landa, Lindén & Kojola 2000; Ferguson, Higdon & Larivière 2006). They give birth to an average of two cubs (Persson *et al.* 2006) in den sites placed in steep, rugged terrain just above the tree line (May *et al.*, unpublished data). Wolverines are typically solitary, which is common among terrestrial mustelids (Dalerum 2005). Although social groups are rarely observed, except for mating pairs or females with cubs, home ranges of males generally overlap with both other males and several females; similarly home ranges of females may partly overlap with other females (Hornocker & Hash 1981; Magoun 1985; Banci & Harestad 1990; Landa, Lindén & Kojola 2000). Young females typically establish residency next to or partly within the natal home range (Magoun 1985). At abundant and concentrated sources of food, such as large carrion, tolerance among adult wolverines appears to increase and adult individuals of the same sex may feed concurrently at the same site, or at the same food source (Banci 1994; Landa 1997).

Study areas

The study areas chosen for the different studies varied from a semi-natural enclosure to the entire wolverine distribution in Norway. The first research question (Paper I) was addressed using a feeding trial which was carried out with two adult wolverines at the Polar Zoo, Troms County, northern Norway. Both wolverines were housed in a semi-natural enclosure of 15,000 m^2 consisting of natural birch forest. The study area for Paper II encompassed the wolverine distribution in southern Norway (Landa, Lindén & Kojola 2000), whereas the study area for Paper III and IV was located in southeastern Norway, in Hedmark County. For Paper V all registered sheep grazing areas in Norway (2001-2004) which either overlapped with wolverine distribution, or for which wolverine predation on sheep had been documented between 2000 and 2005, were used.

Norway exhibits different ecotypes due to the large latitudinal range of the country and its varied topography and climate. The habitat can generally be categorized as mountain plateaus with peaks of bare rock to elevations of 2,000 m, which give way to alpine tundra with heath (e.g. heather *Caluna* spp., crowberry *Empetrum* spp.) and lichen (*Cladonia* spp.) vegetation. At lower elevations, alpine shrub land (e.g. willow *Salix* spp., dwarf birch *Betula nana*) can be found close to tree line. The transition from the shrub land to birch forests below the tree line forms the forest/alpine tundra ecotone (Grytnes 2003). The elevation of tree line decreases with latitude: in the South no trees grow above 1,000 m a.s.l., whereas in the North the tree line is found at 400 m a.s.l. Below tree line, forests are composed 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.), interspersed with open bogs, and some agricultural lands. Human infrastructure is generally concentrated at lower elevations in the valley bottoms although recreational cabins can be found at higher elevations as well. Human activities in the mountains mainly consist of hunting, hiking, camping and cross-country skiing.

Sheep grazing areas are found throughout Norway, but sheep grazing is especially intensive in southwestern Norway, and sheep are largely left unattended during mid-June to mid-September (Landa, Lindén & Kojola 2000). Especially in northern Norway and sporadically in central Norway semi-domestic reindeer herding is also practiced. Unlike sheep husbandry practices, reindeer herds are free-ranging for the entire year, and are therefore vulnerable to predation over a longer period (Landa, Lindén & Kojola 2000). The largest European population of wild reindeer is found in the mountainous areas in the southwestern and southcentral Norway. Moose, roe deer *Capreolus capreolus*, hares *Lepus timidus,* ptarmigan *Lagopus muta,* willow grouse *Lagopus lagopus*, lemmings *Lemmus lemmus*, various rodents (*Microtus* spp. and *Clethrionomys* spp.) and insectivores *Insectivora* spp. (lemming, various rodents and insectivores are hereafter called rodents) form possible sources of food for the wolverine in both northern and southern Norway; either as hunted prey or through scavenging.

In Hedmark County in southeastern Norway where boreal forest dominates the landscape, wolverines, lynx, wolves, and brown bears occur at relatively low densities due to management policies. During the winters of 2002-2003 and 2003-2004 there were two wolf packs within the study area with a minimum of five individuals per pack, in addition to two lone wolves that roamed the southern border of the study area (Wabakken et al. 2004). The National Large Carnivore Monitoring Program (Andrén *et al.* 2002; Swenson *et al.* 2003; Brøseth & Andersen 2004; Brøseth, Odden & Linnell 2004; State of the Environment Norway 2005) estimated that 32 wolverines, 50 lynx and 10-15 brown bears were present in Hedmark County. Red foxes were common within the study area but no population estimate exists.

Study methods

The papers included within this thesis are based on different data sources, varying from experimentally obtained data on two captive wolverines, scat collections, snow tracking data, locational data from radio-marked individuals in the different study areas, to data on documented kills of lambs by wolverines.

For research question I (Paper I) a feeding trial was carried out in which five important prey species for wolverines in Norway (i.e., reindeer, sheep, hares, ptarmigans and rodents;

Landa *et al.* 1997) were offered to two adult wolverines at the Polar Zoo. Scats resulting from the feeding trial were collected and analyzed. Hairs and feathers within the scat were identified to species level using macroscopic and microscopic characteristics following published identification keys (Williamson 1951; Day 1966; Teerink 1991) and comparison with reference collections. Dry weights (Johnson & Hansen 1979; Reig & Jedrzejewski 1988), index of relative contributions (Berducou, Faliu & Barrat 1983), frequency of occurrence (Berducou, Faliu & Barrat 1983; Corbett 1989) and percentage of occurrence (Ciucci *et al.* 1996) for the different prey species within the hair and feather category were calculated. Frequency of occurrence and percentage of occurrence were used to determine the importance of the prey species (i.e. how often do wolverines eat a certain prey species). Dry weight and the index of relative contribution provided insight into the nutritional significance of each prey species to the predator (i.e. how much of each prey species do wolverines eat). Diets calculated using the four methods, were compared with the diet provided to the wolverines through concordance of species ranking of importance.

Paper II was based on scats collected in southern Norway by the Norwegian State Nature Inspectorate during late winter- early spring, as part of the national large carnivore monitoring program. From each scat individual identification (ID) and sex was obtained in cases where faecal DNA was successfully extracted (Flagstad *et al.* 2004b). Scats were analyzed after Ciucci *et al.* (1996) resulting in percentage of occurrence data and for each scat's location habitat type (with use of a 1x1km land cover map) and a prey density index (based on hunting statistics) was assessed. Diet breadth per habitat and sex was calculated in combination with presence or absence of wolf packs using the standardized Levin's measure of niche breadth (see Hurlbert 1978). Occurrence of reindeer, moose and small prey species (i.e., hare, birds and rodents taken together) in the diet were assessed using generalized mixed effect models.

In Hedmark County where wolverines are sympatric with wolves, lynx and red foxes, wolverines were tracked in the snow during two winter seasons (Paper III). Observations of locations of marking behaviour (i.e., secretions, bite marks and claw marks), defecations, urinations, resting places, hunting attempts and food sources, and observations of red fox, lynx and wolf trails were recorded along the wolverine track. Using multivariate regression and fractal dimension analyses (i.e., tortuousness of a wolverine's track as a characteristic of its searching behaviour; Krebs 1999; Nams 2005) wolverine's foraging strategies were analyzed with regard to the presence of other carnivore species and to prey availability.

Paper IV was based on radio-tracking data gathered from field research projects on wolverines, lynx, wolves and brown bears in Hedmark County. 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. Differentiation of habitat use 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. Each covariate was obtained from different background maps (i.e., Digital Elevation Model, MODIS map and 1:50,000 topographic maps). Analysis showed that the best fit was a landscape approach, where we chose to study patterns of selection of geographical ranges within the landscape (first order selection, Johnson 1980), using resource selection function models.

The number of documented kills of lambs by wolverines (confirmed or assumed by the State Nature Inspectorate) during the grazing season was used to analyze spatio-temporal variation in lamb depredation rates and seasonal lamb depredation patterns (Paper V). Spatio-temporal variation in lamb depredation rates were analysed using mixed effects Poisson regression with year and grazing area as random grouping factors to account for replication over grazing areas and years. The number of documented kills of lambs by wolverines per total number of lambs released onto the grazing pastures was taken as measure for lamb depredation rates. The geographic positions of documented wolverine reproductions and removed wolverines (i.e., wolverines killed during license hunts, predator removal, family removal and cub removal) were buffered with a 10 km radius (i.e., the approximate mean radius of the home range of female wolverines; Landa *et al.* 1998). When the buffer overlapped with a sheep grazing area the reproduction or removed wolverine was assumed to be present in this area. Presence of reproductions, removed wolverines, the dominant habitat types (i.e., forest, alpine shrub land or alpine tundra) of each grazing area and region (i.e., northern or southern Norway) were included in the models as explanatory variables. Seasonal depredation patterns were analyzed using information (i.e., number of bite mark locations and whether and how sheep carcasses were hidden in the terrain) recorded on the registration forms of carcass autopsies performed by field personnel of the State Nature Inspectorate in Oppland, Sør-Trøndelag and Hedmark Counties.

Results and discussion

Spatio-temporal distribution of primary food sources is one of the most important spacing patterns in carnivores (Sandell 1989). In multiple-use landscapes, the sustainability of large carnivore populations depends on their ability to co-exist with humans, and is dependent upon societal acceptance of their use of primary food sources (i.e., both wild prey and livestock) (Landa, Lindén & Kojola 2000; Swenson & Andrén 2005). This especially applies for scavengers like the wolverine. The answers to the following questions will shed light on wolverine foraging strategies in the multiple-use landscapes of Scandinavia.

Question 1: *Which analytical method is most appropriate to analyze wolverine diet? [Paper I]*

Wolverines depend on both hunting and scavenging for food (Haglund 1966; Magoun 1987), and their diet has often been described using the frequency of occurrence method (Berducou, Faliu & Barrat 1983; Corbett 1989), in North America (Hornocker & Hash 1981; Magoun 1987; Banci 1994) and Fennoscandia (Haglund 1966; Myhre & Myrberget 1975; Landa *et al.* 1997).

Of the four quantitative methods used, frequency of occurrence and percentage of occurrence resulted in the lowest deviation from the actual diet provided. Although frequency of occurrence had a low concordance with the other three methods, it may still be advisable to include it in diet analyses since it enables comparison with former wolverine studies (e.g., Myhre & Myrberget 1975, Magoun 1987, Landa et al. 1997). Given the opportunistic and varied diet of wolverines, the percentage of occurrence provides a better indication of the relative frequency with which each prey species was consumed (Berducou, Faliu & Barrat 1983; Ciucci *et al.* 1996). It not only indicates how common a prey species is in the diet but also accounts for the relative importance of the different prey species found in the diet (Ackerman, Lindzey & Hemker 1984).

During our analyses of scats sheep hair was only identifiable when present in larger amounts. This resulted in an underestimation of sheep in comparison to actual diet given. In their dietary study on wolverines in the wild Landa *et al.* (1997) argue that the low representation of sheep occurred because sheep wool is likely to fall off during decomposition of sheep carcasses after being hoarded by wolverines during late summer. In our study, however, this could not explain the under-representation of sheep since all food items had been eaten. The under-representation of sheep in our study may have been the result of wolverines plucking the wool from the meat prior to consumption. This behaviour was repeatedly observed when portions of sheep carcasses were offered to the wolverines in our study and we found wool on the ground where plucking behaviour was observed.

Question 2: *Do wolverines shift their food habit in areas where they co-exist with wolves? [Paper II]*

The results of this study revealed that concurrent with the presence of wolves in an area, the amount of moose in wolverine winter-spring diets increased and that wolverines switched to scavenging when scavenging opportunities became more plentiful. We controlled for potential confounding factors such as the local availability of prey species that wolverines could either hunt or scavenge.

Because adult male wolverines have larger home range sizes than females (Landa *et al.* 1998); especially compared to the restricted range of females with offspring (Landa *et al.* 1998; Magoun & Copeland 1998), we expected that scavenging opportunities may be more important for male than female wolverines. We also assumed that females with offspring, who employ a central place foraging strategy (May *et al*. unpublished data) and therefore have smaller home ranges, would compensate the lower opportunity of finding carrion with hunting on small prey species (i.e., hare, birds, rodents). Although female wolverine diet outside wolf territories consisted of more small prey than male wolverine diet, there was a tendency for females to opportunistically utilize the highly available moose carrion and hunt less for small prey within wolf territories.

This study highlighted how scavenging opportunities for wolverines increase in the presence of wolves, and how sexual differences in diet may apply to large scavengers such as the wolverine. The relative high occurrence of wolf kills forms an important food source to wolverines in this area. The recolonization of the area by wolves might thus have contributed to the recolonization of wolverines into the same area.

Question 3: *Which foraging strategies do wolverines employ within a predator guild? [Paper III]*

Given that intra-guild interactions (Holt & Polis 1997; Creel, Spong & Creel 2001) could result in increased competition for food sources (Paquet 1992; Creel & Creel 1996; Linnell & Strand 2000), and intra-guild predation is a widespread phenomenon in mammalian carnivores (Palomares & Caro 1999; Linnell & Strand 2000), wolverines may well face a trade-off between the risk of being killed by other predators and the benefits provided by the increased scavenging opportunities from the kills made by these larger predators (Burkholder 1962; Hornocker & Hash 1981; Bjärvall 1983; Banci 1994; Copeland 1996; Magoun & Copeland 1998).

In this study we recorded more observations of wolf trails at lower than at higher elevations and increased wolverine territorial and resting behaviours (i.e., active marking behaviour, defecation, resting places and hunting attempts) at higher elevations than lower elevations. Similarly, in Paper IV we determined that wolverines use higher elevations than wolves in this region. Wolves tend to follow moose which use lower elevation habitats when snow becomes deeper (Cook, Norris & Theberge 1999; Kunkel & Pletscher 2001).

Of the 23 carcasses visited by wolverines, 19 carcasses were from moose and only four were bird species. No hares, roe deer or rodents were found. Moose carcasses were apparently preferred or abundant enough that scavenging or hunting other prey was either less likely or not energy efficient. Similarly, neither Haglund (1966) nor Myhre (1968) found evidence of successful hunts during their efforts to follow wolverine tracks in the snow. This lack of documented successful hunts may well indicate that in this boreal forest ecosystem wolverines seldom kill their own prey during the winter season but rather depend on carrion or sometimes cached food. Our findings support the suggestion by Magoun (1987) that both prey species composition and availability of carrion influence wolverine hunting activity.

Predation of wolverines by wolves has previously been documented (Novikov 1962; Hornocker & Hash 1981; Bjärvall & Isakson 1982; Banci 1994; Copeland 1996; Magoun & Copeland 1998), and the lack of observations in which wolverines followed wolf trails may indicate that wolverines experience intra-guild predation and interference by wolves (Linnell & Strand 2000). This risk may be reduced by avoiding direct confrontation with wolves and temporal and/or spatial exclusion at carcass sites (see also Paquet 1992; Cohn 1998). Wolverines changed their searching behaviour directly after encounters with lynx trails, with the wolverine track being more tortuous directly after these encounters. Conversely, the wolverine track became less tortuous directly after encounters with fox trails. Wolverine searching behaviour may be influenced by red fox and lynx as seen from changes in track tortuousness.

The importance of scavenging from prey killed by other guild species, in addition to the observed spatial and/or temporal separation between wolverines and wolves or lynx, presumably to avoid intra-guild predation, suggests that maintaining a wolverine population in the presence of other guild species is ecologically feasible within the boreal ecosystem (see also Paper IV). However, wolf, lynx and wolverine populations in Hedmark County are heavily exploited by humans, which likely reduces the magnitude of intra-guild relationships between wolverine, lynx and wolf.

Question 4: *Is the large carnivore community differentiated in habitat tolerances and distribution, and what effect does this have on the potential for regional zoning of large carnivores? [Paper IV]*

Within an intra-guild community setting, sympatry of the wolverine with the three forest-dwelling carnivore species, lynx, wolves and brown bears, appears to depend on the availability of mountainous terrain as a spatial refuge (May *et al.* unpublished data) and the presence of wolves to provide scavenging opportunities (Paper II, III). Brown bears, wolves and lynx were generally associated with rugged, forested areas at lower elevations, while wolverines selected open, rugged terrain at higher elevations. This result fits well with the perception that the wolverine is a carnivore of remote alpine regions (May *et al.* 2006; Carroll, Noss & Paquet 2001; Rowland *et al.* 2003). Despite their similar potential distribution patterns, the three "forest-dwelling" species also displayed clear differences in selection of habitat and location of 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 for the appropriate scale for 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 for all four species found in this region may 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 related to depredations and result in resistance to carnivore conservation by local residents (Wabakken 2001; Linnell *et al.* 2005).

Question 5: *Can spatio-temporal variation in lamb depredation rates be explained by local wolverine density and/or predator removal programs, and are certain demographic classes of wolverines responsible for the increased depredation rate during the latter portion of the grazing season? [Paper V]*

This study revealed that reproductive events, primarily the presence of an adult female with cubs in a given grazing area, resulted in higher depredation rates. Also the removal of adult females during the winter preceding the grazing season resulted in higher depredation rates. The removal of a resident adult female may well lead to local demographic instability (Linnell *et al.* 1996). The gap created in the social mosaic of the population may temporarily lead to higher local densities with the establishment of neighbouring or new individuals in the area (Hornocker 1969; Shaw 1982; Lindzey *et al.* 1992; Thomson, Rose & Kok 1992; Laing & Lindzey 1993; Corbett 1995). Because wolverines can roam over long distances (Hornocker & Hash 1981; Vangen *et al.* 2001) the potential for other wolverines re-establishing home ranges in an area where another one has been removed is high (Landa *et al.* 1998). Landa *et al.* (1999) found, however, that killing of wolverines led to fewer lambs being lost in the same year, but this effect did not carry over to the next year, and depredations resumed, implying a rapid re-establishment of new individuals. Similar results have been found for other carnivores such as wolves (Bjorge & Gunson 1985), lynx (Stahl *et al.* 2001; Herfindal *et al.*

2005), bears (Sagør, Swenson & Røskaft 1997) and red foxes (Reynolds, Goddard & Brockless 1993).

In an area used by a female wolverine accompanied by cubs, not only the resident adult female and her cubs are present, but the father of the cubs and sub-adults from previous litters may also frequently use the same area. This may lead to locally higher densities of wolverines, which fits the suggestion made by Landa *et al.* (1999) that differences in sheep losses among grazing areas were probably related to local variation in wolverine density. According to our model depredation rates were best explained by different demographic groups sharing the same area on a temporal basis at the same time (higher local densities) and by demographic instability, which may be enhanced by predator removal programs.

Lamb depredation rates by wolverines were lower when lamb availability increased, as was also found with lynx depredation (Negård *et al.* 1998; Herfindal 2000; Herfindal *et al.* 2005), brown bear depredation (Camarra 1986; Sagør, Swenson & Røskaft 1997; Kaczensky 1999) and large felids depredation (Michalski *et al.* 2006). This suggests that the availability of sheep does not affect the wolverine's natural foraging behaviour or rate of off-take (i.e., surplus prey).

Depredation rates were highest in alpine shrub land (i.e., forest/alpine tundra ecotone), with a typical depredation increase during the latter portion of the grazing season. According to Mysterud, Iversen & Austrheim (in press) sheep begin the grazing season at lower elevations and move to higher elevations as the it proceeds. At the end of the grazing season, sheep gradually move to lower elevations and tend to use the forest/alpine tundra ecotone during late summer (Mysterud, Iversen & Austrheim in press). GPS analyses on ranging behaviour in wolverines revealed that wolverines prefer to use the forest/alpine tundra ecotone not only at night during the entire summer season but used the ecotone increasingly during daytime as the summer season progressed (May *et al.* unpublished data). The pattern that both sheep and wolverine occupy the same forest/alpine tundra ecotone at the end of the grazing season may explain seasonal depredation patterns in general.

Results from a study on maternal care in wolverines (Landa *et al.* unpublished data) revealed that wolverine cubs become nutritionally independent in August. Seasonal depredation patterns coincide with cub independence; therefore it is likely that these young individuals are at least partly responsible for the increased depredation during the latter portions of the grazing season. It is possible that the independent cubs use lambs as surplus prey (i.e., easy "test-object") to perfect their hunting skills before the onset of winter.

Management implications for an endangered wolverine population in a multiple-use landscape

Conserving large carnivores in landscapes that are also used by humans is a complex and dynamic problem, involving ecological, economic, institutional, political, and cultural factors. The wolverine is protected by the Bern Convention which requires signatories, including Norway, to contribute to viable populations (Ministry of the Environment 2003). Still, the Scandinavian wolverine population is a non-continuous population which is often at risk at some localities (Landa *et al.* 2000; Flagstad *et al.* 2004). Given the large areas of continuous habitat that are required by carnivores (Crooks & Soulé 1999; Purvis *et al.* 2000; Sunquist & Sunquist 2001; Cardillo *et al.* 2004), a successful management strategy is only possible when we succeed in effectively integrating them into the multiple-use landscapes. This can be realized by applying our knowledge on inter-specific relationships among carnivores (Paper II, III & IV), while aiming to minimize livestock depredation conflicts with help of the findings in Paper IV & V.

Within the predator guild, the wolverine has evolved as a scavenger of prey killed by more effective predators. The observed spatial and temporal separation between wolverines and wolves and lynx (Paper III & IV), presumably to avoid intra-guild predation, suggests that maintaining a wolverine population in the presence of other guild species is ecologically feasible within the boreal ecosystem. Although wolves provide wolverines with scavenging opportunities (Paper II & III), further wolverine recovery in forest ecosystems might be difficult given the reproductive den site requirements (May *et al.*, unpublished data), the concentrated human development in forested areas at lower elevations (May *et al.* 2006), and the continuing encroachment of human activity on wilderness areas (Landa 1997). These limitations force us to integrate large carnivores into the multiple-use landscapes and minimize livestock depredation conflicts.

The number of documented family groups of female wolverines with cubs in Norway has increased from 44 in 2000 to 62 in 2005, but the population is still considered to be endangered (Kålås *et al.*, 2006). In 2003 the Norwegian government adopted a new large carnivore management policy (Ministry of the Environment 2003; Committee on Energy and Environment 2004) in which the goal was set to reduce the wolverine population size that includes a documented annual average of 39 reproduction events. The goal of this reduction in population size is to minimize the livestock depredation conflict to an acceptable level. However, since wolverine depredation especially affects herders at a local level, reductions in wolverine population numbers may not have the desired effect of reducing conflict levels or enhancing the level of acceptance for wolverines by local people. Even if the wolverine population is reduced to a level that supports 39 females with cubs, there will still be 39 different areas with heightened depredation losses each year, while most grazing areas within the wolverine distribution are likely to be affected periodically. Successful conservation of wolverines can therefore only be achieved by seeking a balance between local social acceptance, management practices and biological processes.

Future research

This thesis has provided insight into the foraging strategies of wolverines in the multiple-use landscape of Norway. But as all science does, this thesis has not only given us knowledge, it has also generated new questions that should be addressed. Although Paper II and III clearly revealed how wolverine take advantage of carcasses left by wolves and Paper IV indicated that spatial processes enables intra-guild species to co-exist within the boreal ecosystem, Paper II, III, IV and V also suggest various questions on wolverine foraging strategies in a multiple-use landscape. The scope of this thesis didn't allow me to document interactions or address the dependency of wolverines on scavenging prey that brown bears may kill. Bears hibernate during winter months and we can therefore assume that dependency of wolverines on bear for the provision of food during this time can be neglected. On the other hand we can speculate that wolverine use of (wild) food resources left by more efficient guild species may result in fewer depredations of sheep and other livestock by wolverines during the summer season. In areas where locally high sheep depredation by bears may occur (Swenson & Andrén 2005), the availability of bear-killed carcasses on wolverine foraging strategies merits further research.

Apart from the lack of knowledge on wolverine's foraging strategies with regard to bear presence, the interactions we found between wolverine-lynx and wolverine-red fox were not straightforward or in agreement with earlier studies (e.g., Mårell 1997; Mathisen *et al.* 2002). Especially the interactions between wolverine and red fox need further research to understand the impact of these two species on each other and their significance for high alpine ecosystems. With regard to depredation losses and its relevance for successful integrating conservation of wolverines in a multiple-use landscape, more knowledge is needed on the importance of sheep as temporarily abundant food source on wolverine demography (reproduction, survival, dispersal). Management strategies should be explored that could reduce the vulnerability of lambs to wolverine depredation and benefit both agricultural interests and allow wolverine populations to reach reasonable levels. Both in Landa et al. (1997) and Paper II no sheep remains were found within the winter diet of wolverines. Analyses of stable isotopes have been shown to be a powerful complement to traditional diet analyses (Hobson 1999; Kelly 2000) and together with analyses on stomach contents of shot animals it could give us insight into the use of sheep as food source.

The research topics mentioned above will furthermore enhance our knowledge on wolverine's foraging strategies in a multiple-use landscape, which in turn enables successful conservation and management of this elusive species in the future.

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Paper I

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Paper II

Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves

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Running heading: Wolverine diet shift after wolf recolonization

Summary

1. Wolves *Canis lupus* L. recolonized the boreal forests in the southern part of the Scandinavian peninsula during the late 1990's, but so far there has been little attention to its effect on ecosystem functioning. Wolf predation increases the availability of carcasses of large prey, especially moose *Alces alces* L., which in turn may lead to a diet switch in facultative scavengers like the wolverine *Gulo gulo* L.

2. Using 459 wolverine scats collected during winter-spring 2001-2004 for DNA identity and dietary contents, we compared diet inside and outside wolf territories while controlling for potential confounding factors like prey density. We tested the hypothesis that wolverine diet shifted towards moose in the presence of wolves, while taking into account possible sexual segregation between the sexes. Occurrence of reindeer, moose and small prey was modelled against explanatory covariates using logistic mixed-effects models. We furthermore compared diet composition and breadth among habitats and sexes.

3. Occurrence of reindeer, moose and small prey in the diet varied with prey availability and habitat. As expected, diet contained more moose and less reindeer and small prey in the presence of wolves. Their diet in tundra consisted of 40% reindeer *Rangifer tarandus* L., 39% moose and 9% rodents. In forest with wolf, their diet shifted to 76% moose, 18% reindeer, and 5% rodents; compared to 42% moose, 32% reindeer and 15% rodents in forest without wolf. This diet switch could not be explained by higher moose density in wolf territories. Female diet consisted of more small prey than for males, but there was a tendency that females opportunistically utilized the highly available moose carrion and hunted less on small prey within wolf territories.

4. Our study highlights how wolves increase scavenging opportunities for wolverines, and that sexual differences in diet may also apply to large scavengers. Due to their more restricted home range female wolverines are forced to rely more on hunted small prey. The relative high occurrence of wolf kills, however, forms an important food source to wolverines in this area. The recolonization of wolves might therefore have contributed to the consequent recolonization of wolverines into the same area.

Key words hunting, intra-guild interactions, large carnivores, scavenging, sexual segregation

Introduction

The recent recolonization of large carnivores such as wolves *Canis lupus* L. and bears *Ursus arctos* L. to their former range in both Europe and North America seems to be linked to legal protection, reduced hunting and to increased ungulate populations (Berger, Swenson & Persson 2001; Kunkel *et al.* 2004; Massolo & Meriggi 1998; Oakleaf *et al.* 2006). This has sparked great interest into how ecosystem function has changed after the return of these top predators, particularly in studies on wolves in Yellowstone. Attention has focussed mainly on the effect of wolves on deer populations, and how this in turn affects vegetative cover (Fortin *et al.* 2005; Ripple *et al.* 2001; Ripple & Beschta 2006; Vucetich & Peterson 2004). Surprisingly little attention has been paid to the influence of top predators on scavengers, with a few notable exceptions in North America and Poland (Berger 1999; Ripple & Beschta 2004; Selva & Fortuna 2007; Wilmers *et al.* 2003; Wilmers & Post 2006). Wilmers *et al.* (2003) found that before the reintroduction of wolves to Yellowstone National Park in 1995, the timing of elk carrion was a pulsed resource at the end of severe winters. After the reintroduction of wolves this changed to a more constant resource throughout the winter, thus leading to a more constant food source for scavengers.

In 1966 the wolf was regarded as functionally extinct in Norway and Sweden, but slowly recovered after 1978 when the first reproduction was confirmed in the northernmost part of Sweden (Wabakken *et al.* 2001b). In southern Norway, wolverines were hunted to functional extinction and received protection in 1973. However, a small population of wolverines remained in the mountain areas along the Swedish-Norwegian border which received protection in Sweden from 1969. During the late 1970's they recolonized the Snøhetta plateau in south-central Norway (Landa, Lindén & Kojola 2000) but it wasn't before the late 1990's that their range extended from these western mountainous areas to the eastern boreal forest (Brøseth & Andersen 2004a; Flagstad *et al.* 2004a; Flagstad *et al.* 2004b) after wolves recolonized the same region a few years earlier (Wabakken *et al.* 2001a). Wolverines can both hunt and scavenge for food (Haglund 1966; Krott 1982; Magoun 1987). In Scandinavia the wolverine has mainly been regarded to be a scavenger on large ungulates (Haglund 1966; Landa *et al.* 1997; Myhre & Myrberget 1975) with the ability to switch between different food sources if one prey species is getting rare (Landa *et al.* 1997). The high degree of utilization by wolverines on wolf-killed moose *Alces alces* L. in the boreal forests in southern Norway (van Dijk *et al*. unpublished data), suggests that wolf presence may be important to the wolverine diet. However, quantitative information is lacking.

Populations of large mammals are generally strongly structured according to age and sex, and it is central to understand if and how the ecology of the two sexes differ. Many studies of large herbivores focus on sexual segregation (review in Ruckstuhl & Neuhaus 2005), but few studies of sexual segregation exist on large predators (see Rode, Farley & Robbins 2006; Wielgus & Bunnell 1994), and none on scavengers. Adult male wolverines have larger home range sizes and have a more opportunistic life style than females (Landa *et al.* 1998); especially compared to the restricted range use in reproducing females (Landa *et al.* 1998; Magoun & Copeland 1998). We therefore expect that scavenging opportunities may be more important for male than female wolverines. In addition we can assume that the more restricted female will compensate the lower opportunity of finding carrion with hunting on small prey.

In this study we examined the winter-spring diet of wolverines throughout their range in southern Norway between 2001 and 2004. The presence of wolves was expected to increase scavenging opportunities for wolverines, leading to a diet switch to scavenging, and increasing the occurrence of moose in their diet. We controlled for potential confounding factors such as the local availability of prey species that could either be hunted or scavenged upon. We furthermore predicted this diet switch to differ between male and female wolverines since females have relative smaller home ranges compared to male wolverines and are therefore more restrictive in their search for wolf-kills.

Methods

STUDY AREA

In southern Norway the range of wolverines encloses many different ecological conditions, from remote mountainous areas in the west and centre with peaks up to 2,000 m to more accessible forest areas and low mountain ranges in the east. The tree line can be found around 900 to 1,000 m above see level. In southern Norway snow is present from October/November until May/June depending on elevation.

In the mountainous areas in the west and centre high densities of unattended free-ranging sheep graze in their summer pastures from June to September. Also in the low mountain ranges and forest areas in the east free-ranging sheep graze in their summer pastures, but at lower densities. The largest European population of wild reindeer *Rangifer tarandus* L. is found in the mountainous areas in the west and centre. In the north-eastern, north-western and south-eastern part, herding of semi-domestic reindeer is practised. Moose, roe deer *Capreolus capreolus* L., hare *Lepus timidus* L., ptarmigan *Lagopus muta* M., lemming *Lemmus lemmus* L. and various rodents (*Microtus* spp. and *Clethrionomys* spp.) and insectivores *Insectivora* spp. form possible sources of food for the wolverine in southern Norway; either as hunted prey or through scavenging.

The estimated wolverine population in southern Norway increased from 83 to 130 adult individuals (≥ 1 year old) between 2001 and 2004 (Brøseth & Andersen 2003; Brøseth *et al.* 2004a). They share the boreal forests with wolves, bears, lynx *Lynx lynx L.* and red foxes *Vulpes vulpes* L. but live alone in the higher alpine habitat. The general location of the wolf area, where 2 to 3 wolf packs with 2 to 11 members per pack lived between 2001 and 2004, is shown in Fig. 1 (Wabakken *et al.* 2004a; Wabakken *et al.* 2001a, 2002; Wabakken *et al.* 2004b; Wabakken *et al.* 2005). Low numbers of bears were found both in the wolf area and in the north-eastern part of the study area, but no bear reproductions have officially been documented in the study area between 2001 and 2004 (State of the Environment Norway 2005; Swenson *et al.* 2003). Lynx are found at lower elevations within the study area, and the number of registered family groups ranged from 43 to 39 for 2001 and 2004 respectively (Brøseth, Odden & Linnell 2004b). Red foxes are also common in the study area but no population estimates exist.

SCAT COLLECTION AND DIET ANALYSIS

As part of the National Large Carnivore Monitoring program wolverine scats are collected yearly in southern Norway by the Norwegian State Nature Inspectorate during late winter-early spring (i.e., April-May depending on snow conditions). A small portion of each scat sample is used within the DNA-based monitoring programme (Flagstad *et al.* 2004b) resulting in individual identification (ID) and sex when DNA is successfully extracted. Scat samples collected in 2001-2004 for which DNA was successfully extracted ($N = 459$; 86 in 2001, 104 in 2002, 144 in 2003, and 125 in 2004) were analysed for dietary contents (Fig. 1). The DNA-analysis identified 162 different individuals (72 males and 90 females).

Each scat sample was washed in a sieve with diameter of 0.5 mm until the water was clear. Hairs and feathers were separated from other dietary remains (e.g., bones, plant material, non-food items) and the hairs and feathers were oven dried at 70˚C for 24 hours. The relative contribution of the hairs and feathers was visually estimated with use of a superimposed grid (van Dijk *et al.* in press). Hairs and feathers were identified to species level using macroscopic and microscopic characteristics following published identification keys (Day 1966; Teerink 1991; Williamson 1951) and reference collections.

ECOLOGICAL CONDITIONS AND PREY AVAILABILITY

For each scat sample's location habitat type (i.e., tundra, forest, and shrub land) was derived from a 1x1km land cover map (classified AVHRR image, United States Geological Survey: http://edcdaac.usgs.gov/glcc/background.html), using Geographic Information System software package ArcView 3.3 (ESRI, Environmental Systems Research Institute, Redlands, California).

As an index for prey density, hunting statistics from Statistics Norway (http://www.ssb.no) were used, as has been done and validated in earlier studies on Cervids from Norway (for moose, see Herfindal *et al.* 2006). Numbers of wild reindeer and moose shot during the hunting season (i.e., autumn) before the scat sample was collected (i.e., late winter following the hunting season) were divided by the municipality surface area in which the scat sample was collected. Statistics for semi-domestic reindeer were obtained from data available from the Directorate of Reindeer Husbandry (2000-2003, http://www.reindrift.no). Numbers of semi-domestic reindeer for the different herds were divided by municipality surface area of where the scat sample was collected to obtain a relative measure for semi-domestic reindeer density. Average annual densities for wild and semi-domestic reindeer and moose are given in the supplementary material, Fig. S1. Since hunting statistics on small game (i.e., Galliform spp., Passeriform spp., Columbiform spp., mustelids, beaver *Castor fiber* L., mountain hare and red squirrel *Sciurus vulgaris* L.) were only available on county level, numbers of small game were divided by the county surface area. Because small game hunting statistics were only available from 2001 to 2004 (thus not from the hunting season in 2000 representing small prey density for the scat samples collected in 2001) we used the statistics of 2002 to represent small prey density in 2001. To include possible annual fluctuations in rodent and insectivore (hereafter called rodents) densities, monitoring data (2000-2003) from the Directorate for Nature Management's programme for terrestrial nature monitoring on rodents at a study site in the west, Åmotsdalen (latitude 62º27', longitude 9º30'), and at a study site in the east, Gutulia (latitude 62º00', longitude 12º13') (http://tov.dirnat.no), were included for comparison.

STATISTICAL ANALYSES

Based on the geographical position of the scat samples and sex of the wolverine the percentage of occurrence for the prey species were calculated (Table 1.; after Ciucci *et al.* 1996; van Dijk *et al.* in press). Diet breadth per habitat and sex was calculated using the standardized Levin's measure of niche breadth B_j following equation 1.

$$B_j = \frac{\left(\sum p_{ij}^2\right)^{-1} - 1}{i - 1} \qquad \text{eqn 1}$$

where p_{ij} represents the proportion of occurrence for prey species i in subset j (Hurlbert 1978). We checked for possible dietary differences among the habitats and between the sexes by comparing percentage of occurrence with the overall percentage of occurrence using Chi-square tests.

Occurrence of reindeer, moose and small prey species (i.e., hare, birds and rodents taken together) in the diet were assessed using generalized mixed-effects models with presence/absence of prey species as a binary categorical response variable (i.e., logistic model) and ID as random factor to control for repeated observations of the same individuals. Explanatory variables included were year (categorical), wolf presence (i.e., the scat sample was found inside or outside the area where wolves were present, Fig. 1), sex, habitat type (i.e., tundra, shrub land, forest) and the density index for wild reindeer, semi-domestic reindeer, moose, and small prey. The variable year was included in the models to capture annual fluctuations in rodent densities, since no spatially explicit data on rodents was available. Also other factors varying between years will be captured by this variable, such as snow conditions. Model selection was conducted using a backward stepwise procedure, where the most parsimonious model corresponded to the model with the lowest corrected Akaike Information Criterion (AIC_c) (Anderson, Burnham & Thompson 2000; Burnham & Anderson 2002). Models with $\Delta\ AIC_c$ scores lower than 2, compared to the most parsimonious model, were included as possible alternative models (Burnham & Anderson 2002).

Statistics were performed in the statistical software programme R 2.4.0 (R Development Core Team 2006) using the lmer function with a binomial distribution of the lme4 library (Bates & Sarkar 2005). Model fit was calculated using the Laplace approximation of the maximum likelihood. All other statistical analyses were done with SPSS, version 14 (SPSS Inc. 2005) and Microsoft Excel, version 2003.

Results

WOLVERINE DIET AND NICHE BREADTH

Of the analysed scat samples, 135 were collected in tundra, 189 in shrub land, and 135 in forest habitat. Number of yearly collected scat samples did not significantly vary by habitat in which the scats were found (ANOVA, $F_{2,9} = 1.733$, $P = 0.231$).

Dietary contents expressed as Percentage of Occurrence (*PO*) showed that moose was the most important prey species for wolverines in southern Norway in late winter-early spring followed by reindeer and rodents (Table 1). In tundra however, reindeer was more important than moose in the diet of wolverines. The diet of wolverines in tundra was significantly different from the overall diet in southern Norway ($\chi^2 = 19.149$, df = 6, $P = 0.004$), while the diet in shrub land and forest was not ($\chi^2 = 4.757$, df = 6, $P = 0.575$ and $\chi^2 = 4.461$, df = 6, $P = 0.615$ for shrub land and forest respectively). Niche breadth in tundra was broadest, while niche breadth in forested areas was narrowest ($B_{tundra} = 0.341$, $B_{shrub\ land} = 0.307$ and $B_{forest} = 0.291$; Table 1). In forest, we found a significant difference in the diet with wolf presence versus without wolf presence ($\chi^2 = 31.154$, df = 6, $P < 0.001$). Niche breadth of wolverines in forested areas with wolf presence was narrower than without wolf presence (respectively, $B = 0.103$ and $B = 0.382$; Table 1).

As predicted from the sexual segregation hypothesis, a significant difference in the diet of male and female wolverines was found in forest habitat ($\chi^2 = 12.905$, df = 6, $P = 0.045$). This effect was similar both in forested areas with wolf presence and without wolf presence ($\chi^2 = 9.218$, df = 2, $P = 0.010$ and $\chi^2 = 13.570$, df = 6, $P = 0.035$ for wolf presence and wolf absence respectively), with females having a higher percentage of occurrence of small prey and moose in their diet, but a lower occurrence of reindeer. No tendency for a sex effect was found in shrub habitat ($\chi^2 = 10.420$, df = 6, $P = 0.108$), and in tundra ($\chi^2 = 5.554$, df = 6, $P = 0.475$).

EXPLAINING PREY SPECIES IN WOLVERINE DIET

The logistic mixed-effects regression models showed that in the best model explaining reindeer occurrence in the scat samples, reindeer occurrence was lower in the area with wolf presence and higher in areas with higher wild reindeer densities. The next best model also indicated that reindeer occurrence was higher in tundra (Table 2).

The best model for moose occurrence in the scat samples varied per year and wolf presence had a positive effect on moose occurrence. The next best model for moose occurrence indicated that moose density also had a positive effect on moose occurrence in the diet. According to the third model shrub land and forest had a positive effect on moose occurrence.

The best model explaining small prey occurrence in the scat samples showed that small prey occurrence was lower in scat samples from male wolverines. Furthermore, small prey occurrence varied per year and increased with small prey densities, but was negatively affected by moose density. In the next best model small prey occurrence was also found to be higher in tundra, relative to shrub land and forest (Table 2).

PREY DENSITIES AND ANNUAL VARIATION

The study was not long-term enough to explicitly test for factors causing annual variation in the wolverine diet. However, since rodents constituted 69 % of small prey occurrence in the faeces, the yearly density-index for rodents derived from the Directorate for Nature Management's programme for terrestrial nature monitoring on rodents was plotted against the average percentages of rodents, moose and reindeer found within the scat samples collected in the areas with or without wolf presence (Fig. 2). In areas without wolf presence the average percentage of rodents occurrence in the scat samples qualitatively followed the yearly density index of rodents, showing an increase in the percentage of moose occurrence when the yearly density index of rodents was low (Fig. 2, panel A). In the area with wolf presence the average percentage of rodents occurrence in the scat samples did not follow the yearly density index of rodents, and moose occurrence was relatively high regardless of the fluctuating density index of rodents (Fig. 2, panel B). This evidence indicates that also the dynamics of rodents plays a role in wolverine diet.

Discussion

THE WOLVERINE IN THE FOOTSTEPS OF WOLVES

Our study revealed that during the winter-spring period wolverines ate more moose within than outside wolf territories, suggesting that wolf recolonization have induced a diet shift in a facultative scavenger, the wolverine. Wolverines both scavenge and predate, and switch between the two strategies depending on what is most profitable (Haglund 1966; Stephens & Krebs 1986). Carrion has proven to be an important winter and spring food resource for the wolverine both in North-America (Houston 1978; Magoun 1987; Wilmers *et al.* 2003) and Scandinavia (this study, Landa *et al.* 1997) when carrion supply is more abundant (Selva *et al.* 2005). The availability of carcasses due to natural mortality is seasonally pulsed, while wolf kills form a more constant resource for scavengers (Wilmers *et al.* 2003; Selva & Fortuna 2007). Moose is assumed to be available to the wolverine as carcasses and although high moose densities imply a high availability of carcasses due to natural mortality and traffic kills (Solberg *et al.* 2006), in wolf areas the number of available carcasses increases enormously (Wilmers *et al.* 2003, Smith *et al.* 2004, Sand *et al.* 2005). Indeed, wolf presence had a strong effect on moose occurrence in the wolverine's diet in our study. Both reindeer occurrence and small prey occurrence in the wolverine's diet were lower in scats found in the area where wolves were present. Apparently the increase of available scavenging opportunities provided by wolves enables the wolverine to shift from a broad diet with reindeer, mountain hare, birds and rodents to a narrower diet with almost only moose, as niche breadth for wolverines co-existing with wolves was remarkably narrower (Table 1). Both rodents and wild reindeer, as traditional wolverine diet species (Landa *et al.* 1997), are however also more abundant in the mountainous areas in the western region of southern Norway (see also Fig. 2 with rodent index from study site Åmotsdalen in the west and Gutulia in the east). Whether the increase in scavenging opportunities provided by wolves have actually triggered wolverines to re-colonize previously occupied areas clearly merits further research. The samples did not enable us to highlight the potential role of other large carnivores, such as bears (low numbers) or lynx (widely distributed). The lynx is a roe deer specialist (Andersen *et al.* 1998; Odden, Linnell & Andersen 2006), and since we found very little roe deer in wolverine diet, lynx presence might not be important for the wolverine's diet confirmed also by snow tracking studies (van Dijk *et al.* unpublished data).

THE ROLE OF PREY AVAILABILITY

It is also clear that prey availability is important for wolverine diet, as local availability of reindeer, moose and small prey were all part of the best models explaining occurrence in the diet. Though data was available only from a limited number of years, the occurrence of rodents in wolverine diet outside wolf territories seemed to follow the yearly fluctuations in small rodent availability (Fig. 2, panel A). In autumn 2002, when the yearly rodent index was low, wolverines switched to scavenging on moose carcasses during winter 2002-2003. Interestingly, such a switch was not apparent within the wolf territories (Fig. 2, panel B). Landa *et al.* (1997) showed that the reproductive success in wolverines was correlated with the density cycle of rodents, but this may thus not be the case in areas where wolves have recolonized.

The two previous studies conducted on wolverine winter diet in Norway reported that reindeer was their most important prey species (Landa *et al.* 1997; Myhre & Myrberget 1975), whereas this study revealed moose as being the most important prey species for the wolverine. Especially during the last decades moose densities have increased enormously (Lavsund *et al.* 2003; Solberg *et al.* 2006), which might explain the diet shift from reindeer to moose in a historical perspective. Also, the study from Landa *et al.* (1997) and Myhre & Myrberget (1975) were conducted in the high mountainous areas in south-central Norway and northern Norway, respectively, where moose densities are relatively low (Lavsund *et al.* 2003) and reindeer more abundant. Our study, however, included both the south-central mountain region and the forest region towards the east. When only considering wolverine diet in tundra habitat, reindeer was in fact the most important prey species; consistent with the two earlier studies. Wild reindeer densities in our study area have more or less been constant over the years due to a hunting management regime that aims to keep the population stable (Punsvik & Jaren 2006; Solberg *et al.* 2006).

SEXUAL SEGREGATION IN DIET

Our study revealed that more small prey species were found in the diet of female wolverines relative to males. To which extent the differences in diet is the result of sexual segregation due to differences in body sizes or resource use (forage selection or body size hypotheses; Main, Weckerly & Bleich 1996; Ruckstuhl & Neuhaus 2002) is difficult to assess, especially because differing diet and foraging behaviour between individuals of different sex in the wild have rendered varying results (e.g. Begg *et al.* 2003; Ruggiero *et al.* 1994). Although sexual dimorphism in body size is apparent in mustelids (Moors 1980), anatomical analyses have demonstrated that the carnassials and skull size of mustelids were less dimorphic than were the rest of their bodies (Holmes 1987; Holmes & Powell 1994; Landa and Skogland 1995) suggesting that dietary specialization of the sexes due to body size differences would be unlikely. On the other hand, however, Rode, Farley & Robbins (2006) suggested that as a result of larger body size, males can experience disproportionate nutritional costs during times of low resource availability and might therefore have larger home ranges to maximize their foraging opportunities. The fact that male wolverines have 2 to 3 times larger home range sizes compared to females (Landa *et al.* 1998) might increase their chances for encountering large prey to scavenge upon compared to the more restricted female. The observed differences in diet are therefore likely the result of sexual segregation due to different space use between the sexes.

Although only 11 scat samples from female wolverines were found in wolf territories (versus 31 scat samples from male wolverines) there was a tendency that females opportunistically utilized the highly available moose carrion and hunted less on rodents. The two to three times larger home ranges of male wolverines likely enables them to come in contact with reindeer either as carrion or as hunted prey more than females. The more restricted home ranges of females force them to rely more on small prey that is locally available. Since scavenging on moose carrion will have a relatively low energetic cost the female wolverine may switch to this food resource when abundant, despite the fact that females with dependent cubs may face an increased risk of intra-guild predation by wolves (c.f. May *et al.* unpublished data).

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Table 1. Percentage of occurrence for the different prey species found within different subsets of wolverine scat samples. The final row gives the standardized Levin's niche breadth for the different subsets. The three main prey species are given in bold.

	Southern Norway			Tundra	Shrub land	Forest	Forest wolf absent			Forest wolf present		
	All	Male	Female				All	Male	Female	All	Male	Female
Number of scats	459	202	257	135	189	135	93	44	49	42	31	11
Reindeer	**31.4**	**34.2**	**29.3**	**40.2**	**27.8**	**27.9**	**31.9**	**36.4**	**27.7**	**18.4**	**22.2**	**9.1**
Moose	**47.5**	**49.5**	**45.9**	**38.6**	**50.6**	**51.9**	**41.8**	**43.2**	**40.4**	**76.3**	**74.1**	**81.8**
Roe deer	1.1	2.1	0.4	0.8	1.1	1.6	2.2	2.3	2.1	0.0	0.0	0.0
Sheep	2.8	2.1	3.3	0.8	5.0	1.6	2.2	4.5	0.0	0.0	0.0	0.0
Hare	3.2	2.1	4.1	9.4	0.6	0.8	1.1	0.0	2.1	0.0	0.0	0.0
Birds	2.3	1.1	3.3	0.8	2.2	3.9	5.5	2.3	8.5	0.0	0.0	0.0
Rodents	**11.7**	**8.9**	**13.8**	**9.4**	**12.8**	**12.4**	**15.4**	**11.4**	**19.1**	**5.3**	**3.7**	**9.1**
Niche breadth	0.323	0.282	0.355	0.341	0.307	0.290	0.382	0.331	0.419	0.103	0.111	0.076

Table 2. Results of the logistic regression models used within the dietary analyses of wolverine scat samples in southern Norway. The models represent the variables explaining the diet of wolverines based on all scats for which DNA was successfully extracted (459 scat samples, 162 individuals). Each first model corresponds to the most parsimonious model with the lowest corrected Akaike Information Criteria (AIC$_c$). The next models, with $\Delta AIC_c < 2$ compared to the most parsimonious model, are included as possible alternative models. One, two or three asterisks indicate significance at $P < 0.05$, $P < 0.01$, or $P < 0.001$, respectively.

Models	**Variables**	**Coef.**	**S.E.**	**Z-value**	**P**		**AIC$_c$**	**ΔAIC$_c$**
Reindeer occurrence, model I	Intercept	-1.144	0.197	-5.801	0.000	***	541.234	0.000
	WOLF PRESENCE	-1.240	0.464	-2.674	0.008	**		
	WILD REINDEER DENSITY	3.479	1.804	1.928	0.054			
Reindeer occurrence, model II	Intercept	-0.906	0.274	-3.308	0.001	***	542.656	1.422
	WOLF PRESENCE	-1.206	0.484	-2.492	0.013	*		
	WILD REINDEER DENSITY	3.676	1.846	1.991	0.047	*		
	SHRUB LAND^{B}	-0.482	0.297	-1.624	0.104			
	FOREST^{B}	-0.196	0.347	-0.566	0.571			
Moose occurrence, model I	Intercept	-0.636	0.243	-2.619	0.009	**	614.164	0.000
	YEAR-2002^{A}	-0.149	0.320	-0.466	0.641			
	YEAR-2003^{A}	0.855	0.296	2.890	0.004	**		
	YEAR-2004^{A}	0.166	0.306	0.541	0.589			
	WOLF PRESENCE	1.165	0.319	3.648	0.000	***		
Moose occurrence, model II	Intercept	-0.716	0.250	-2.866	0.004	**	614.671	0.507
	YEAR-2002^{A}	-0.200	0.321	-0.622	0.534			
	YEAR-2003^{A}	0.792	0.299	2.653	0.008	**		
	YEAR-2004^{A}	0.131	0.307	0.428	0.669			
	WOLF PRESENCE	1.001	0.340	2.947	0.003	**		
	MOOSE DENSITY	1.470	1.148	1.280	0.201			
Moose occurrence, model III	Intercept	-0.989	0.301	-3.285	0.001	**	615.456	1.292
	YEAR-2002^{A}	-0.112	0.323	-0.348	0.728			
	YEAR-2003^{A}	0.857	0.302	2.843	0.004	**		
	YEAR-2004^{A}	0.171	0.307	0.557	0.577			
	WOLF PRESENCE	0.969	0.344	2.819	0.005	**		
	MOOSE DENSITY	1.532	1.273	1.203	0.229			
	SHRUB LAND^{B}	0.441	0.253	1.747	0.081	.		
	FOREST^{B}	0.132	0.317	0.417	0.677			

Small prey occurrence, model I	Intercept	-3.167	0.720	-4.400	0.000	***	378.804	0.000
	YEAR-2002^{A}	2.083	0.541	3.853	0.000	***		
	YEAR-2003^{A}	0.487	0.574	0.848	0.396			
	YEAR-2004^{A}	0.889	0.560	1.590	0.112			
	MALE^{C}	-0.737	0.347	-2.127	0.033	*		
	MOOSE DENSITY	-2.696	1.784	-1.511	0.131			
	SMALL PREY DENSITY	0.373	0.234	1.595	0.111			
Small prey occurrence, model II	Intercept	-2.961	0.756	-3.914	0.000	***	379.936	1.132
	YEAR-2002^{A}	2.042	0.556	3.671	0.000	***		
	YEAR-2003^{A}	0.436	0.589	0.740	0.459			
	YEAR-2004^{A}	0.868	0.576	1.506	0.132			
	MALE^{C}	-0.777	0.361	-2.154	0.031	*		
	MOOSE DENSITY	-2.896	2.059	-1.406	0.160			
	SMALL PREY DENSITY	0.425	0.244	1.747	0.081			
	SHRUB LAND^{B}	-0.632	0.382	-1.654	0.098			
	FOREST^{B}	-0.153	0.467	-0.327	0.744			

^{A} year effect is given relative to year 2001

^{B} habitat effect is given relative to tundra

^{C} sex effect is given relative to female

Figure captions

Fig. 1. Overview of the wolverine scat samples analysed within the dietary study in southern Norway. Black circles represent scat samples collected within the area with wolf presence whereas white circles represent scat samples collected outside the area with wolf presence. The wolverine range in southern Norway is indicated with a solid line, whereas the wolf area is indicated with a dotted line.

Fig. 2. The average percentage of rodent species (black columns), moose (grey columns) and reindeer (white columns) occurrence found in the scat samples in the area outside wolf territories (panel A) and inside wolf territories (panel B) per winter plotted against the yearly density index for rodents in that area (♦) during the autumn before. The error bars indicate the standard deviations of the average percentages.

Supplementary material

Fig. S1. Average densities of moose (grey columns), wild reindeer (black columns) and semi-domestic reindeer (white columns) for the different study years (plus standard deviation error bars). Based on the hunting statistics, moose was hunted in 56 of the 56 communities in which scat samples were collected, whereas wild reindeer was hunted in 31 and semi-domestic reindeer was herded in 29 of the 56 communities.

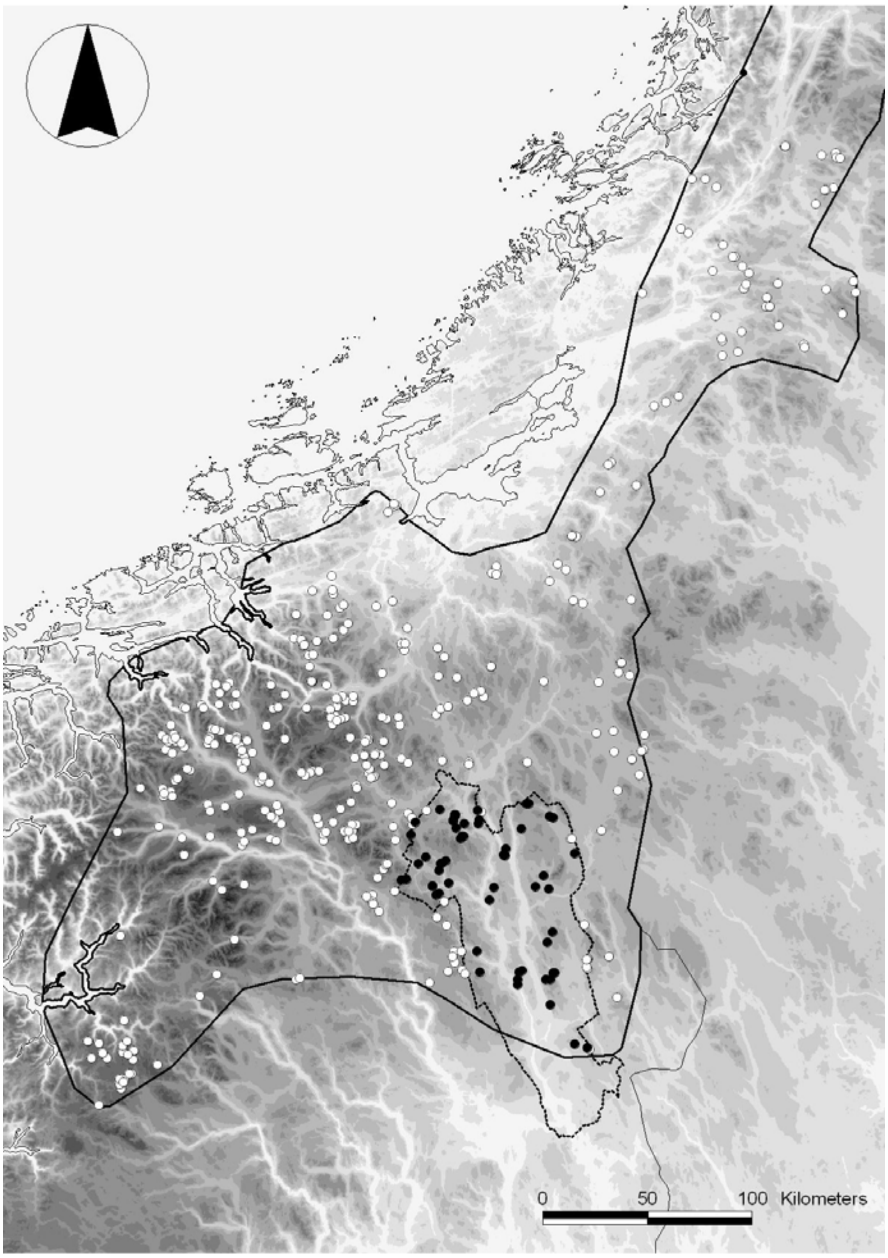


Fig. 1.

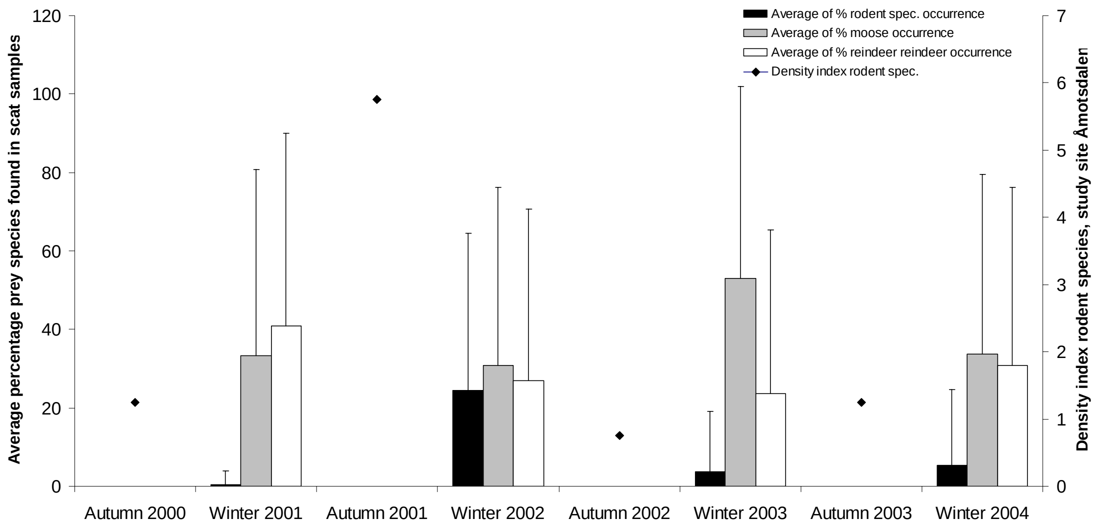


Fig. 2. panel A

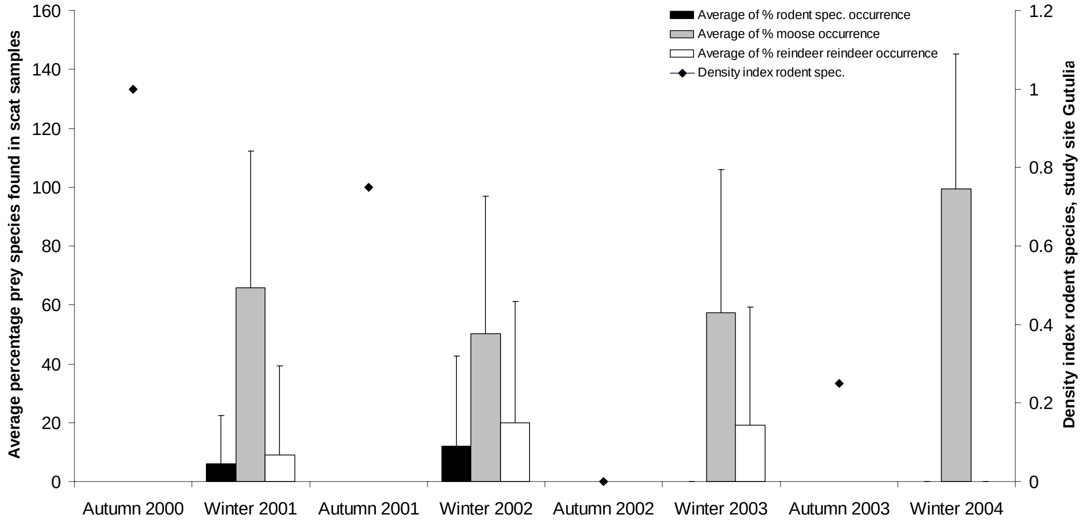
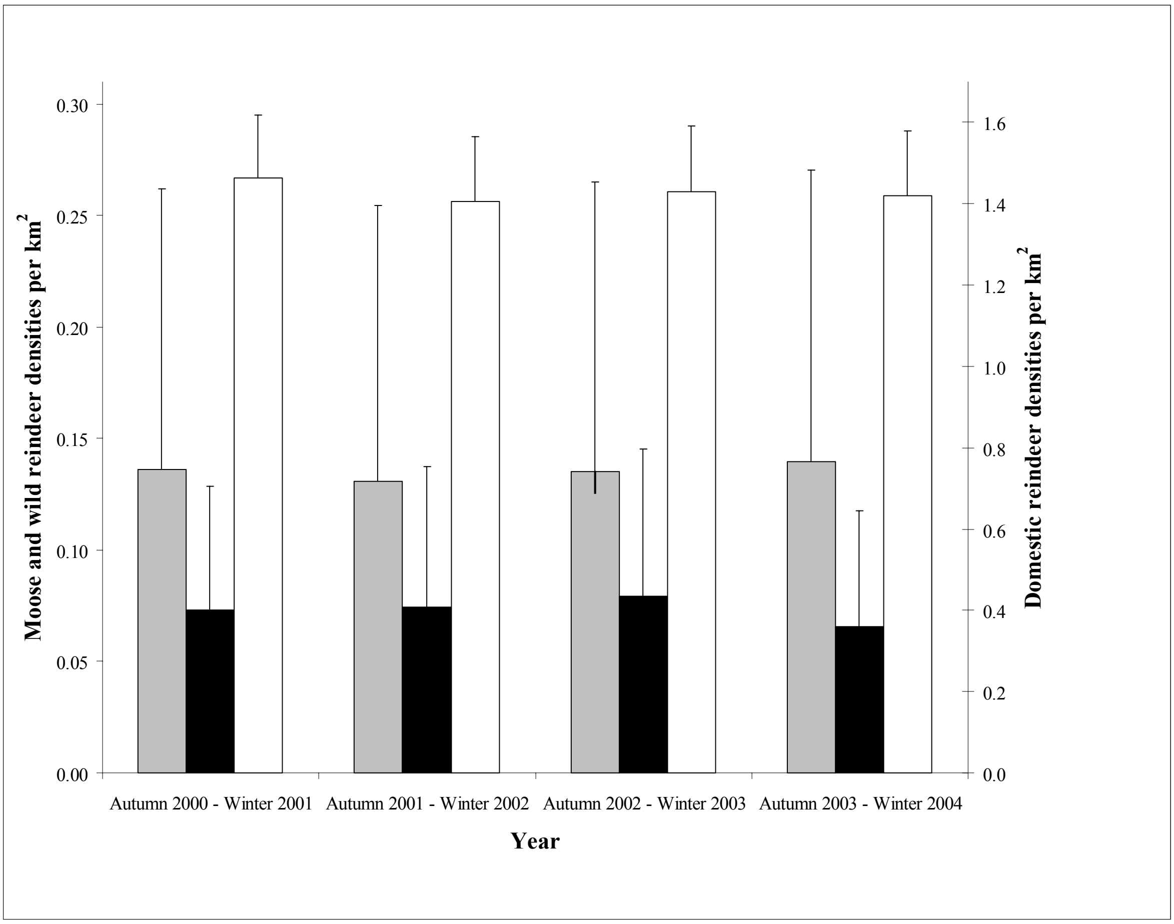


Fig. 2. panel B

Supplementary material



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Paper III

FORAGING STRATEGIES OF WOLVERINES WITHIN A PREDATOR GUILD

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Abstract: Within the predator guild, the wolverine (*Gulo gulo* (L., 1758)) has evolved as a generalist and scavenging on dead animals, including prey killed by other more effective predators, is believed to be an important feature. The removal of the wolf (*Canis lupus* (L., 1758)) is therefore likely to have had a negative effect on wolverine density because fewer carcasses were available for scavengers. It can thus be speculated that the recent recolonization of the boreal forests by wolverines in southern Norway followed the recovery of wolves in this region. We investigated the winter foraging behavior of wolverines in the boreal forest and their interactions with wolves, lynx (*Lynx lynx* (L., 1758)) and red foxes (*Vulpes vulpes* (L., 1758)). We followed 55 wolverine tracks in the snow from at least nine individuals for a total length of 237 km during the winters of 2003-2004. We documented 23 carcasses (19 moose and four birds), and recorded 16 unsuccessful hunting attempts on small prey. Observations of wolf trails were found at lower elevations, while wolverine marking behavior, defecations, urinations, resting places and hunting attempts all tended to be found at higher elevations. Wolverines did not follow guild species’ trails directly to carcasses. However, the tortuousness of the tracks increased when the tracks led to a carcass. Wolverines tended to change their searching behavior directly after encounters with lynx trails, with the wolverine track being more tortuous directly after these encounters. Conversely, the wolverine’s track became less tortuous directly after encounters with fox trails. The higher number of observations of wolf trails found at lower elevations and increased wolverine marking, defecations, urinations, resting places and hunting attempts at higher elevations suggests a spatial separation between wolverines and wolves, where wolverines only travel down to lower elevations to scavenge on wolf kills. Although wolverines seem to depend on wolf for carrion during the winter, we did not observe wolverines following wolf trails to carcasses. This may indicate that wolverines experience intra-guild predation by wolves and reduce this risk by avoiding direct confrontation with wolves. However, foraging behavior in wolverines may also be influenced by red fox and lynx as seen from changes in track tortuousness. The importance of scavenging from prey killed by other guild species, suggests that maintaining a wolverine population in an intra-guild setting is ecological feasible within the boreal forest ecosystem.

Introduction

Successful conservation of biological diversity involves an understanding of ecosystem dynamics and the role that species play in a community. All species are organized into communities within ecosystems and among carnivores complex systems of interactions including intra-guild competition (Caro 1994; Peterson 1995; Creel and Creel 1996; Landa 1997; Crooks and Soulé 1999; Creel et al. 2001), mutualism and commensalism are likely to exist (Haglund 1966; Fedriani et al. 1999; Ray and Sunquist 2001; Amarasekare 2004; Hooper et al. 2005). Although the role of top predators in ecosystems is still not well understood, they are increasingly recognized as keystone species in the structuring of communities, and ultimately of the integrity and health of ecosystems (Terborgh 1988; Kucera and Zielinski 1995; Berger 1999; Crooks and Soulé 1999; Terborgh et al. 1999).

Given the large and continuous habitat area required by carnivores (Crooks and Soulé 1999; Purvis et al. 2000; Sunquist and Sunquist 2001; Cardillo et al. 2004), a successful conservation strategy requires an understanding of both the biology of these species and their inter-specific relationships.

After nearing extinction due to excessive human exploitation, the wolverine (*Gulo gulo* (L., 1758)) population in Scandinavia has increased in number and distribution after protective legislation was passed in the 1970's (Landa et al. 2000). During the late 1970's wolverines recolonized the mountainous areas around Snøhetta in southern Norway (Kvam 1979; Landa et al. 1998; Landa et al. 2000) and during the last decade extended their distribution from western mountainous areas to the eastern boreal forest (Brøseth and Andersen 2004; Flagstad et al. 2004a; Flagstad et al. 2004b).

Within the predator guild, the wolverine (*Gulo gulo* (L., 1758)) has been observed scavenging on prey killed by other more effective predators and Bjärvall and Lindstrøm (1991) hypothesized that the removal of more effective predators like the wolf (*Canis lupus* (L., 1758)) could have a negative effect on wolverine density because fewer carcasses would be available. Landa and Skogland (1995) found evidence for this food limitation hypothesis. It can thus be speculated that the recolonization of the boreal forests by wolverines in southern Norway followed the recolonization by wolves in this same region which occurred a few years earlier (Wabakken et al. 2001). Despite reported observations of wolverines scavenging on carcasses of prey killed by wolves, lynx (*Lynx lynx* (L., 1758)) and brown bears (*Ursus arctos* (L., 1758)) (Haglund 1966; Bjärvall and Isakson 1982; Magoun 1987), responses of wolverines to increased scavenging opportunities have never been investigated in detail.

Given that intra-guild interactions (Holt and Polis 1997; Creel et al. 2001) could result in increased competition for food sources (Paquet 1992; Creel and Creel 1996; Linnell and Strand 2000), and intra-guild predation is a widespread phenomenon in mammalian carnivores (Palomares and Caro 1999; Linnell and Strand 2000), wolverines may well face a trade-off between the risk of being killed by other predators and the benefits of the scavenging opportunities they provide (Burkholder 1962; Hornocker and Hash 1981; Bjärvall 1983; Banci 1994; Copeland 1996; Magoun and Copeland 1998).

In this study we investigated the winter foraging behavior of wolverines in a boreal forest habitat shared with wolves, lynx and red foxes (*Vulpes vulpes* (L., 1758)). Because bears hibernate during winter months we were not able to neither document interactions nor address the dependency of wolverines on bears for the provision of food. We expected that wolverines relied on more effective predators to provide sufficient nutrition during the winter where encounters with intra-guild species' trails enabled them to find food sources. Foraging behavior was expected to be triggered by the presence of guild species, which would eventually lead to food sources to scavenge on. Because of possible intra-guild competition and interference (Linnell and Strand 2000) wolverines were expected to avoid direct interactions with lynx and especially wolves. Foxes however, as a subordinate guild species could help wolverines in finding food sources, in addition to being possible prey for them. We therefore expected that wolverines would concentrate their foraging activities in the more predation exposed, lower-lying lynx and wolf habitat, whereas behaviors such as marking and resting would be expected to be placed at higher elevations.

Methods

Study area

Our study took place in Hedmark County of southeastern Norway (Fig. 1). The area included approximately 2,700 km^2; primary vegetation type was boreal coniferous forest with Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* (L.)), birch (*Betula pubescens* Ehrh. and *B. pendula* Ehrh.) and aspen (*Populus tremula* (L.)) dominating the landscape from valleys to the tree line at 900 m above sea level (asl). Low mountain ranges interspersed the forested areas. The climate is typical for inland Norway, with warm summers and cold winters, and snow covering the area for five to seven months from October-November to April-May.

Wolverines, lynx, wolves, and brown bears co-exist in relatively low densities in the area. During the winters of 2002-2003 and 2003-2004 there were two wolf packs within the study area with a minimum of five individuals per pack, in addition to two lone wolves that roamed the southern border of the study area (Wabakken et al. 2004). The National Large Carnivore Monitoring program (Andrén et al. 2002; Swenson et al. 2003; Brøseth and Andersen 2004; Brøseth et al. 2004; State of the Environment Norway 2005) estimate that 32 wolverines, 50 lynx and 10-15 brown bears were present in Hedmark County. Red foxes were common within the study area but no population estimate existed. Estimated density of large prey species in Hedmark County included 0.9 moose (*Alces alces* (L., 1758))/km^2 and 0.8 roe deer (*Capreolus capreolus* (L., 1758))/km^2 (Solberg et al. 2003). Few semi-domestic reindeer (*Rangifer tarandus* (L., 1758)) were herded in the northern periphery of the study area. Tetraonids and other bird species, hare (*Lepus timidus* (L., 1758)), rodent and insectivore species as well as small mustelids were also potential prey for wolverines in the area.

Field work

Wolverines were tracked for a total of 237 km during two winter seasons: March-April, 2003 and December 2003-January 2004. We opportunistically searched for wolverine tracks in the snow inside the study area or followed tracks located by local people. Information on moose carcasses found by local people was not used to locate wolverine tracks since this would have resulted in an overrepresentation of wolverine tracks near carcasses. Wolverine tracks were followed (back- or front-tracked) for as far as possible depending on snow conditions and daylight. We noted when a track was lost due to poor tracking conditions in closed forests or open windy areas, or when the wolverine used a cleared road or snowmobile trail. Relatively fresh tracks were only back-tracked to avoid disturbing the wolverine and possibly affecting its behavior.

The tracks were logged in a hand-held global positioning system (GPS) eTrex or 12XL receivers (Garmin International, Inc.; Olathe, Kansas) stored at a rate of 1 track point per minute. Observations of locations of marking behavior (i.e., secretions, bite marks and claw marks), defecations, urinations, resting places, hunting attempts and food sources, and observations of red fox, lynx and wolf trails were recorded along the wolverine track. From the temporal sequence of the tracks in the snow it was possible to determine when a wolverine encountered the trail of another guild species or when the other guild species encountered the wolverine track. When either the wolverine or the other guild species *followed* the other species' trail we measured the distance that the trail was followed. Elevations of track points and observations were determined with use of a 100x100 m digital elevation map (Norwegian State Mapping Authority), recorded in meters asl. Wolverine scats were collected, frozen and analyzed for faecal DNA at the Evolutionary Biology Centre in Uppsala, Sweden (for general methodology on DNA sequencing see Flagstad et al. 2004b).

Cause and time of death of the food sources were determined based on the presence of other species tracks, bite marks and state of the remains. Verification for certain wolf kills and remains left from hunter kills, together with the verification for time of death were given by the Scandinavian wolf project and local hunters.

Data analyses

Wolverines often move or cache body parts from carcasses of prey they have killed or scavenged (Haglund 1966; Landa et al. unpublished data). Because intact remains were rarely observed, we defined an independent carcass (hereafter referred to as carcass) as containing the bulk of remains of individual prey or at least its head or rib cage. By following the wolverine's track we were able to determine whether the located prey remains were from a single carcass.

We checked for possible temporal and spatial clustering of the total number of observations along each track by regressing the observations against date (in days of the winter season, where the first tracking day was set to day 1) and elevation, while correcting for variation in track length, using multivariate regression (MANOVA). We further assessed how the number of these observations was distributed by distance to the nearest carcass in intervals of 100 m. The number of observations were regressed (MANOVA) against distance to carcass, while correcting for the number of wolverine tracks per interval.

Tortuousness of a wolverine's track is a characteristic of its searching behavior (Nams 2005). We investigated whether wolverine's searching behavior along their entire tracks, as measured by the fractal dimension for each track (for general methodology see Nams 2005), was affected by the presence of guild species and of food sources. The fractal dimension for each track was regressed against the number of guild species encounters (only including those observations where the tracked wolverine encountered trails of other guild species), whether or not the track led in to a carcass, while correcting for the variation in track length. To provide a measure for the direct behavioral response of a wolverine to a guild species' encounter, we calculated the tortuousness of wolverine track segments 100 m prior to and 100 m following each encounter (arbitrarily chosen segments which were based on the average distance between encounters). Tortuousness was calculated as the measured walking distance (d_w) of the wolverine within 100 m straight-line distance prior to or following the encounter and divided by the 100 m straight-line distance (i.e., $d_w/100$). To avoid a cause-and-effect bias, only those walking distances were included in which no other guild species' encounters or other species' encounters, such as small mustelids, were recorded. Possible differences among guild species in tortuousness of the wolverine's track before or after a guild species' encounter were tested using a BACI modeling approach (Before_After-Control-Impact, c.f., Krebs 1999). The observed tortuousness of track segments before and after an encounter (i.e., impact) was regressed against the tortuousness of randomly chosen segments without any encounters (i.e., control).

Results

We followed 55 wolverine tracks for a total length of 237 km. The average distance that wolverines were tracked was 4.7 km per tracking day. We ceased following six tracks due to poor snow conditions in closed forests, open windy areas and when the wolverine entered snow-mobile trails or cleared roads where tracks were not visible. Locations of followed tracks, carcasses and observations of lynx and wolf trails are shown in Fig. 1, and the numbers of all the different observations are given in Fig. 2. Faecal DNA was successfully amplified for 21 of the 31 scats collected, from which nine individual wolverines were identified (five males and four females). We observed more hunting attempts earlier in the winter season, but we found no temporal clustering in the number of the other observations (Table 1). However, wolf trails were found at lower elevations (Table 1), while wolverine marking behavior, defecations, urinations, resting places and hunting attempts tended to be found at higher elevations (Fig.3).

Foraging behavior: food sources and hunting

We documented 57 food sources from 23 individual carcasses: 19 moose carcasses and four birds (1 grouse (*Lagopus lagopus* (L., 1758)), 1 magpie (*Pica pica* (L., 1758)), 1 *Tetrao spp*. (L., 1758) and 1 unknown bird species). The four bird carcasses and one fresh moose carcass were less than 2 weeks old; the remaining carcasses (18 moose carcasses) were older than 2 weeks. Of the 19 moose carcasses, four were known to be killed by wolves (the fresh moose carcass and three old carcasses) and four (all old carcasses) were known remains left from hunter kills. The cause of death for the remaining 11 moose carcasses could not be determined with certainty. Although the moose carcasses were clearly scavenged on by the wolverine, the cause of death of the bird carcasses was unknown to us. They were either killed by other predators and scavenged on by the wolverine, or killed, possibly cached, and consumed by the wolverine. We recorded 16 hunting attempts by wolverines: four on hares, four on bird species and eight on small mammals likely to be rodents. None of these hunting attempts was successful.

Intra-guild interactions

The number of guild species encountering the wolverine’s track increased with increasing distances from a carcass (Table 2). All but for wolverine encountering wolf trails, the number of encounters increased with the number of tracks per track interval (i.e., higher chance of encounter). We found no increased number of observations where wolverines encountered trails of guild species closer to carcasses. Based on those observations where a wolverine *followed* another guild species and for which it was possible to record the start and end position of these observations with certainty, the average distance of wolverines following red fox trails was 153.1 m (±120.4 SD, n=17), 421 m (n=1) for lynx trails and 168.7

m (± 141.6 SD, n=6) for wolf trails. However, none of these encounters resulted in wolverines following guild species' trails directly to carcasses or other scattered food sources.

The tortuousness (fractal dimension) of the (entire) wolverine tracks, while correcting for the variation in track length, increased when the track led to a carcass, and decreased with the number of encounters the tracked wolverine had with other guild species (Table 3, $F_{3,51}$ = 8.568, R^2 = 0.335, $P < 0.001$). When specifying the number of these encounters per species, foxes negatively affected overall tortuousness of the wolverine tracks, whereas lynx and wolf did not affect tortuousness at all (Table 3, $F_{5,49}$ = 6.159, R^2 = 0.386, $P < 0.001$). Directly after an encounter with a guild species' trail, the wolverine's searching behavior changed significantly ($F_{3,912}$ = 12.724, $P < 0.001$). Encounters with lynx caused the wolverine to directly change its searching behavior, and the track to become more tortuous (Table 4; Fig. 4). However after one of the lynx encounters, the wolverine track was extremely tortuous (tortuousness of 12). When excluding this encounter from the model, searching behavior (i.e., tortuousness) did not change after an encounter with a guild species ($F_{3,911}$ = 1.598, P = 0.188), but the effect for fox became significant, with the wolverine track being less tortuous directly after an encounter with fox ($ß$ = -0.102 ± 0.050, P = 0.041).

Discussion

Seasonal and geographical variation

Successful DNA amplification revealed that at least nine different wolverines were tracked in this study. The wolverine tracks that we followed were distributed over the study area. These two factors increased the likelihood that behaviors observed were representative of the population and reduced potential bias that observed behaviors were specific to area or habitat type. The higher number of observations of wolf trails at lower elevations may have been because wolves tend to follow the moose which use lower elevation habitats when snow becomes deeper (Cook et al. 1999; Kunkel and Pletscher 2001). As seen by their tendency to active marking behavior (i.e., territoriality), defecation, resting places and hunting attempts at higher elevations, wolverines seems to concentrate their main activity at higher elevations during the entire winter season. May et al. (unpublished data) found that wolverines use higher elevations than wolves and lynx in this region. The higher number of observations of wolf trails found at lower elevations and increased wolverine’s own specific behaviors at higher elevations may therefore suggest a spatial separation between wolverines and wolf, where wolverines travel down to lower elevations to scavenge on wolf kills.

Foraging behavior: hunting versus scavenging; hunter kills versus wolf kills

Diet studies from Fennoscandia revealed that large ungulates constitute the main food source for the wolverine during the winter (Haglund 1966; Pulliainen 1968; 1988; Landa et al. 1997). Large ungulates have also been found to be the most important winter food source outside Fennoscandia (Rausch and Pearson 1972; Hornocker and Hash 1981; Gardner 1985; Magoun 1987). The fact that no hares, roe deer or rodent species and only four bird species were found among the 23 carcasses visited by wolverines indicates that moose carcasses were preferred or abundant enough that scavenging or hunting other prey was either impossible or not energy efficient. Similarly, neither Haglund (1966) nor Myhre (1968) found evidence of successful hunts during their efforts to follow wolverine tracks in the snow. This lack of documented successful hunts may well indicate that in this boreal forest ecosystem wolverines seldom kill their own prey during the winter season but rather depend on carrion and possibly cached food. Our findings thus support the suggestion by Magoun (1987) that both prey species composition and availability of carrion influence wolverine hunting activity.

We found that moose carcasses comprised the most important food source for wolverines in this study and did not observe evidence that any moose were killed by wolverines. This pattern that moose are rarely obtained by wolverines except as carrion has been widely reported by others (Hornocker and Hash 1981; Banci 1987; Magoun 1987; Landa et al. 1997). Thus, seeking out carcasses was an important foraging strategy for the wolverines during the winter within our study area. Of the 19 moose carcasses that wolverines scavenged on, 18 had been dead for >2 weeks. We were not able to determine the cause of death for 11 of these 18 carcasses, but it is reasonable to assume that none were killed by wolverines. Due to high hunting pressure, the moose population in our study area has a young age and sex composition (Gundersen 2003) which results in very low natural mortality during winter. Also, the remains of moose kills left by hunters in autumn are of limited value to wolverines during winter as hunters bring out most of the animal and consumable remnants (highly decomposable entrails) are quickly eaten by birds and red foxes (Wilmers et al. 2003). Thus it is likely that the moose carcasses for which the cause of death could not be ascertained were also killed by wolves, especially considering the domination of moose in the diet of wolves in Hedmark County (Wabakken et al. 2003; Sand et al. 2005).

Based on the moose hunting statistics of Hedmark County (see Statistics Norway, http://www.ssb.no), the estimated percentage of slaughter remains left behind by moose hunters (Wilmers et al. 2003), the killing rate of moose by the different wolf packs in the area (Wabakken et al. 2003; Sand et al. 2005), and the estimated percentage of carcasses left behind by wolves (Mech et al. 1998; Wilmers et al. 2003), the amount of leftovers from the moose hunt would be expected to be much higher than the amount left by wolves. However, because the hunting season occurs during a short time window during Autumn (October) while wolves kill moose throughout the winter, carcasses from wolf kills should be more important to nutritional needs of wolverines that those from hunter kills. Wilmers et al. (2003; 2004) and Wilmers and Stahler (2002) came to a similar conclusion when they compared biomass available to scavengers from wolf-killed wapiti (*Cervus Canadensis* (Erxleben, 1777)) with remains of wapiti left by hunters in and near Yellowstone National Park. Where wolf packs are stable and not hunted, their kill rate is also relatively stable and therefore reduces the temporal variation in the quantity of carrion and extends the period over which carrion is available (Wilmers et al. 2004).

Intra-guild species

We observed no cases in which wolverines followed the trails of other guild species to locate carcasses or other scattered food sources during our study. Following guild species' trails might therefore be better explained as a strategy to save energy when traveling through deep snow rather than to improve foraging success. Also, as guild species encountering wolverine tracks increased further away from carcasses and wolverines did not encounter more guild species trails when approaching carcasses, it may imply that either wolverines did not use guild species' trails to locate carcasses or that they even avoided using other guild species' trails when approaching carcasses. The tortuousness of the entire tracks increased when they led to a carcass, which indicates that the wolverine actively sought for these carcasses (i.e., foraging behavior movement pattern) on their own. Despite the low number of observed encounters, we found a slight tendency for a wolverine's path to become more tortuous after encountering lynx trails. Seemingly, wolverines may associate a lynx trail with possible food sources, and thus would be more likely to actively search the immediate area after encountering a lynx trail. The fact that wolverine's path became less tortuous after encountering red fox trails is difficult to explain since one would actually expect an increase in tortuousness because red fox trails could also be associated with possible food sources. The relationship between wolverines and red foxes clearly merits further research.

Haglund (1966) suggested that during the 1960's, when wolves were absent as a result of the predator control programs (c.f., Landa et al. 2000), the wolves' role as a major predator was taken by the lynx. During that period, the remains of lynx-killed prey would have served as the primary winter food supply of carrion for wolverines. The diet of lynx is more varied in areas with low roe deer densities, but Linnell et al. (1996) and Andersen et al. (1998) found the diet of lynx in eastern Hedmark County was composed of 75% roe deer. Pedersen et al. (1999) found in northern Sweden that lynx consumed an average of 61% of the reindeer body that they killed; leaving 39% for scavengers. It might therefore still be energetically profitable for a wolverine to investigate lynx trails for food remains. Neither Myrberget et al. (1969) nor Kvam et al. (1979), however, observed occasions during their wolverine tracking surveys in which wolverines followed lynx trails or scavenged on lynx kills. In contrast to these and our results, Mathisen et al. (2002) recorded that wolverines utilized reindeer carcasses killed by lynx in Troms in northern Norway and Mårell (1997) found that the home ranges of wolverines and lynx were more closely associated in northern Sweden than expected by chance. These differences indicate that the relationships between wolverines and lynx vary in space and time. Interacting with lynx might be a trade-off for the wolverine due to potential risk of intra-guild predation and injuries. However, as both lynx and wolverine are of similar body size interference is expected to be lessened (Linnell and Strand 2000). Also lynx, which are solitary hunters, are less likely to be a threat to a wolverine than wolves which operate in packs.

Although, we did not observe wolverines following wolf trails directly leading to food sources, carcasses from (likely) wolf-kills provided a primary food source for wolverines. This would imply that wolverines depend on wolf predation on moose to provide them with carrion in the boreal forests during the winter. The lack of observed encounters between wolverine and wolf may indicate that wolverines experience intra-guild predation and interference by wolves (Linnell and Strand 2000) and reduce this risk by avoiding direct confrontation with wolves and temporal and/or spatial exclusion at carcass sites (see also

Paquet 1992; Cohn 1998). In July 2003 a radio-marked female wolverine was assumed killed by wolves together with one of her three cubs within the study area. The leftovers, with bite marks from large canids, were found only several kilometres from a rendezvous site of a wolf pack followed by GPS-transmitters and no (feral) dogs are known to use the area (Landa et al. unpublished data). Also predation of wolverines by wolves has previously been documented (Novikov 1962; Hornocker and Hash 1981; Bjärvall and Isakson 1982; Banci 1994; Copeland 1996; Magoun and Copeland 1998). Spatial and temporal avoidance of wolves is furthermore, indicated by our observations of wolverines making primary use of high elevations (based on their marking behavior, defecations, urinations, resting places and hunting attempts) with short-term excursions to find food sources at lower elevations.

The importance of scavenging from prey killed by other guild species together with the spatial and temporal separation between wolverines and wolves and lynx, presumably to avoid intra-guild predation, suggests that maintaining a wolverine population in the presence of other guild species is ecological feasible within the boreal ecosystem (May et al. unpublished data). However, we have to keep in mind that wolf, lynx and wolverine populations in Hedmark County are heavily exploited by humans, which likely reduces the magnitude of intra-guild relationships between wolverine, lynx and wolf.

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Table 1. Multivariate regression assessing possible temporal (date) or spatial (elevation) effects (last two columns) in the number of observations found along wolverine tracks in southeastern Norway, while correcting for variation in track length. The last four columns give the estimates, standard errors and significance level of the model coefficients. One, two or three asterisks indicate $P < 0.05$, $P < 0.01$, or $P < 0.001$.

Dependent	**$F_{3,51}$**	**P-value**	**R^2**	**Intercept**	**Track length**	**Temporal**	**Spatial**
Marking	11.131	0.000	0.396	-2.905 ± 2.974	0.905 ± 0.188***	0.016 ± 0.020	0.002 ± 0.005
Defecation	1.407	0.251	0.076	1.155 ± 0.971	0.118 ± 0.062	-0.007 ± 0.006	-0.001 ± 0.002
Urinating	9.369	0.000	0.355	0.130 ± 2.052	0.649 ± 0.130***	-0.012 ± 0.014	0.000 ± 0.004
Resting place	2.320	0.086	0.120	1.588 ± 1.093	0.183 ± 0.069*	-0.004 ± 0.007	-0.002 ± 0.002
Hunting attempt	3.011	0.039	0.150	0.642 ± 0.514	0.082 ± 0.033*	-0.007 ± 0.003*	0.000 ± 0.001
Carcass	2.499	0.070	0.128	3.427 ± 1.505*	0.181 ± 0.095	-0.019 ± 0.010	-0.004 ± 0.003
Fox trail	12.605	0.000	0.426	5.852 ± 4.893	1.861 ± 0.310***	-0.034 ± 0.032	-0.007 ± 0.009
Lynx trail	0.920	0.438	0.051	1.700 ± 1.028	0.071 ± 0.065	0.004 ± 0.007	-0.003 ± 0.002
Wolf trail	5.130	0.004	0.232	5.142 ± 1.343***	0.201 ± 0.085*	-0.016 ± 0.009	-0.007 ± 0.002**

Table **2**. Multivariate regression explaining number of encounters at different actual distances from a carcass (intervals of 100m), while correcting for the number of wolverine tracks per interval. The second column gives the number of observed encounters. The last three columns give the estimates, standard errors and significance level of the model coefficients. One, two or three asterisks indicate $P < 0.05$, $P < 0.01$, or $P < 0.001$.

Dependent	**N**	**$F_{2,101}$**	**P-value**	**R^2**	**Intercept**	**Number of tracks**	**Distance to carcass**
fox encounters wolverine	214	37.091	0.000	0.423	-2.263 + 0.723**	0.289 + 0.051***	$2.4E^{-4}$ + $7.9E^{-5}$**
lynx encounters wolverine	22	18.450	0.000	0.268	-0.530 + 0.145***	0.049 + 0.010***	$5.1E^{-5}$ + $1.6E^{-5}$**
wolf encounters wolverine	22	20.990	0.000	0.294	-0.790 + 0.310*	0.090 + 0.022***	$7.2E^{-5}$ + $3.4E^{-5}$*
wolverine encounters fox	222	72.224	0.000	0.589	-1.187 + 0.804	0.297 + 0.057***	$1.0E^{-4}$ + $8.8E^{-5}$
wolverine encounters lynx	12	4.293	0.016	0.078	-0.179 + 0.181	0.023 + 0.013	$1.7E^{-5}$ + $2.0E^{-5}$
wolverine encounters wolf	25	0.550	0.579	0.011	0.006 + 0.492	0.015 + 0.035	$3.7E^{-6}$ + $5.4E^{-5}$

Table 3. Linear model regressing tortuousness (fractal dimension) of the entire wolverine track against the explanatory effects of the presence food sources (leads to carcass) and encounters with guild species, while correcting for the variation in track length.

Model	**Covariate**	**ß**	**SE**	**t-value**	**P-value**
Wolverine encountered guild species, total	Intercept	1.094	0.009	123.009	< 0.001
	Track length	-4.0E^{-6}	1.9E^{-6}	2.127	0.038
	Leads to carcass	0.070	0.015	4.778	< 0.001
	Total encounters	-1.8E^{-3}	9.1E^{-4}	1.941	0.058
Wolverine encountered guild species, per species	Intercept	1.092	0.009	123.523	< 0.001
	Track length	-3.1E^{-6}	1.9E^{-6}	1.647	0.106
	Leads to carcass	0.075	0.015	5.085	< 0.001
	Fox encounters	-3.6E^{-3}	1.3E^{-3}	2.822	0.007
	Lynx encounters	1.6E^{-3}	8.4E^{-3}	0.194	0.847
	Wolf encounters	7.9E^{-3}	4.9E^{-3}	1.618	0.112

Table 4. BACI-model assessing tortuousness of wolverine track segments in a 100 m straight-line distance prior to or following the encounter as a measure of direct changes in wolverine's searching behavior before and after an encounter with a trail of another guild species. “before_after” indicates changes in tortuousness after relative to before an encounter irrespective of species, whereas “species-” indicates changes in tortuousness per species irrespective of before or after an encounter. The last three rows indicated as “encounter-” measure the effect of the interaction term between “before_after” and “species-”, thus indicating the changes in tortuousness after a species’ encounter relative to before.

Covariate	**ß**	**SE**	**t-value**	**P-value**
intercept	1.379	0.140	9.865	0.000
before_after	0.033	0.037	0.886	0.376
species-fox	0.003	0.052	0.060	0.952
species-lynx	0.061	0.188	0.324	0.746
species-wolf	-0.022	0.174	0.124	0.901
encounter-fox	-1.000	0.070	1.424	0.155
encounter-lynx	1.485	0.253	5.877	0.000
encounter-wolf	0.048	0.225	0.216	0.829

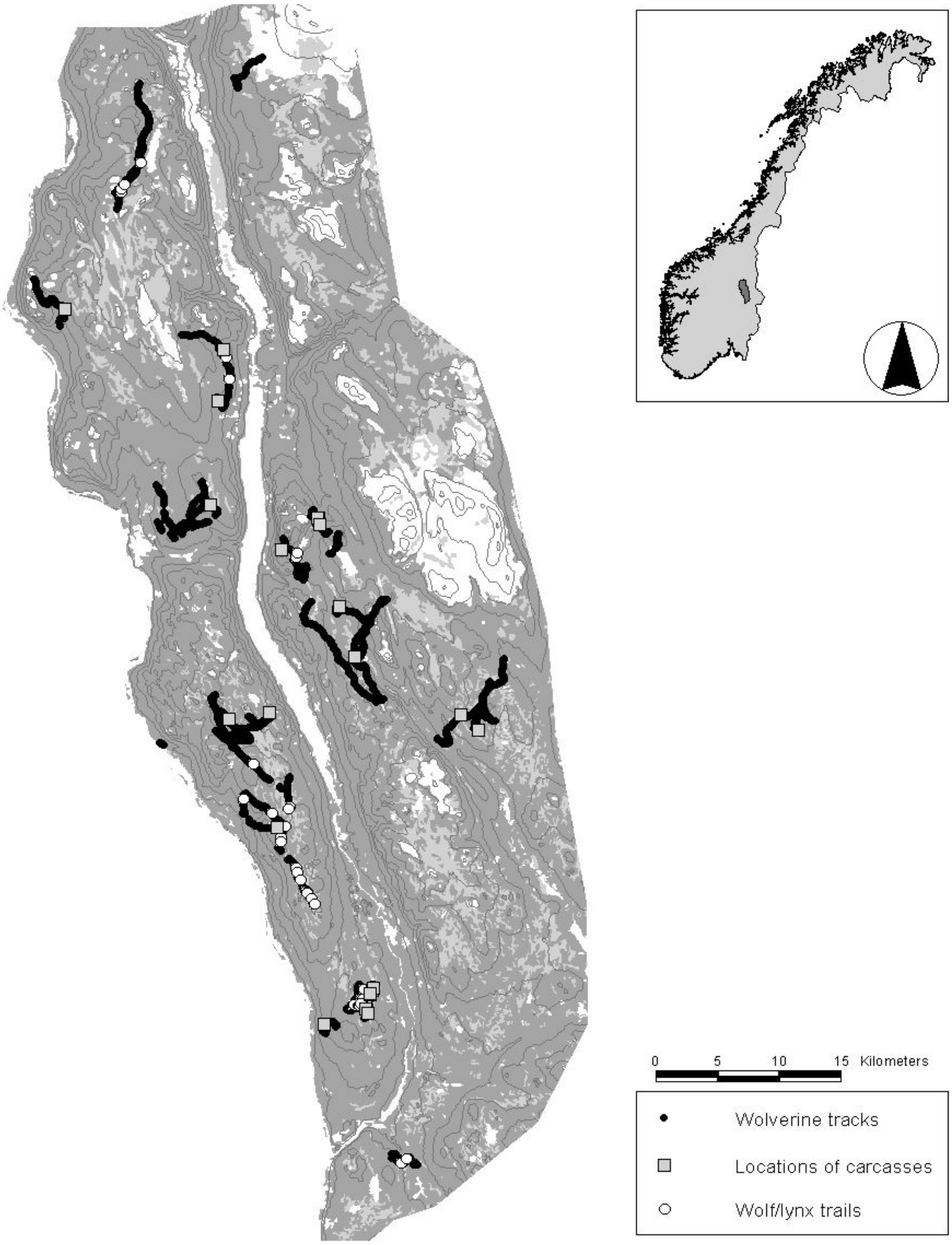

Fig. 1. The study area in northwestern Hedmark County, Norway where wolverine tracks were followed in the snow during March-April, 2003 and December 2003-January 2004. Solid lines indicate wolverine tracks followed, squares indicate locations of carcasses scavenged by wolverines, and circles indicate location of the encounters between wolverines and wolf or lynx trails.

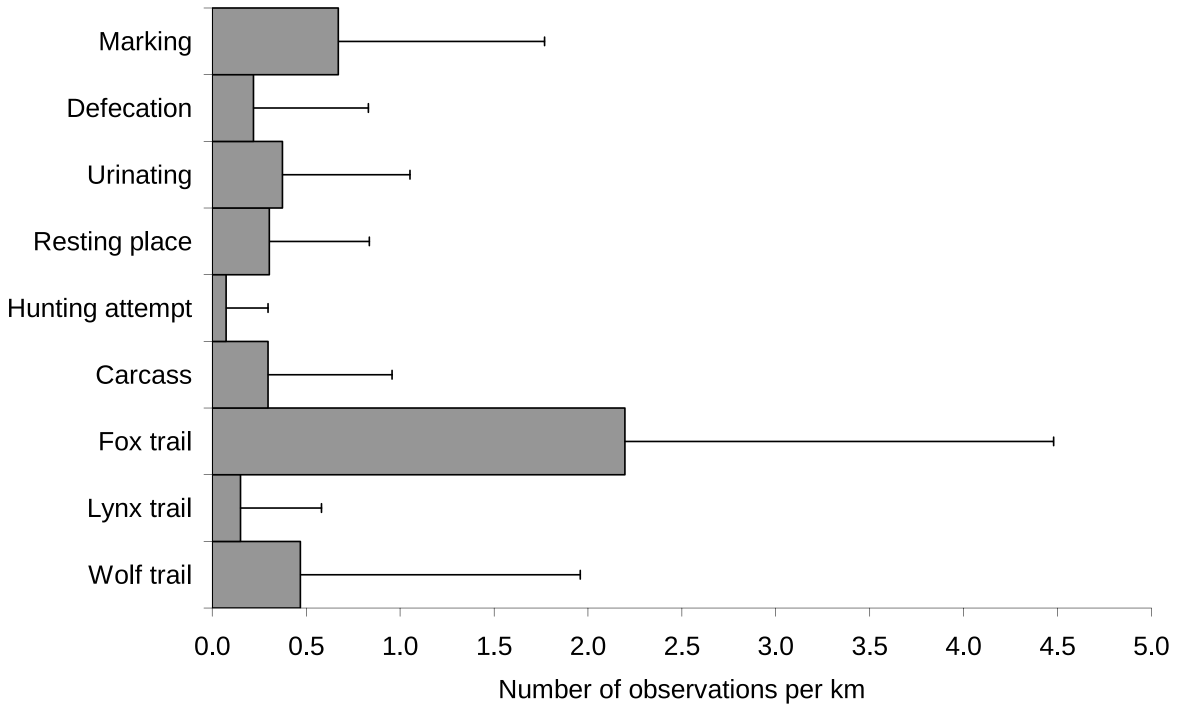

Fig. 2. Number of observations (+SD) per km tracked along wolverine tracks in southeastern Norway.

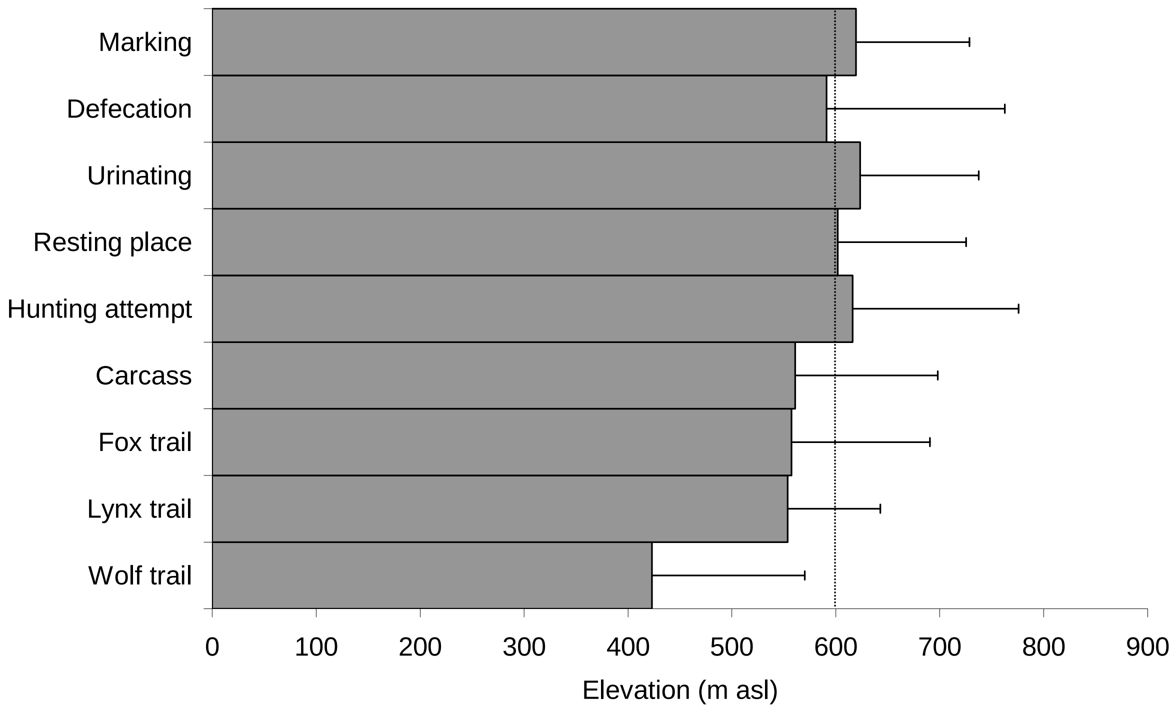

Fig. 3. Average elevation (+ SD) of each observation along wolverine tracks in southeastern Norway. The dotted vertical line indicates average elevation of the wolverine tracks.

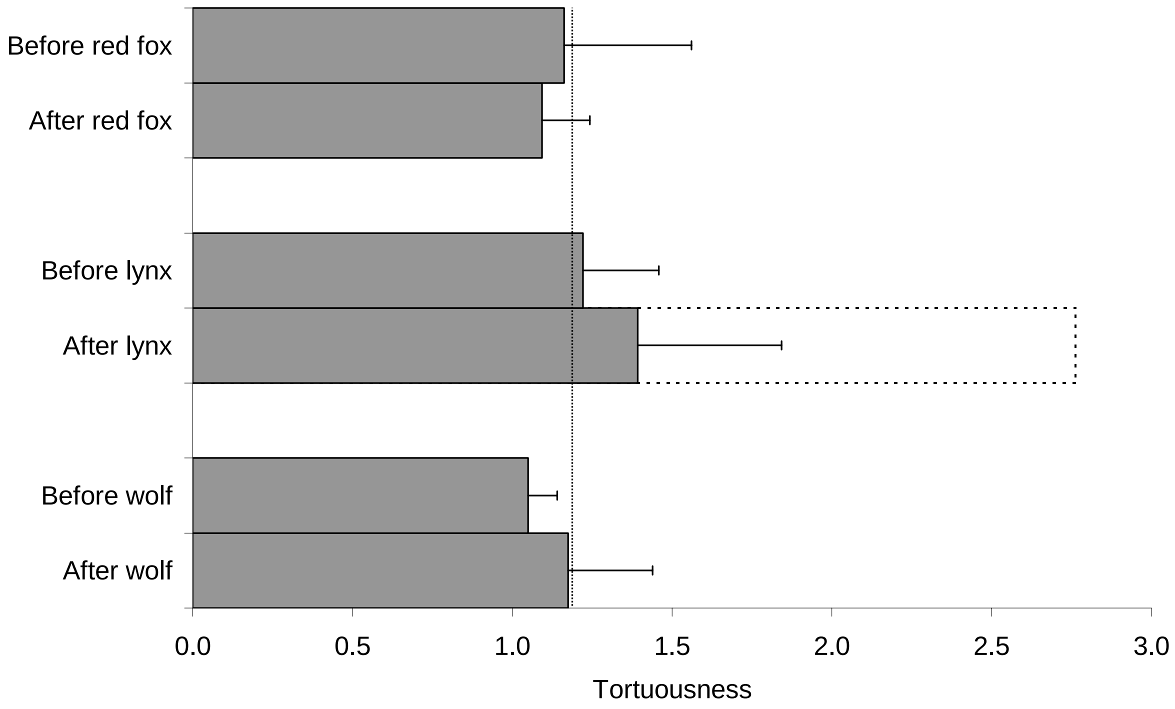

Fig. 4. Average tortuousness (+ SD) of wolverine track segments in a 100 m straight-line distance prior to or following the encounter as a measure of wolverine's searching behavior before and after an encounter with a trail of another guild species. The striped bar indicates the average tortuousness including an outlier encounter with a tortuousness of over 12. The dotted vertical line indicates average tortuousness of random track segments.

Paper IV

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: brown bear, grey wolf, Eurasian lynx, wolverine, habitat and predation patterns, intra-guild competition, species co-existence, regional zoning, elevational gradients

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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 in 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 lynx 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 also 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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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**

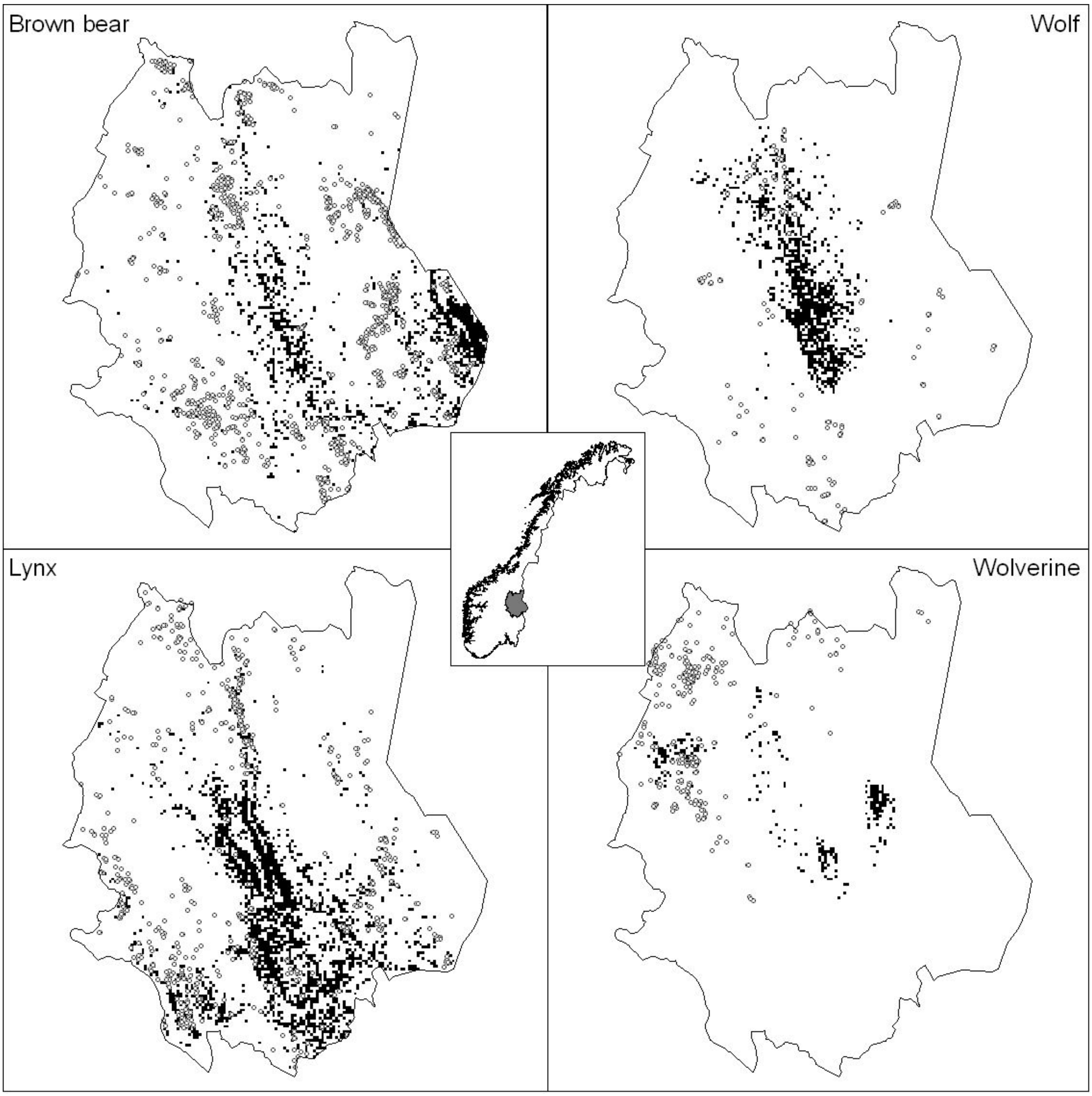

Figure 1. Presence maps for four large carnivore species within the study area in southeast Norway (see inset). The presence pixels from the radio-tracking data are given in black; locations of predator-killed sheep are given as white circles.

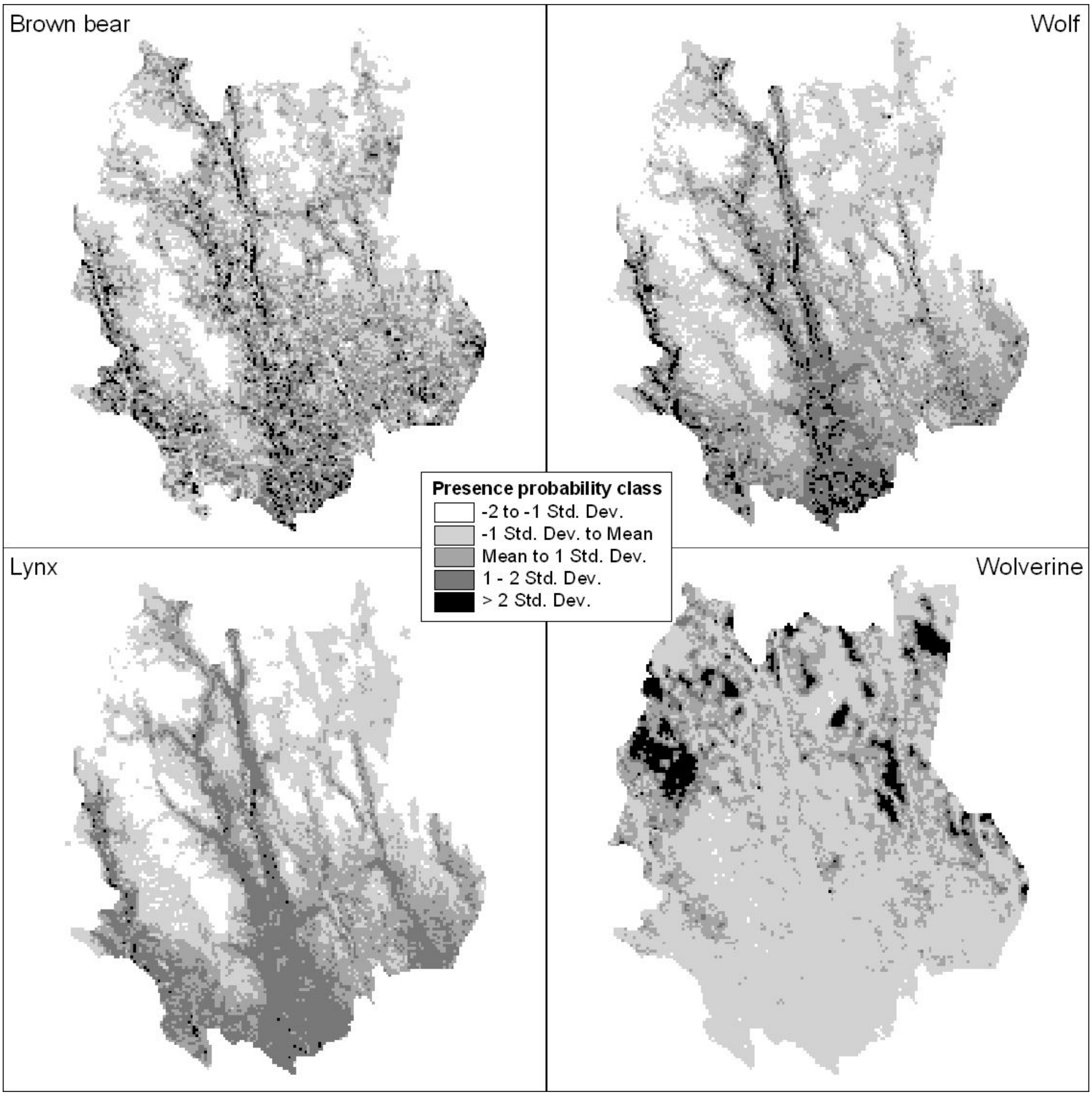

Figure 2. Probability maps for four large carnivore species within the study area in southeast Norway. The probability distributions were based on species-specific resource selection function models given in Table 1.

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 V

Wolverine predation on domestic sheep: explaining spatio-temporal variation in lamb losses

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Running title: Wolverine predation on domestic sheep

Summary

1. In Norway wolverines *Gulo gulo* L. are involved in conflicts with human interests because of their predation on free-ranging domestic sheep *Ovis aries* L. during summer. Despite license hunts during winter, predator-control during summer and the removal of females with cubs during spring, depredation losses are still documented and the conflict continues to exist. It has however never been clear why certain grazing areas have high wolverine depredation losses during certain years and why depredation losses increase during the development of the sheep-grazing season.

2. We analysed spatio-temporal variation in lamb depredation rates within the sheep grazing areas in Norway during 2000 and 2005. We modelled (mixed effects Poisson regression) spatio-temporal variation in lamb depredation rates using data on stock numbers and numbers of documented kills of lambs by wolverines, and data on wolverine reproductions and removals. Seasonal depredation patterns were analyzed using information (i.e., killing and hoarding techniques) recorded on registration forms of carcass autopsies performed by the State Nature Inspectorate.

3. Spatio-temporal variation in lamb depredation rates was best explained by the presence of reproductive females with her cubs together with the removal of sub-adults. Removal of adult wolverines had varying effects on depredation rates. Depredation rates were highest in alpine shrub land, with a typical depredation increase during the latter portion of the grazing season. Although the seasonal depredation pattern coincided well with cub independence, no evidence in the form of changing killing techniques was found. Also the number of hoarded carcasses didn’t increase during the latter portion of the grazing season.

4. *Synthesis and applications:* This study may help to explain why depredation-control measures have failed to reduce depredation rates in the past. The removal of wolverines may locally lead to temporary demographic instability and fluctuating local densities with the establishment of neighbouring or new individuals in the area, explaining the variation in lamb depredation rates. Because lamb depredation increases during the latter portion of the grazing season when sheep and wolverines overlap in habitat use and cubs become independent, depredation may be minimized by systematically rounding-up sheep earlier in grazing areas with wolverine reproduction.

Key words: demographic instability, lamb depredation, local density, predator removal, wolverine reproduction.

Introduction

Predation on domestic livestock by large carnivores has resulted in conflicts that limit human tolerance of carnivore conservation (Vittersø, Bjerke & Kaltenborn 1999; Treves *et al.* 2002; Linnell *et al.* 2005). Reducing these conflicts therefore is a prerequisite to successfully conserving large carnivore species (Linnell *et al.* 1996; Sagør, Swenson & Røskaft 1997). In Norway, wolverines *Gulo gulo* L. are involved in conflicts with human interests because of their predation on free-ranging domestic sheep *Ovis aries* L. during summer (Aanes, Swenson & Linnell 1996; Landa *et al.* 1999) and their predation on semi-domestic reindeer *Rangifer tarandus* L. year-round (Landa, Lindén & Kojola 2000). In Norway wolverine predation on unattended sheep during summer is well documented, whereas in Sweden and Finland little documentation exists, because almost no unattended sheep graze in the same areas where wolverines live. On the other hand wolverine predation on semi-domestic reindeer is well documented in all of the Nordic countries. Wolverine predation on livestock has been one of the main reasons for their control and historical population decline (Landa, Lindén & Kojola 2000). After nearing extinction due to hunting and predator removal programs, the wolverine population in Scandinavia has increased in number and distribution after protective legislation was passed in the 1970's (Landa, Lindén & Kojola 2000). Since the 1970's wolverine recovery in Norway has occurred, but also sheep stock numbers have increased while herding and livestock traditions had been lost (Landa, Lindén & Kojola 2000). License hunts during the winter, predator-control during the summer and the removal of females with cubs during the denning period in spring have been used in attempts to reduce depredation losses after their official legal protection during the 1970's and 1980's. Despite these wolverine removals, depredation is still documented and the conflict continues to exist. It has however never been clear why certain grazing areas have high depredation rates during certain years and why depredation rate increases during the development of the sheep-grazing season.

The aim of the study was to identify parameters that explain the spatio-temporal variation in sheep depredation rates between grazing areas and years, and the increase of depredation rates during the development of the grazing season. The results may also help to identify specific demographic classes of wolverines (i.e., adult females, adult males, sub-adults, cubs) that might be responsible for the losses. The main hypothesis was that predation on unattended, free-ranging sheep is best explained by temporal variation in local wolverine density, i.e. several wolverines sharing the same area at a certain period. Although home ranges of females with cubs are restricted while the cubs are growing up (Hornocker & Hash 1981; Banci & Harestad 1990), the mating period coincides partly with the cub-rearing period (Rausch & Pearson 1972; Persson *et al.* 2006) meaning that adult males also frequent cub-rearing areas. Together with sub-adult wolverines from previous litters (especially female offspring tend to stay within the home range of a female with dependent young; Magoun 1985) these demographic classes increase local wolverine density. Removal of adult females or entire families (i.e., female with her cubs) through licence hunts and depredation-control measures may disrupt local wolverine densities and generate a shift in home ranges of neighbouring wolverines and the establishment of new individuals. This might cause a temporary higher local density that increases depredation until the local wolverine density has stabilized again. Although all adult wolverines are known to hoard (Haglund 1966; Magoun 1987; Banci 1994; Landa *et al.* 1997), we expected that especially adult female wolverines would contribute to the depredation increase during the latter portion of the grazing season in order to secure food caches for next spring's reproduction (Haglund 1966; Vander Wall 1990). Furthermore, cubs were expected to contribute to this depredation increase when they become nutritionally independent from their mother by the end of August. A typical killing strategy of the wolverine is a powerful bite mark in the neck of the sheep, breaking the neck vertebra. Although the majority of sheep killed by wolverines show only a bite mark in the neck, either or not accompanied with a bite mark on the nose (A. Landa pers. comm.), some carcasses are found with bite marks around the throat, legs, tail, back and/or belly region. Because cubs are likely less experienced in killing sheep, we assumed the number of bite mark locations on the lamb carcasses to increase during the latter portion of the grazing season (see also Stirling & Latour 1978; Seidensticker & McDougal 1993; Watt 1993; Caro & Laurenson 1994).

Our study renders insight into the variation in lamb depredation rates between grazing areas and years, and into seasonal depredation patterns. Since one of the main barriers to large carnivore conservation is their predation on domestic livestock (Kaczensky 1996; Linnell *et al.* 1996), a better understanding of wolverine predation on lambs enhances the sustainable management of the Norwegian wolverine population considerably.

Material and methods

STUDY AREA

Data was collected for all sheep grazing areas in Norway (Norwegian Institute for Forest and Landscape, NIJOS, 2001-2004) which either overlapped with wolverine distribution (Landa, Lindén & Kojola 2000), or for which wolverine predation on sheep had been confirmed or assumed (hereafter called documented) between 2000 and 2005 by the State Nature Inspectorate (SNO) (see Figure 1). In total 71 and 143 registered sheep grazing areas were included for northern and southern Norway respectively.

Norway exhibits different ecotypes due to the large latitudinal range of the country and its varied topography and climate. The habitat can generally be categorized as mountain plateaus with peaks of bare rock to elevations of 2,000 m, which give way to alpine tundra with heath (e.g. heather *Caluna* spp., crowberry *Empetrum* spp.) and lichen (*Cladonia* spp.) vegetation. At lower elevations, alpine shrub land (e.g. willow *Salix* spp., dwarf birch *Betula nana* L.) can be found close to tree line. The transition from the shrub land to birch forests below the tree line forms the forest/alpine tundra ecotone (Grytnes 2003). The elevation of tree line decreases with latitude: in the South no trees grow above 1,000 m a.s.l., whereas in the North the tree line is found at 400 m a.s.l. Below tree line, forests are composed of mountain birch *Betula pubescens* Ehrh., 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.), interspersed with open bogs, and some agricultural lands. Human infrastructure is generally concentrated at lower elevations in the valley bottoms although recreational cabins can be found at higher elevations as well. Human activities in the mountains mainly consist of hunting, hiking, camping and cross-country skiing.

Sheep grazing areas are found throughout Norway, but sheep grazing is especially intensive in southwestern Norway, and sheep are largely left unattended during mid-June to mid-September (Landa, Lindén & Kojola 2000). Especially in northern Norway and sporadically in central Norway semi-domestic reindeer herding is also practiced. Unlike sheep husbandry practices, reindeer herds are free-ranging for the entire year, and are therefore vulnerable to predation over a longer period (Landa, Lindén & Kojola 2000). The largest European population of wild reindeer is found in the mountainous areas in the southwestern and southcentral Norway. Moose *Alces alces* L., roe deer *Capreolus capreolus* L., hares *Lepus timidus* L., ptarmigan *Lagopus muta* M., willow grouse *Lagopus lagopus* L., lemmings *Lemmus lemmus* L., various rodents (*Microtus* spp. and *Clethrionomys* spp.) and insectivores (*Insectivora* spp.) form possible sources of food for the wolverine in both northern and southern Norway; either as hunted prey or through scavenging.

LIVESTOCK HUSBANDRY AND DEPREDATION MANAGEMENT

Because of winter weather conditions, sheep are grazed on mountain and forest pastures only between mid-June and mid-September. In former times sheep were commonly protected from predation by the presence of shepherds, but the dramatic reduction in large carnivore populations during the last century changed the herding system. Now sheep are largely left without supervision or protection during the grazing season and about 2.4 million sheep are released for free-ranging grazing each summer (Landa, Lindén & Kojola 2000).

Because of the low intensity of supervision by herders, many sheep that die due to accidents, illness, predation, or other causes are never found. Losses of 2% ewes, and 5% lambs are regarded as “normal” (i.e., to sources other than predation) (Landa, Lindén & Kojola 2000; Swenson & Andrén 2005). During the 1990’s, 10 to 20% of the lambs lost on the Snøhetta plateau, southern Norway, had been found and 50 to 85% of these had been killed by wolverines (Børset 1995; Mortensen 1995); which mostly comprised lambs (Landa *et al.* 1999).

A compensation system for depredation losses was introduced in southern Norway in 1973 and in northern Norway in 1982 (Landa, Lindén & Kojola 2000). Herders are required to document large carnivore predation on livestock, although not all missing animals need to be found (Landa, Lindén & Kojola 2000). Since the late 1990's SNO assumed responsibility for the registration of large carnivore depredation, where field personnel examine carcasses reported as depredation and document the cause of death through autopsy (Landa *et al.* 1999). Documented predator-killed livestock are registered in the national predator database Rovbase, and are used by the Directorate for Nature Management (DN) and the County managers to set compensation levels to herders. Compensation is directly paid by the County managers to the herders.

Apart from sporadic rounding-up sheep from the pastures during late August instead of mid-September, and the rare application of electric fencing and livestock guarding dogs to protect sheep, the primary management approach for reducing wolverine depredation has been direct removals of wolverines. During September to February, "licence hunts" are held, in which a set quota of animals may be killed by local hunters. In addition, separate "predator removal" permits may be issued by the management authorities for the killing of wolverines in areas associated with high rates of depredation. Predator removal permits are usually issued during the grazing season. However two thirds of the wolverines were removed prior to the onset of the depredation increase during the latter portion of the grazing season, decreasing the bias that increased depredation rates had already occurred during the summer season before wolverines were removed.

As depredation is generally perceived to be tied to reproduction events, management authorities can, in addition to these two types of control, decide to conduct "family removal" in which an adult female and her cubs are killed at the den site during spring. The decision to conduct a family removal in a certain area is based on depredation rates during the previous year(s). In practice this type of control measure results either in the removal of the entire family when the adult female is in the den or in "cub removal" when only the cubs are killed but the mother escapes. In about one third of the cases the female escapes when family removal is attempted and the adult female may reproduce again the following year. Female wolverines tend to den within a limited area, and are known to re-use the same denning locations over several years. Even when females are removed the same locations are often used again by newly established females. Therefore, systematic monitoring of den sites throughout Norway has been a standard monitoring tool for wolverines during the last 15 years (for methods see Landa *et al.* 1998b). The numbers of documented reproductions in both southern and northern Norway between 2000 and 2005 are listed in Table 1 (Brøseth & Andersen 2003, 2004, 2005). Annual wolverine control, including those killed in licence hunts, predator removal, family removal and cub removal in southern and northern Norway between 2000 and 2005 are listed in Table 2.

DATA ON DEPREDATION LOSSES

Data on sheep depredation losses are available from three different sources: i.e. the number of documented kills of lambs by wolverines during the development of the grazing season (SNO), the number of compensated lambs of which it was assumed they were killed by wolverines (DN) and the number of total lamb-losses given by NIJOS (see supplementary material, Fig. S1. Panel A, B & C). However the numbers of sheep losses given by NIJOS (panel C) do not distinguish between losses caused by different predators, such as wolverine, golden eagle *Aquila chrysaetos* L. or lynx *Lynx lynx* L., or caused by accidents or illness. It only gives an overview of all animals that failed to return after the grazing season. On the other hand, DN (panel B) has a complete overview over the number of sheep for which the sheep owners, organized within grazing areas, got compensation for, and of which was assumed to have been killed by wolverines. The assessment of how many lost sheep are compensated for is based not only on what SNO personnel documents in the field and the number of missing animals given by the sheep owners (NIJOS data), but it also takes into account whether the grazing area has been affected by wolverine depredation before and if the area lies close to or within a known wolverine reproduction area. The inclusion of this kind of history is likely justifiable in terms of economic losses but does not enable us to distinguish between assumptions and the actual number of depredation rates in a particular area for a particular year. The documented kills of lambs by wolverines in the SNO database Rovbase (panel A) is an underestimation of the actual depredation losses (~10% of those that failed to return after the grazing season - NIJOS) since many carcasses are never found, and therefore poorly reflects the actual losses sheep owners face. However, it does form the most unbiased data available representing a relative measure for the actual wolverine depredation rates. Records compiled by the SNO indicate that 5,968 lambs, 765 sheep of >1 year of age, and 128 of unknown age were documented killed by wolverines between 2000 and 2005. We used this data to analyze spatio-temporal variation in depredation rates and seasonal depredation patterns in combination with statistics from the different sheep grazing areas (i.e., number of sheep released each year per grazing area).

TOPOGRAPHIC DATA AND INDIVIDUAL, TEMPORAL AND SPATIAL INFORMATION

The geographic positions of documented wolverine reproductions (excluding the family removals and cub removals) and removed wolverines (i.e., wolverines killed during license hunts, predator removal, family removal and cub removal) were buffered with a 10 km radius (i.e., the approximate mean radius of the home range of female wolverines; Landa *et al.* 1998a), with use of Geographic Information System software package ArcView 3.3 (ESRI, Environmental Systems Research Institute, Redlands, California). When the buffer overlapped with a sheep grazing area the reproduction or removed wolverine was assumed to be present in this area. The documented kills of sheep by wolverines were assigned to the different grazing areas with the nearest feature extension of ArcView and checked for errors with regard to this spatial procedure. The most dominant habitat category, being forest, alpine shrub land or alpine tundra, of each grazing area was derived from a 1x1 km land cover grid (a reclassified AVHRR image, United States Geological Survey, http://edcdaac.usgs.gov/glcc/background.html).

Landa *et al.* (unpublished data) found that wolverine cubs become nutritionally independent from their mothers by August-September, but generally disperse 13 months after birth (Vangen *et al.* 2001). Assuming that independent wolverine cubs are responsible for the increased sheep killed during the latter portion of the grazing season, depredation rates were compared with the independence curve (i.e., as measured by the increasing distance between females and their cubs). Seasonal depredation patterns were furthermore analyzed using information (i.e., killing and hoarding techniques) recorded on the registration forms of carcass autopsies performed by field personnel of the State Nature Inspectorate. 1,739 (1,624 lambs, 102 sheep of >1 year of age, and 13 of unknown age) registration forms of carcass autopsies in Oppland, Sør-Trøndelag and Hedmark Counties in southern Norway (2000-2005) were manually checked. Only those registration forms were included of which field personnel of SNO performed the autopsy on the carcasses and confirmed the carcass as wolverine kill.

DATA ANALYSIS

Wolverines killed more lambs than ewes with a lamb-ewe ratio of 9:1. Since this ratio was constant during the development of the grazing season we limited our analysis to lamb depredation. Spatio-temporal variation in lamb depredation rates were analysed using Poisson regression with year and grazing area as random grouping factors to account for replication over grazing areas and years. The number of documented kills of lambs by wolverines divided by total number of lambs released onto the grazing pastures (included as offset) was taken as measure for sheep depredation rates. Explanatory variables explaining spatio-temporal variation in depredation rates included in the analyses are listed in Table 3. Model parsimony of the entire set of 16,384 possible models was based on the corrected Akaike Information Criterion (AIC_c) (Anderson, Burnham & Thompson 2000; Burnham & Anderson 2002). The relative importance of each of these explanatory variables on depredation rates was assessed by calculating the summed AIC_c weights for each variable across all models. We used model averaging to obtain estimates and standard error of the variables (Anderson & Burnham 2004). Statistics were performed in the statistical software programme R 2.4.0 (R Development Core Team 2006) 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.

Whether the extent of hoarding behaviour was affected by reproduction in the year after, we analyzed the number of hidden carcasses per total number of carcasses documented as binary response variable in a binomial mixed effects model (lmer) with grazing area as a random grouping factor and reproduction in the year after as explanatory fixed effect factor. All other statistical analyses were done with Microsoft Excel, version 2003.

Results

SPATIO-TEMPORAL VARIATION IN LAMB DEPREDATION RATES

Lamb density per km^2 grazing area in northern Norway was slightly lower than in southern Norway (8.781 ± 7.107 SD, 95% C.I.: 7.128 – 10.435 for northern Norway and 11.556 ± 10.894 SD, 95% C.I.: 9.771 – 13.342 for southern Norway). Similarly, average lamb depredation rates in northern Norway were lower (0.0025 ± 0.0042 SD, 95% C.I.: 0.0015 – 0.0034) than in southern Norway (0.0040 ± 0.0063 SD, 95% C.I.: 0.0030 – 0.0051). Still, these regional differences had no significant effect on the spatio-temporal variation in lamb depredation rates (Table 4). The calculated relative importance of the different covariates showed that grazing areas with alpine tundra and especially with alpine shrub land had higher depredation rates. Increased lamb availability led to lower lamb depredation, but according to the Wald statistic its relative importance within the models was low.

According to the Wald statistics, reproductions in the current and the following year were the most important factors explaining increased depredation rates. Conversely, the removal of sub-adults and cubs during the winter preceding the grazing season was the most important factor explaining decreased depredation rates. While adult males removed during the winter preceding the grazing season also resulted in decreased depredation rates, did removal of adult females increase depredation rates. Also, removal of sub-adults and cubs during the grazing season led to increased depredation rates, while removal of adult males and females during the grazing season did not have any significant effect. The removal of females with cubs during spring reduced depredation rates, but according to the Wald statistic its relative importance within the models was low. Neither removal of only the cubs during spring nor reproduction in the previous year affected depredation rates (Table 4). The summed AIC_c weights over the 10 best models ($\Delta AIC_c<2$), which estimates the proportional support of the data for the given models to explain spatio-temporal variation in depredation rates, was 49.5%.

SEASONAL DEPREDATION PATTERNS

Since we expected a bias in the seasonal depredation pattern due to the fact that more kills of lambs may be found at the end of the grazing season when many locals are traversing the grazing areas fetching sheep, we examined the seasonal pattern also for fresh kills only with absolute certain kill dates as indicated on the autopsy sheets from SNO. The seasonal depredation pattern based on fresh kills only was, however, the same as for all documented kills of lambs with estimated kill dates.

Most documented kills of lambs by wolverines were found in alpine shrub land, where also the increase in depredation during the latter portion of the grazing season was most pronounced. We observed a similar pattern for lambs killed in forest, whereas it was less apparent in alpine tundra (Fig. 2).

The independence curve, based on the increasing distance between females and their cubs over weeks presented by Landa *et al.* (unpublished data), closely followed the seasonal pattern of increased lambs killed towards the end of the grazing season ($R^2 = 0.430$, Fig. 3). Also, the number of bite mark locations on lamb carcasses was found to increase towards the end of the grazing season (Fig. 4); however this pattern was similar for areas with and without reproductions the year after. The number of hidden carcasses, as a possible measure of female hoarding behaviour to secure food sources for next year's reproduction, did not increase towards the end of the grazing season (Fig. 5). The number of hidden carcasses per total number of carcasses found was not affected by wolverine reproduction in the area the year after ($\beta = -0.130 \pm 0.140$ SE, $z = 0.923$, $P = 0.356$).

Discussion

SPATIO-TEMPORAL VARIATION IN LAMB DEPREDATION RATES EXPLAINED BY LOCAL VARIATION IN WOLVERINE DENSITY

Our study revealed that reproductive events, representing the presence of an adult female with her cubs in a given grazing area, resulted in higher depredation rates. This result was also found by Landa *et al.* (1999). We also found that the removal of adult females during the winter preceding the grazing season resulted in higher depredation rates. The removal of a resident adult female may well lead to local demographic instability (Linnell *et al.* 1996). The gap created in the social mosaic of the population may temporarily lead to fluctuating local densities with the establishment of neighbouring or new individuals in the area (Hornocker 1969; Shaw 1982; Lindzey *et al.* 1992; Thomson, Rose & Kok 1992; Laing & Lindzey 1993; Corbett 1995). Because wolverines can roam over long distances (Hornocker & Hash 1981; Vangen *et al.* 2001), the potential for their re-establishment is relatively large (Landa *et al.* 1998a). Landa *et al.* (1999) found, however, that killing of wolverines led to fewer lambs being lost in the same year, but this effect did not carry over to the next year, and depredations resumed, implying a rapid re-establishment of new individuals. Similar results have been found for other carnivores such as wolves *Canis lupus* L., lynx (Stahl *et al.* 2001; Herfindal *et al.* 2005), brown bears *Ursus arctos* L. (Sagør, Swenson & Røskaft 1997) and red foxes *Vulpes vulpes* L. (Reynolds, Goddard & Brockless 1993), although the period in which predation was reduced varied between two years for wolves in Canada (Bjorge & Gunson 1985) and lynx in Norway (Herfindal *et al.* 2005) to less than one year for brown bears in Norway (Sagør, Swenson & Røskaft 1997), lynx in the French Jura (Stahl *et al.* 2001) and red foxes in England (Reynolds, Goddard & Brockless 1993).

In an area with wolverine reproduction not only the resident adult female and her cubs are present, but also the father of the cubs and sub-adults from previous litters may frequent the same area. This thus leads to locally higher densities of wolverines, which fits the suggestion made by Landa *et al.* (1999) that differences in sheep losses among grazing areas were probably related to local variation in wolverine density. Given our model results, there are clear indications that depredation rates are best explained not only by different demographic groups sharing the same area at the same time (higher local densities) but also by demographic instability which might be enhanced by the predator removal programs.

Lamb depredation rates by wolverines were lower when lamb availability increased, as was also found with lynx depredation (Negård *et al.* 1998; Herfindal 2000; Herfindal *et al.*

2005). This suggests that the availability of sheep does not affect the wolverine's natural foraging behaviour or rate of off-take (i.e., surplus prey). According to Kaczensky (1999), Camarra (1986) and Sagør, Swenson & Røskaft (1997) bear depredation levels were also unrelated to the number of sheep available, whereas the mean proportion of cattle lost to large felids varied according to the herd class size but not linear (Michalski *et al.* 2006). Landa *et al.* (1999), on the other hand, found that an increase in the number of sheep in grazing areas containing a stable wolverine population would lead to higher, but not proportionally higher, number of losses.

SEASONAL DEPREDATION PATTERNS

Within this study we found that depredation rates were higher in grazing areas where alpine shrub land was dominant and that the pattern of increased depredation rates during the latter portion of the grazing season was especially apparent in alpine shrub land. In general, sheep start grazing on lower elevations at the beginning of the grazing season and move to higher elevations as the grazing season proceeds. At the end of the grazing season the sheep gradually move down to lower elevations and tend to use the forest/alpine tundra ecotone (i.e., the alpine shrub land) during late summer (Mysterud, Iversen & Austrheim in press). According to Warren, Mysterud & Lynnebakken (2001) wolverines seemed to venture little below the tree line earlier in the season but between the end of June and the beginning of August when sheep grazed in the more open birch forest and in more precipitous terrain they apparently used the same habitat as wolverines. GPS analyses on ranging behaviour in wolverines revealed that they preferred to use the forest/alpine tundra ecotone not only at night during the entire summer season but used the ecotone increasingly during daytime as the summer season proceeded (May *et al.* unpublished data). Sheep exploit the entire elevation gradient with varying vegetation profiles, and traverse the habitats of different predators during the grazing season (Warren, Mysterud & Lynnebakken 2001), thus explaining seasonal depredation patterns.

Although reproduction in the following year increased depredation rates, we found no increase in hoarding behaviour during the development of the grazing season nor was hoarding behaviour related to reproductions in the following year. However, the number of recorded hoarded carcasses is likely to be an underestimate because especially these carcasses will be difficult to find. Possibly adult females start hoarding carcasses after mating has taken place; which may explain the lack of recorded hoarding in the beginning of the season. Still female wolverines are not likely solely responsible for the increased depredation rates at the end of the season. Although results from a study on maternal care in wolverines (Landa *et al.* unpublished data) revealed that wolverine cubs become nutritionally independent in August, no clear evidence was found that cubs were solely responsible for the increased depredation rates during the latter portion of the grazing season, when looking at the number of bite mark locations on the carcasses. It is however possible that in August, independent cubs are already as effective and strong as their mother and might thus have the same killing skills. The observed increase of number of bite mark locations during the latter portion of the grazing season had no relationship with reproductive events, and might therefore rather be a reflection that grown-up lambs are more difficult to kill during this period. The good fit between the seasonal depredation pattern and cub independence gives clear indication that inexperienced young individuals may be responsible. Possibly independent cubs use lambs as surplus prey (i.e., easy “test-object”) to perfect their hunting skills before the onset of winter.

MANAGEMENT IMPLICATIONS

The number of annual wolverine reproductions in Norway has increased from 44 in 2000 to 62 in 2005, despite the depredation-control measures. At a regional scale however (see supplementary material, Fig. S1. Panel A, B & C), there was a slight decrease in number of documented kills of lambs, compensated losses and registered losses instead of the expected increase with increasing numbers of wolverine reproductions. The differences in the number of documented kills of lambs, compensated losses and registered losses may therefore be a result of changes in social perceptions of the conflict (e.g., ability to find carcasses, acceptance of losses) rather than a result of changes in biological processes.

Several studies on large carnivore livestock depredation in Norway (Landa *et al.* 1999; Odden *et al.* 2002; Moa *et al.* 2006) argue that depredation-control measures will only be effective if eradication or severely reduction in population numbers is implemented as management goal. In 2004 the Norwegian government adopted a new large carnivore management policy (Committee on Energy and Environment 2004) in which the goal was set to reduce the wolverine population and to have a wolverine population based on an average of 39 reproductions per year in entire Norway. This reduction in population size should minimise the livestock depredation conflict to an acceptable level. Since wolverine depredation on lambs especially affects herders at a local level, it is questionable whether a reduction in wolverine population numbers will have its desired effect in reducing conflict levels and enhancing the level of acceptance. Even with the minimal number of wolverine reproductions, there will still be at least 39 different areas with heightened depredation losses each year, while most grazing areas within the wolverine distribution are likely to be affected periodically. In our opinion the most effective measures to minimise the wolverine depredation are therefore to focus on mitigation measures and prevention. Because this study revealed that grazing areas were increasingly affected by depredation when reproduction was documented in the area, the most effective mitigation measure would be to systematically round-up sheep earlier in the season.

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Table 1. Numbers of annual wolverine reproductions in southern Norway (Counties south of and including Sør-Trøndelag) and northern Norway (Counties north of Sør-Trøndelag), 2000-2005. Reproductions that were terminated following family removals and cub removals are also included.

Year	reproductions in southern Norway	reproductions in northern Norway
2000	10	34
2001	12	29
2002	8	22
2003	17	30
2004	26	21
2005	18	44

Table 2. Numbers of wolverines killed in depredation control programs in southern Norway (South: Counties south of and including Sør-Trøndelag) and northern Norway (North: Counties north of Sør-Trøndelag), 2000-2005 during the summer and winter seasons. Licensed hunting occurs during winter season, family and cub removal takes place during spring season, while predator control takes place during summer season. For ease of presentation, family and cub removals during spring are presented as summer figures. Family removals include the removal of an adult female with her cubs, whereas cub removals include the removal of only the cubs. In the family removal and cub removal columns the number of den sites involved is given in parentheses. The numbers of adult females in the fourth column and the numbers of sub-adults in the sixth column exclude those individuals killed within the family and/or cub removal programs.

	Family removal (during spring)		Cub removal (during spring)		License hunts (during winter) and Predator control (during summer)					
Seasonal periods of wolverines killed	Females with cubs		Cubs only		Adult female (>1yr old)		Adult male (>1yr old)		Sub-adults (≤1 yr old)	
	North	South	North	South	North	South	North	South	North	South
summer 2000	2(1)	-	-	-	1	-	2	-	7	1
winter 2000-2001	-	-	-	-	9	2	9	1	8	1
summer 2001	4(1)	6(2)	2(1)	6(2)	1	3	2	2	10	11
winter 2001-2002	-	-	-	-	3	2	3	1	5	3
summer 2002	-	-	2(1)	-	1	-	-	-	2	1
winter 2002-2003	-	-	-	-	8	1	3	2	8	3
summer 2003	2(1)	-	-	1(1)	2	-	-	1	2	5
winter 2003-2004	-	-	-	-	4	-	6	1	6	3
summer 2004	-	12(4)	2(1)	-	-	5	-	-	5	11
winter 2004-2005	-	-	-	-	2	-	2	3	5	5
summer 2005	9(3)	4(1)	-	-	3	1	2	1	9	5
total	17(6)	22(7)	6(3)	7(3)	34	14	29	12	67	49

Table 3. Explanatory variables included in the Poisson regression models explaining inter-annual lamb depredation rates. All variables, apart from "number of lambs" and "habitat", represent binary categorical covariates. "Habitat" is included in the models as a categorical covariate with three groups.

Variable	**Measures the effect of…**
number of lambs (log-transformed)	lamb availability
region (South/North)	regional differences
habitat	habitat (forest, alpine shrub land, alpine tundra)
reproduction year X_{t-1}	presence of sub-adults
reproduction year X_t	presence of adult female with cubs
reproduction year X_{t+1}	presence of adult female securing food sources for next year reproduction
cubs removal year X_t	reduced presence of cubs
family removal year X_t	reduced presence of adult female with cubs
sub-adults removed in the winter preceding grazing season of year X_t	reduced presence of sub-adults prior to the grazing season
sub-adults removed during grazing season of year X_t	reduced presence of sub-adults during the grazing season
adult females removed in the winter preceding grazing season of year X_t	reduced presence of adult females prior to the grazing season
adult females removed during grazing season of year X_t	reduced presence of adult females during the grazing season
adult males removed in the winter preceding grazing season of year X_t	reduced presence of adult males prior to the grazing season
adult males removed during grazing season of year X_t	reduced presence of adult males during the grazing season

Table 4. The relative importance of each of the explanatory variables included in the Poisson regression models explaining spatio-temporal variation in lamb depredation rates. The relative importance of each of the explanatory variable was assessed by calculating the summed AIC_c weights for each variable across the entire set of 16,384 possible models. Model averaging was used to obtain unbiased estimates and standard errors for the variables. The five variables below the dotted line had no significant effect on depredation rates. The number of best models ($\Delta AIC_c<2$) in which each variable is included is denoted in column n.

Variable	**AIC_cw**	**Est**	**SE**	**Wald**	**P**	**n**	**lower 95%**	**upper 95%**
(Intercept)	1.000	-4.740	0.837	5.666	0.000	10	-6.379	-3.100
Reproduction year X_t	1.000	0.439	0.054	8.138	0.000	10	0.333	0.545
Reproduction year X_{t+1}	1.000	0.333	0.050	6.701	0.000	10	0.236	0.431
Sub-adults removed in the winter preceding grazing season of year X_t	1.000	-0.520	0.081	6.438	0.000	10	-0.678	-0.361
Sub-adults removed during grazing season of year X_t	1.000	0.434	0.087	5.008	0.000	10	0.264	0.603
Adult females removed in the winter preceding grazing season of year X_t	1.000	0.495	0.104	4.771	0.000	10	0.292	0.699
Habitat - Shrub land†	1.000	1.312	0.279	4.695	0.000	10	0.764	1.859
Number of lambs (log-transformed)	0.996	-0.417	0.113	3.706	0.000	10	-0.638	-0.197
Adult males removed in the winter preceding grazing season of year X_t	0.998	-0.371	0.100	3.700	0.000	10	-0.568	-0.175
Habitat - Tundra†	1.000	0.861	0.264	3.259	0.001	10	0.343	1.379
Family removal year X_t	0.863	-0.259	0.125	2.065	0.039	10	-0.504	-0.013
Adult males removed during grazing season of year X_t	0.517	-0.128	0.148	0.861	0.389	5	-0.418	0.163
Cubs removal year X_t	0.419	0.065	0.101	0.639	0.523	4	-0.134	0.263
Adult females removed during grazing season of year X_t	0.375	0.054	0.105	0.517	0.605	4	-0.152	0.260
Region - South‡	0.336	0.081	0.188	0.431	0.666	2	-0.287	0.449
Reproduction year X_{t-1}	0.270	-0.004	0.034	0.112	0.911	0	-0.071	0.063

† Habitat effect is given relative to Habitat–Forest.

‡ Regional effect is given relative to Region–North.

Figure captions

Fig. 1. Overview of the registered sheep grazing areas (dark grey polygons) in northern (on the left) and southern Norway (on the right) used within the analyses on wolverine sheep depredation patterns. White polygons are the grazing areas not included in the analyses. The white dots represent wolverine reproductions between 2000 and 2005.

Fig. 2. Number of documented kills of lambs by wolverines found in forest (black), alpine shrub land (grey), or alpine tundra (white) during the development of the grazing season.

Fig. 3. Number of documented kills of lambs by wolverines and the degree of wolverine cub independence, as measured by the increasing distance between females and their cubs (after Landa *et al.* unpublished data), during the development of the grazing season.

Fig. 4. Percentage of lamb carcasses with more than two bite mark locations on their body of the total number of carcasses found with bite mark locations, as a measure of killing experience of wolverine cubs, during the development of the grazing season with (black squares and solid line; $R^2 = 0.185$) and without reproduction (white circles and dotted line, $R^2 = 0.343$).

Fig. 5. Percentage of hidden (black) and not hidden (grey) lamb carcasses of total lamb carcasses found, as a possible measure of female wolverine hoarding behaviour to secure food sources for next year's reproduction, during the development of the grazing season.

Supplementary material

Fig. S1. Overview of the percentage documented kills of lambs by wolverines (**Fig. S1.A**: data from the State Nature Inspectorate and used in the regression models), the percentage of compensated lambs of which it was assumed they were killed by wolverines (**Fig. S1.B**: data from the Directorate for Nature Management) and the percentage of lamb-losses (**Fig. S1.C**: data from NIJOS) of the total lambs released per county per year (2001: white bars, 2002: light grey, 2003: dark grey, 2004: black bars). The first six counties on the horizontal axes (i.e., Hedmark, Oppland, Buskerud, Sogn og Fjordane, Møre og Romsdal and Sør-Trøndelag) are the counties where wolverine depredation occurred in southern Norway. The last four counties (i.e., Nord-Trøndelag, Nordland, Troms and Finmark) are the counties where wolverine depredation occurred in northern Norway.

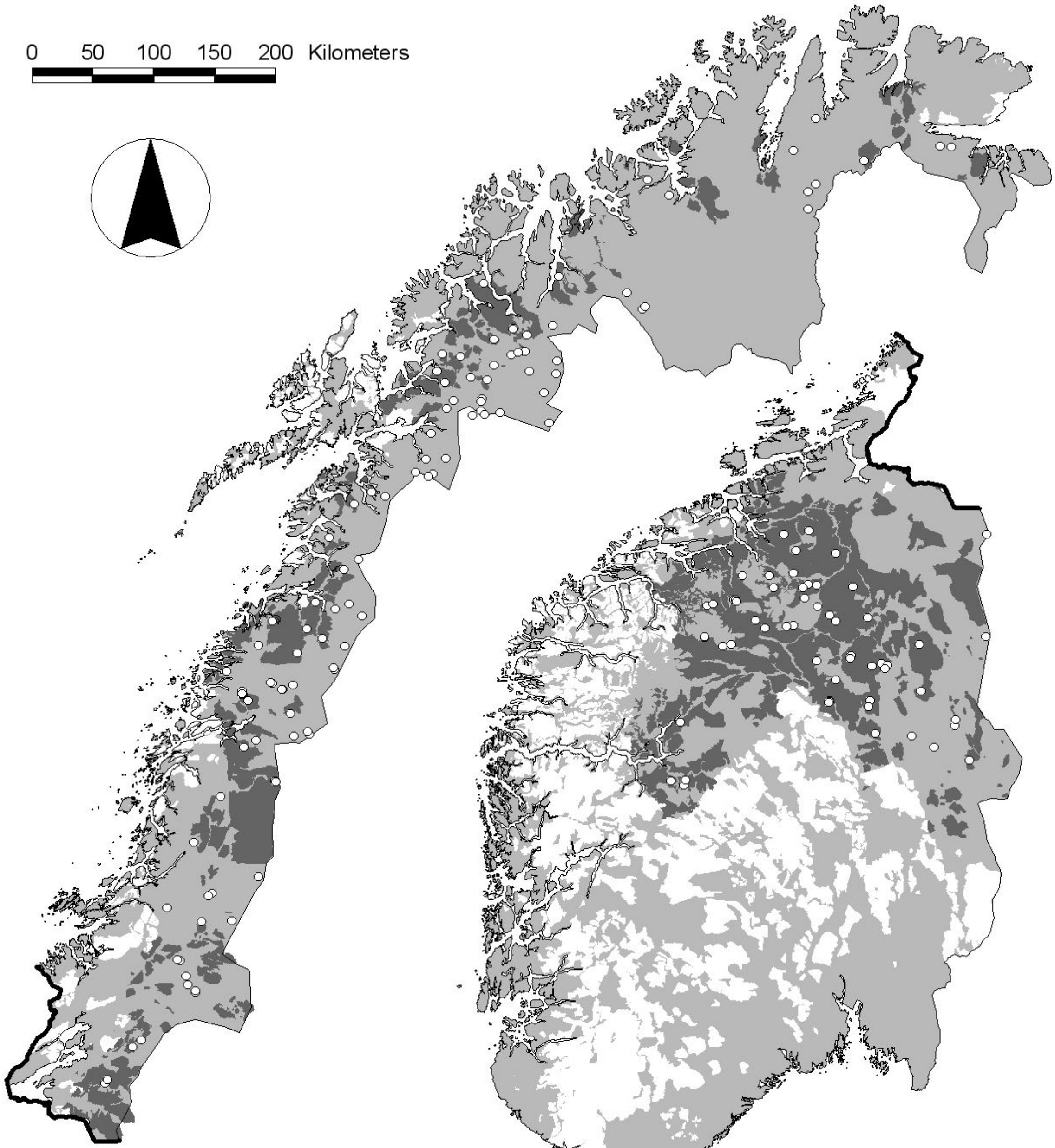
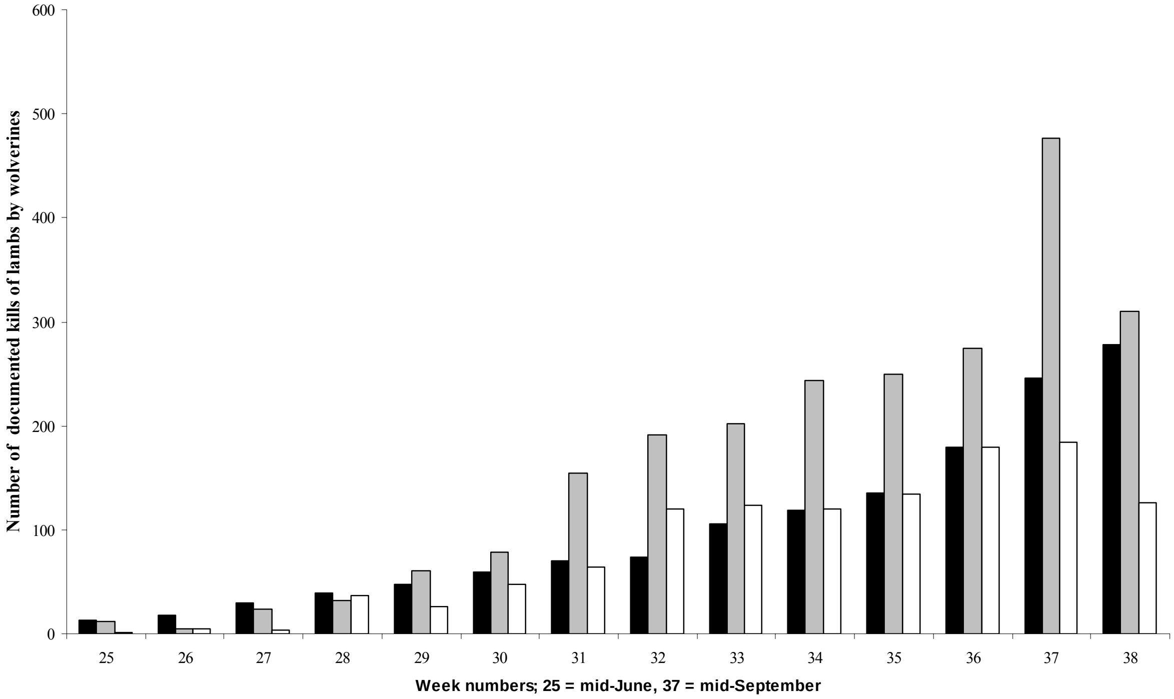


Fig. 1.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Number of documented kills of lambs by wolverines
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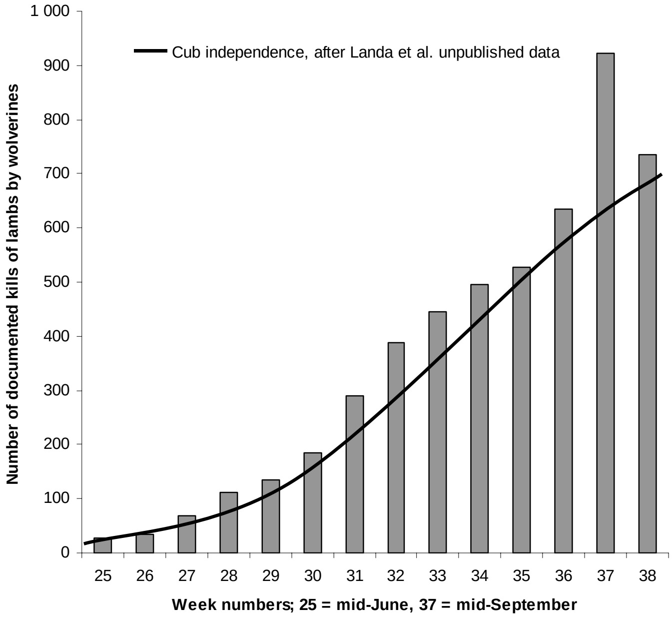
Week numbers; 25 = mid-June, 37 = mid-September

Fig. 2.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Number of documented kills of lambs by wolverines
Cub independence, after Landa et al. unpublished data
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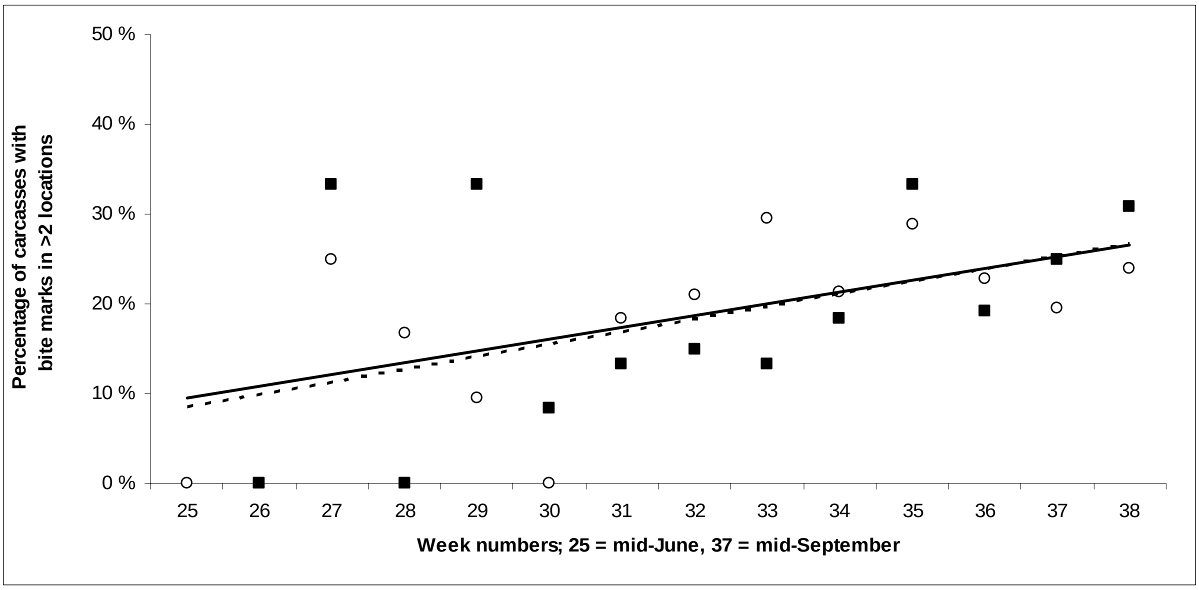
Week numbers; 25 = mid-June, 37 = mid-September

Fig. 3.


Percentage of carcasses with bite marks in >2 locations
50 %
40 %
30 %
20 %
10 %
0 %
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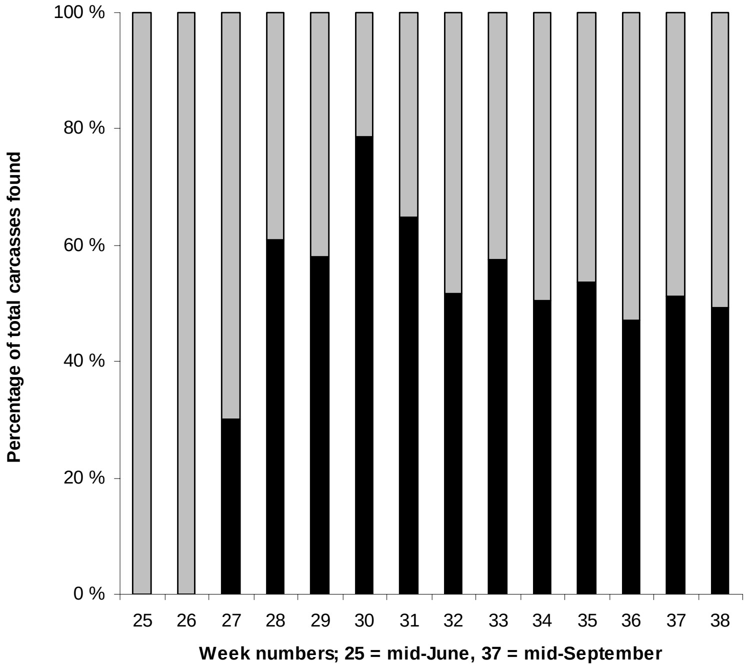
Week numbers; 25 = mid-June, 37 = mid-September

Fig. 4.


100 %
80 %
60 %
40 %
20 %
0 %
Percentage of total carcasses found
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Week numbers; 25 = mid-June, 37 = mid-September

Fig. 5.

Supplementary material

Fig. S1.A: data from the State Nature Inspectorate and used in the Poisson regression models

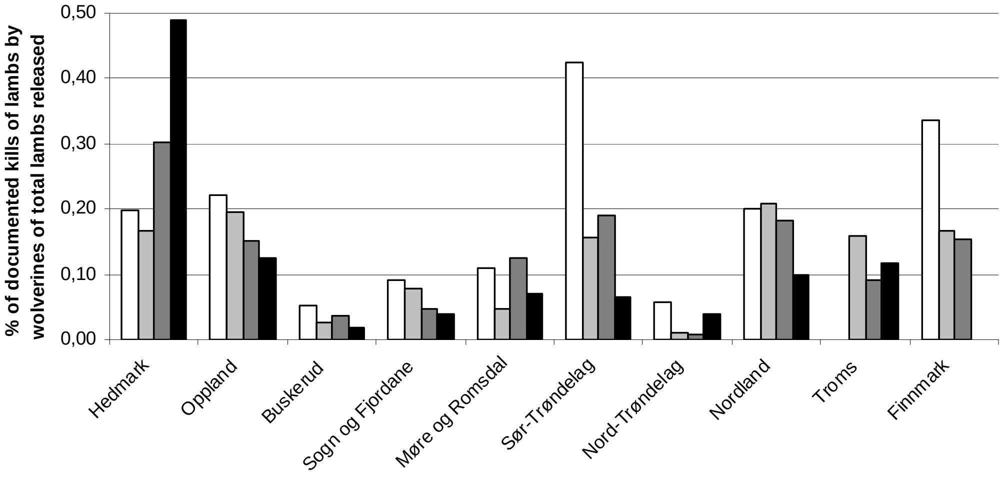


Fig. S1.B: data from the Directorate for Nature Management

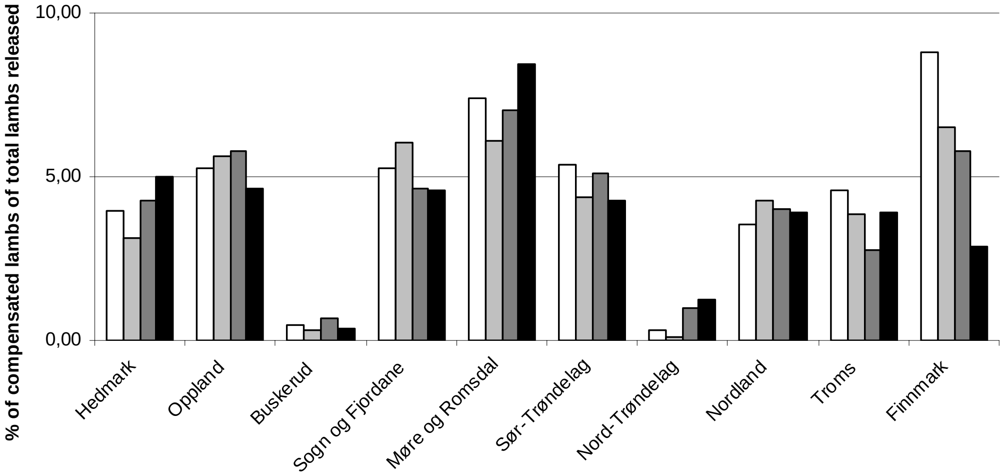
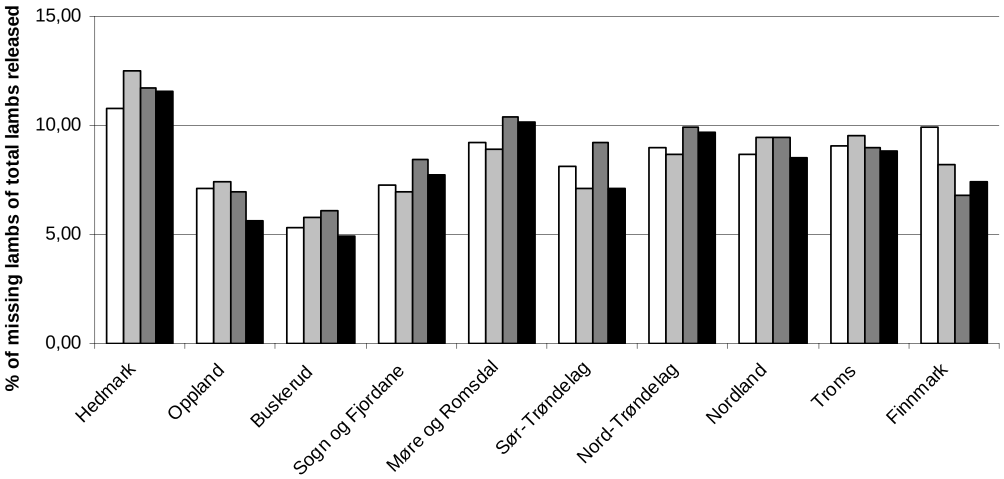


Fig. S1.C: data from NIJOS



Supplementary Fig. S1. Overview of the percentage documented kills of lambs by wolverines (**Fig. S1.A**: data from the State Nature Inspectorate and used in the regression models), the percentage of compensated lambs of which it was assumed they were killed by wolverines (**Fig. S1.B**: data from the Directorate for Nature Management) and the percentage of lamb-losses (**Fig. S1.C**: data from NIJOS) of the total lambs released per county per year (2001: white bars, 2002: light grey, 2003: dark grey, 2004: black bars). The first six counties on the horizontal axes (i.e., Hedmark, Oppland, Buskerud, Sogn og Fjordane, Møre og Romsdal and Sør-Trøndelag) are the counties where wolverine depredation occurred in southern Norway. The last four counties (i.e., Nord-Trøndelag, Nordland, Troms and Finmark) are the counties where wolverine depredation occurred in northern Norway.