

Wolverines in a Changing World

Final report of the Norwegian Wolverine Project 2003-2007

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Norwegian Institute for Nature Research

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**Final report of the Norwegian Wolverine
Project 2003-2007**

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Abstract

May, R., Dijk, J. van, Andersen, R. & Landa, A. 2008. Wolverines in a Changing World. Final report of the Norwegian Wolverine Project 2003-2007. – NINA Report 434. 43 pp.

In 2003 the Norwegian Wolverine Project “Wolverines in a Changing World” was initiated with the principle objective to gain a better insight in the ecological role wolverines *Gulo gulo* have in ecosystem dynamics and their adaptation to multiple-use landscapes. This knowledge is important with respect to achieving the goals of viable and inter-connected wolverine populations, while minimizing conflicts with human interests. The project consisted of two parts; one part focussed on foraging strategies and the other part focussed on spatial ecology. The study area was situated in southern Norway with special focus on Østerdalen where wolverines are sympatric with other large carnivores (i.e., wolf *Canis lupus*, Lynx *lynx lynx* and brown bear *Ursus arctos*), and the Snøhetta plateau in relation to our studies on wolverine-sheep conflicts. During the project period (2003-2007) a total of 56 different individuals were captured (13 adults and 43 cubs), mostly at secondary den sites. All adults and 11 cubs were instrumented with GPS collars and/or VHF implants.

With regard to the study on foraging strategies, wolverine diet inside and outside wolf territories were compared to see if wolverine diet shifted towards moose *Alces alces* (as main prey species for the wolf in this area) in the presence of wolves. As expected, we found that wolverine diet contained more moose and less reindeer *Rangifer tarandus* and small prey species (i.e., rodents and insectivores, birds and mountain hare *Lepus timidus*) in the presence of wolves. Apparently wolves increase scavenging opportunities for wolverines and the recolonization of wolves during the late nineties might therefore have contributed to the consequent recolonization of wolverine into the same area a few years later.

The study where we followed wolverine tracks in the snow revealed that in the area where wolverines are sympatric with wolves, wolverines were more active at higher elevations whereas the probability of encountering a wolf trail was higher at lower elevations. This suggests a spatial separation between wolverines and wolves. Wolverines only moved down into the forest to scavenge on relatively old wolf-killed moose carcasses (i.e., > 2 weeks old) during the winter season. Although wolverines seem to depend on wolf for carrion during winter, they did not use wolf trails to find carcasses. The use of higher elevations and the use of relative old wolf-killed moose carcasses indicate that wolverines reduce risk of intra-guild predation by avoiding direct confrontation with wolves.

Wolverine depredation on sheep *Ovis aries* is a dominant foraging strategy known in the higher alpine habitat where livestock are grazed unprotected. However the observed variation in lamb depredation rates between years and between sheep grazing areas has never been clarified. When analyzing the spatio-temporal variation in lamb depredation rates within sheep grazing areas we found that not only reproductive events resulted in higher depredation rates but also the removal of adult female wolverines during the winter preceding the grazing season increased depredation rates. The removal of a resident adult female may result in a temporal demographic instability with the establishment of neighbouring or new individuals in the area which likely enhances depredation rates. Also a reproductive event in an area implies that not only the female, but also her cubs, the father of the cubs (mating season, maternal care and grazing season overlap with each other) and sub-adults from previous litters are around. This locally and temporarily higher wolverine density also increases depredation rates.

Overall losses to wolverines based on long-term data indicate that male lambs are more prone to predation than females later in the season. A behavioural study revealed that although no differences were found in ewe-lamb distance or locomotor activity in gender, female lambs synchronized their behaviour more with their mother than males. Only for female lambs, increased synchrony resulted in closer ewe-lamb distances. Male lambs can therefore be ex-

pected to be more prone to wolverine predation towards the end of the season, when lambs become independent from the ewe.

For the study on spatial ecology of wolverines, habitat preferences and potential for sympatry of wolverines with wolf, lynx and brown bears was analyzed in Østerdalen, Hedmark County. Whereas the presence of wolves, lynx and brown bears was generally associated with rugged, forested areas at lower elevations, wolverines selected open, rugged terrain at higher elevations. Although nearly one third of the study area was suitable for sympatry of the three forest carnivore species (wolf, lynx and brown bear), only 1% was suitable for all four species. In all, sympatry of the wolverine with the three forest-dwelling carnivore species appears to depend on the availability of mountain ranges as a spatial refuge, combined with the presence of wolves at lower elevations to provide scavenging opportunities. 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.

Based on VHF data obtained from radio-marked individuals on the Snøhetta plateau (southern Norway, wolverine project 1990-1995) and in Troms (northern Norway, wolverine project 1996-2002), wolverines were shown to locate their home ranges away from human disturbance (undeveloped alpine tundra). However within their home ranges, wolverines preferred to use alpine shrub land and forest. We found that habitat selectivity in developed habitats was low, indicating that infrastructure and not habitat was the primary factor for home range location.

Reproducing female wolverines are faced with a continuous, but diminishing, trade-off between providing protection for their dependent cubs and being away searching for food. We investigated the spatio-temporal ranging behaviour of seven reproductive female wolverines in south-central Norway, based on GPS data collected in 2002-2005. Their spatio-temporal ranging behaviour showed a gradual change from a central-place foraging to a more optimal foraging movement pattern. Female wolverines were most active during the night when they preferred to forage in lower-lying patches within the forest-alpine tundra ecotone. As the summer season proceeded, their preference for lower-lying patches increased. It seems that wolverines utilize the forest–alpine tundra ecotone for foraging, where a high abundance of prey could well represent the patches with the highest expected profitability. Reproducing wolverines cope with the trade-off by selecting higher terrain at first, when cubs are placed at rendezvous sites, and moving downhill as cubs grow more mobile and independent.

To study the activity patterns in reproductive females in more detail, we recorded activity patterns and food caching habits of wolverine females through intensive radio-tracking and carcass trials. We found that in the parturition and weaning period, female wolverines relied on food caches and spent most of their time together with the cubs. At this time, denning females had a nocturnal daily activity pattern. After den abandonment, the cubs' continuously increasing ability to accompany the mother optimizes growth, foraging skills, and independence in the cubs. Over the rearing period, the intervening distances between mother and offspring increased significantly and by September, cubs were nearly full-grown and nutritionally independent from their mother. Over the rearing period depredation on domestic sheep had a high positive correlation with proportion of cubs separated from their mother. Insight into maternal care and activity patterns of family groups may provide valuable information for management.

Reproductive den sites in southern Norway were visited to monitor fine-scale spatial characteristics. At the site-specific scale, den sites were associated with steep, rugged terrain with bare rock. At the home-range and landscape scale, den sites were placed in rugged terrain at 1,000 meters above sea level and away from infrastructure. At all spatial scales, the overall ruggedness or steepness of the terrain appeared to be an important feature for den sites. Steep and rugged terrain enables wolverines to dig out den sites in snowdrifts. It is also possible that steep and rugged terrain, especially when placed farther from human infrastructure, is perceived as providing security from humans. Recurrent use of specific topographic features may

provide valuable information for directing monitoring efforts, protecting denning localities from unnecessary human disturbance, and augmenting endangered wolverine populations.

The overall conclusion of the project “Wolverines in a Changing World” is that given the large areas of continuous habitat that are required by wolverines, 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 their spatial requirements and their foraging strategies, while aiming to minimize livestock depredation conflicts. Therefore successful conservation of wolverines can be achieved by seeking a balance between local social acceptance, management practices and biological processes.

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Sammendrag

May, R., Dijk, J. van, Andersen, R. & Landa, A. 2008. Jerven – og en verden i endring. Sluttrapport for Det norske jervprosjektet 2003-2007. – NINA Rapport 434. 43 s.

Det norske jervprosjektet "Jerven – og en verden i endring" ble startet i 2003. Prosjektets formål var å framskaffe en bedre innsikt i den økologiske rollen jerven *Gulo gulo* spiller i forhold til dynamikken i økosystemet og dens tilpasningsevne til flerbrukslandskapet. Slik kunnskap er viktig med hensyn til å oppnå målsetningene omkring levedyktige jervepopulasjoner med god utveksling mellom populasjonene, samtidig som en kan minimalisere konfliktene til beiteinteresser. Prosjektet besto av to deler; en del fokuserte på furasjeringsstrategier og den andre på jervens romlige økologi. Studieområdene var Sør-Norge, med en spesiell fokus på Østerdalen der jerven forekommer sammen med andre store rovdyr (dvs. ulv *Canis lupus*, gaupe *Lynx lynx* og bjørn *Ursus arctos*), og Snøhetta-området for studier omkring konflikten mellom jerv og sau. I løpet av prosjektperioden (2003-2007) ble totalt 56 ulike individer fanget (13 voksne og 43 unger), de fleste av disse i sekundærhi. Alle voksne og 11 av ungene ble instrumentert med GPS-halssendere og/eller implanterte VHF-sendere.

I studiet av næringsstrategier ble det gjort sammenligninger av jervens diett innenfor og utenfor ulveterritorier. Målet var å se om jervens diett endret seg til mer elg *Alces alces* (som er hovedbyttet for ulven i området) når det fantes ulv i området. Som forventet fant vi at jervens diett inneholdt mer elg og mindre rein *Rangifer tarandus* og små byttedyr (dvs. smånagere og insekter, fugler og hare *Lepus timidus*) der ulv var nærværende. Ulven øker øyensynlig jervens tilgang på kadavre, og ulvens reetablering i løpet av slutten av 1900-tallet kan derfor ha bidratt til den etterfølgende reetablering av jerv noen år senere innenfor det samme området.

I områder der både jerv og ulv forekom, observerte vi ved snøsporing at jerven var mer aktiv i høyereliggende områder, samtidig som sjansen til å finne ulvespor økte i de lavereliggende områdene. Dette antyder en romlig separering mellom jerv og ulv. Jerv beveger seg bare ned i skogen for å ernære seg på relativt gamle ulvedrepte elgkadavre (dvs. > 2 uker gamle) under vinterhalvåret. Selv om jerven synes å være avhengig av ulv for å få tilgang på kadavre om vinteren, så benyttet de seg ikke av ulvesporene for å finne kadavrene. Jerven synes å redusere risikoen for direkte konfrontasjoner med ulv, og dermed den interne predasjonen mellom de to artene, ved at de benytter høyereliggende deler av terrenget og bare eldre ulvedrepte elgkadavre.

I høyereliggende alpine områder, der buskap beiter uten beskyttelse, er tap av sau *Ovis aries* til jerv så vanlig at det utgjør en dominerende furasjeringsstrategi for jerven. Likevel har en ikke kunnet forklare den observerte variasjonen i tapsfrekvensen av lam mellom ulike år og beiteområder. Ved å analysere den romlige og tidsmessige variasjonen i tap av lam innenfor områder med sauebeite, fant vi at høye tapsrater ikke bare var relatert til reproduksjon hos jerven, men at beitesesonger med økt predasjonsrate også kunne være påvirket av at voksne hunnjerver var fjernet i løpet av den foregående vinteren. Uttak av voksne stedegne hunnjerver kan forårsake en midlertidig demografisk ustabilitet ved etablering av nabo- eller nye individer i området, noe som sannsynligvis vil forandre predasjonsraten. En reproduksjon i et område medfører at ikke bare er hunnen tilstede, men også hennes avkom, faren til avkommet, og ungdyr fra tidligere kull. Siden tidspunktene for paring og foreldrepass hos jerven overlapper med beitesesongen for sau, fører også lokal og temporær høyere jervetetthet til økt predasjonsrate på sau.

Langsiktige data over tap av sau til jerv indikerer at værlam er mer utsatt for predasjon enn søyelam på slutten av beitesesongen. En atferdsstudie har avdekket at selv om det ikke ble funnet noen forskjell relatert til lammenes kjønn når det gjelder bevegelsesaktivitet eller avstand mellom søya og lammene, så synkroniserte søyelammene sin bevegelsesatferd mer med mora enn værlammene. Økt synkronitet resulterte i en mindre avstand mellom søye og

søyelam. Derfor kan en anta at værlam er mer utsatt for jervepredasjon mot slutten av sesongen, på det tidspunktet når lammene blir uavhengige av mora.

I studiet av den romlige økologien til jervene, ble habitatpreferanser og potensielle overlapp av jerv med ulv, gaupe og bjørn studert i Østerdalen, Hedmark fylke. Mens tilstedeværelsen av ulv, gaupe og bjørn generelt var knyttet til lavereliggende, kupert skogsterreng, så foretrakk jerven mer høyereliggende, åpent og kupert terreng. Selv om 1/3-del av studieområdet var egnet for alle de tre skogtilknyttete rovdyrene, var bare 1 % egnet for alle fire artene. Alt i alt synes sameksistens mellom jerv og de tre skoglevende rovdyrene å være avhengig av tilgang på spredte fjellrefuger i kombinasjon med nærvær av ulv som gir kadavermuligheter innenfor lavereliggende arealer. Når en skal forklare de nåværende utbredelsene, habitatpreferansene og forskjellene i disse mellom de store skandinaviske rovdyrene, må en imidlertid ikke underestimere betydningen av den historiske forvaltningen og rollen mennesket har spilt som en toppredator i disse flerbruksøkosystemene.

På bakgrunn av VHF-data fra radiomerkete individer fra Snøhetta-området (Sør-Norge, Jervprosjektet 1990-1995) og i indre Troms (Nord-Norge, Jervprosjektet 1996-2002) viste det seg at jerven plasserte sitt leveområde i ubebygde alpin tundra lengst borte fra menneskelige forstyrrelser. Innenfor sitt leveområde foretrekker jerven den alpine busk- og skogsonen. I mer bebygde habitater var det ingen tydelig preferanse til spesielle habitater; trolig var det infrastrukturen og ikke habitattypene som var den primære faktoren for lokalisering av leveområde innenfor disse arealene.

Reproduserende jervetisper står overfor en konstant, men avtakende avveining mellom å beskytte sine hjelpeløse unger og det å være borte på næringssøk. Vi studerte bevegelsesatferden i tid og rom til sju reproduserende tisper i sørlige og sentrale deler av Norge på bakgrunn av innsamlete GPS-data fra 2002-2005. Deres bevegelsesatferd viste en gradvis forandring fra en jaktatferd som er konsentrert til nærområdene rundt hiet til et mer optimalt bevegelsesmønster under jakta. Hunnjervene var mest aktive om natta når de jaktet innenfor den lavereliggende overgangssonen mellom tundra og skog. Deres preferanse til de lavereliggende områdene økte etter som sommeren skred fram. Jervene ser ut til å utnytte disse lavereliggende alpine og subalpine arealene til matsøk. Dette er arealer med en høy tetthet av byttedyr, og som dermed meget godt kan representere de delområdene innenfor deres jaktterreng som har størst forventet lønnsomhet. Reproduserende tisper takler avveilingen ved å velge det høyereliggende terrenget når ungene ennå er plassert i dagleier, mens de vandrer nedover i terrenget ettersom ungene vokser til og blir mer mobile og uavhengige.

Gjennom intensiv oppfølging av radiomerkede tisper og kadaverundersøkelser studerte vi i mer detalj aktivitetsmønstre og matforrådsvaner til reproduserende tisper. Vi fant at under fødsels- og avvenningsperioden stolte hunnene på sine matforråd og benyttet mesteparten av sin tid sammen med ungene. På dette tidspunktet hadde tisper med hi et nattlig aktivitetsmønster. Etter at hiet blir forlatt øker ungenes evne til å følge moren, noe som optimaliserer deres vekst, jaktdyktighet og uavhengighet. I løpet av oppfostringsperioden øker avstanden mellom mor og avkom signifikant, og i september er ungene blitt nesten fullt utvokste og er ikke lengre avhengige av at mora finner mat til dem. Under denne tiden er det en høy positiv korrelasjon mellom predasjonen på sau og andelen av unger som er separert fra sin mor. Innsikt i mødrepass og familiegruppers aktivitetsmønstre kan derfor bidra med verdifull informasjon til forvaltningen.

I Sør-Norge ble dokumenterte hiplasser hvor det hadde vært reproduksjon undersøkt for å belyse romlige egenskaper. På den stedsspesifikke skalaen var hiene assosiert med bratt, kupert terreng med bar fjellgrunn. På leveområde- og landskapsskala var hiene plassert i kupert terreng 1000 meter over havet og langt unna infrastruktur. Kuperthet og bratthet i terrenget syntes generelt å være et viktig kjennetegn for hilokalitetene på alle skalaene. I slikt terreng kan jerven grave ut hiplasser i snøfonner. Det er også mulig at denne terrengetypen, spesielt når den finnes langt fra menneskelige infrastruktur, blir oppfattet som å gi beskyttelse fra mennesker. Denne type informasjon over spesifikke topografiske egenskaper for hilokaliteter kan gi nyttig

informasjon til å styre overvåkningsinnsatsen samt å beskytte hiområder fra unødvendig menneskelig forstyrrelse.

Jerven krever store arealer med sammenhengende habitater, og hovedkonklusjonen fra prosjektet "Jerven - og en verden i endring" er at en vellykket forvaltning bare er mulig dersom vi lykkes i reell integrering av jerven i flerbrukslandskapet. Dette kan oppnås ved å bruke vår kunnskap om jervens romlige krav og dens næringsstrategier, samtidig som en søker å minimalisere konfliktene i forhold til tap av bufe.

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Foreword

In the new Red List the wolverine has received the status of endangered species in Norway. Causes for this were its biology, distribution and low numbers. At the same time the wolverine is responsible for the biggest challenges regarding damages to and compensation for loss of sheep (lambs) and semi-domestic reindeer in Norway. Disbursement of compensation for wolverine damages has in many years, and is still today, as large as the damages to wolf, brown bear and lynx together. Management has reacted to these challenges with a strong population regulation with the use of licensed hunting and damage control permits, together with extraordinary removal of females with cubs at their den site. This way of managing an endangered species puts extra demand for knowledge; not just concerning numbers, but also knowledge on demographic effects of removal and effects of removal on reduction of damages to livestock. A long-term conservation depends also on good insight into the ecological role wolverines play in coexistence with other carnivores and especially its ability to adjust to our use of and the changes we inflict on wolverine habitat.

This report summarizes the project “Wolverines in a Changing World” which focused on the problems mentioned above. The results give a great advance in the knowledge on the ecological role of wolverines, their habitat requirements, and losses to livestock and effects of removal of wolverines. The results show that interactions with other carnivores, especially the wolf, are of importance for the possibility of wolverines to re-establish in the vicinity to forest areas. The studies on wolverine foraging and diet, daily activity and spatial habitat use have shown that this species is more vulnerable than the other large carnivores given its need for mountain and forest areas with little human influence and activity. The wolverine prefers shrub vegetation and forest landscapes with little human activity. Also the placement of den sites seems to be affected by the proximity to human infrastructure and activity. Removal of wolverines through hunting or control permits affects the composition of the wolverine population and spatio-temporal use of areas and by this also concentration and temporal changes in livestock damages. Damages to sheep appear to be related to wolverine density in an area. Removal of resident females may create a territorial instability which on the short-term leads to more wolverines and increased losses of sheep. Similarly reproduction may result in a locally higher concentration of wolverines. This indicates that removal of older and resident individuals should be avoided as management measure and that management might need to prioritize a more thorough analysis of removal and its effect on reduced losses. In this way removal can be directed at those categories of individuals that give the most reduction in damages and through this also increased social acceptance for the conservation of the wolverine.

The project has so far been the foundation for two PhD studies and five MSc studies. To day 13 scientific publications, five technical reports, 23 popular articles/media and 18 scientific posters/presentations have been emitted from the project.

Trondheim, 26th of August 2008

Arild Landa
(project leader)

1 Introduction

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 (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 (Cardillo *et al.*, 2004; Crooks & Soulé, 1999; Purvis *et al.*, 2000; Sunquist & Sunquist, 2001), 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.

In Europe, wolverine present fragmented distribution is limited to the central and northern parts of Norway, Sweden and Finland. Within their geographic range, wolverines occupy a variety of habitats (Pasitschniak-Arts & Larivière, 1995). General characteristics of wolverines are their large area requirements, low densities and remoteness from human development (Landa, Lindén & Kojola, 2000; Sunquist *et al.*, 2001). Given their extensive habitat needs and the continuing encroachment of human activity on wilderness areas, provision of adequate habitat has to be realized while integrating wolverines in multiple-use landscapes. However wolverines are increasingly involved in conflicts with man because of their depredation on semi-domestic reindeer *Rangifer tarandus* throughout the year in Fennoscandia, and on free-ranging domestic sheep *Ovis aries* during summer in Norway. Wolverine depredation on livestock has been one of the main reasons for their control, and historical population decline in Fennoscandia. Integrating wolverines in multiple-use landscapes can therefore only be realized while minimizing conflicts with humans.

Wolverines rely on a varied prey base and benefit from other large carnivores that provide carrion (Magoun, 1987). However, the exact nature of wolverine interactions with other large carnivores requires further study. It is important to illustrate the possibilities for co-existence of large carnivores and possibilities for zoning of large carnivores to minimise depredation conflicts and enable an integrated management of the natural environment. Wolverine are known to inhabit inaccessible areas away from human development (Landa *et al.*, 2000; Sunquist *et al.*, 2001) but our knowledge of wolverine habitat requirements and their adaptability to multiple-use landscapes is however poorly documented and need further investigation.

The principal objective of this project was to gain a better insight in the ecological role wolverines have in ecosystem dynamics and their adaptation to multiple-use landscapes. This information is important if management is to achieve the goals of maintaining viable and interconnected wolverine populations. The principal objective was achieved by focussing on the following two research aims.

- Investigate wolverine foraging strategies in a multiple-use landscape; both with regard to co-existence of large carnivores and depredation conflicts.
- Investigate habitat requirements of wolverines and the impact of landscape structure to predict the availability of suitable habitat for wolverines in Scandinavia.

In 2003 NINA's Norwegian Wolverine Project initiated the project entitled "*Wolverines in a Changing World*" which was completed in 2007. The project was financed by the Norwegian Research Council (NFR), Norwegian Directorate for Nature Management (DN), NINA, several Norwegian counties and private funds (e.g., Sparebank-1 Midt-Norge, Alertis-fund for bear and nature conservation). Here, we report the findings from this project.

2 Material and methods

Wolverines have a wide distribution in southern Norway, but to allow for logistics it was necessary to limit the area of our activities. Within our study area we prioritized our capturing and instrumentation based on the different objectives of the project. The most relevant areas lay in the boreal forested landscapes of Østerdalen and on alpine tundra habitats of the Snøhetta plateau.

2.1 Study areas

The study areas chosen for the different studies varied from a study area in Østerdalen where wolverines are sympatric with wolves to the entire wolverine distribution in Norway. The main study area, however, was located in south-central Norway (62°N 9°E). This area encloses many different ecological conditions, from remote mountainous areas in the west and centre where high densities of free-ranging sheep graze unattended in their summer pastures (June – September) to more accessible forest areas in the east where wolverines are sympatric with wolves, lynx and brown bears. In the mountainous regions some of the largest remaining European populations of wild reindeer are found. In the north-eastern part of the study area, herding of semi-domestic reindeer is practised. The habitat in the mountain ranges consist of mountain plateaus with peaks up to 2,286 m with bare rock (high alpine zone down to 1,800 m), which give way to alpine tundra with heath (e.g., heather, crowberry) and lichen vegetations (midalpine zone down to 1,400 m). At lower elevations, alpine shrub land (e.g., willow, dwarf birch) can be found down towards the treeline at 900 – 1,000 m (low alpine zone). From the treeline downwards, forests are comprised of mountain birch, Norway spruce and Scots pine with a varied undercover (e.g., blueberry, grasses, mosses) (subalpine zone). The low alpine zone and the sub-alpine zone form the forest– alpine tundra ecotone (Grytnes, 2003). The mountain ranges are divided by steep valleys. The forest region is mostly characterized by hills or lower mountains up to 1,200 m and wider valleys. In the study area, snow is present from October/November until May/June depending on elevation. Human infrastructure is mainly concentrated at lower elevations in the valley bottoms. Recreational cabins can be found at higher elevations as well. Activities may consist of hunting, hiking and camping, and cross-country skiing.

Parts of the project were also based on radio-tracking and denning activity data collected in Troms County in northern Norway (68°N 19°E), with some additional data on denning activity from Sarek, northern Sweden (67°N 17°E). The landscape, habitats, and climate of the northern areas are broadly similar to the south-central Norway, except that treeline is lower (600 – 700 m) and climate is more continental. In addition, lynx, which are a major predator of semi-domestic reindeer, and brown bears, which can occasionally kill moose *Alces alces* and reindeer, are present in both northern areas, but occur at higher densities in Sarek.

For our study on sheep depredation, all registered sheep grazing areas in Norway which either overlapped with wolverine distribution, or for which wolverine predation on sheep had been documented between 2000 and 2005, were used. Sheep grazing areas are found throughout Norway, but sheep grazing is especially intensive in south-western Norway.

2.2 Wolverine capture and instrumentation

Capture and instrumentation of wolverines was carried out with permits from the Norwegian Directorate for Nature Management (DN), the Committee for Animal Experiments (FDU) and the Norwegian Post and Telecommunications authority (Post- og teletilsynet; permits for use of radio frequencies). Throughout the project we were allowed to capture and instrument a maximum of nine adult wolverines and five cubs per year. In addition a maximum of 20 cubs per year could be captured in order to collect tissue samples for DNA-analyses. Capturing, handling and instrumentation followed the "*Biomedical Protocol for Free-ranging Wolverines (Gulo gulo) in Scandinavia*".

Wolverines were captured using live-traps and captured at secondary den sites. We also recaptured animals in June with use of helicopter. The live-traps were placed at locations with regular wolverine activity, and were fitted with an alarm system and checked by local personnel. Capture at secondary den sites was done in spring (April – May), after the family group had left the primary (natal) den site. These sites were located as part of the on-going large carnivore monitoring programme which was conducted by the staff of the Norwegian Nature Inspectorate (SNO). Placement of live-traps and use of snow scooter or helicopter were all according to permits given to us by municipalities and local landowners. The use of snow scooter and helicopter was minimized in order to avoid unnecessary disturbance of other mountain species (e.g., wild reindeer during calving).

Between 2003 and 2005 caught individuals were implanted with a VHF radio transmitter, which allowed for localisation of these animals throughout their life. In 2003 and 2004 cubs were implanted with special cub-implant transmitters at the den site; in 2005 cubs were only implanted during recapture in June. From 2006 and onwards, no animals (both adults and cubs) were implanted. In order to get a better insight into the precise movement patterns of wolverines, adults were equipped with a GPS radio-collar. Between 2003 and 2005 GPS radio-collars were used in addition to the implanted radio transmitters, but from 2006 adults were only equipped with GPS-collars. These collars provide up to 7-15 positions a day, but have a life span of only 5 months after which they automatically dropped off the animal. After drop-off an internal VHF system is activated to enable relocation of the collar.

During the project period (2003-2007) a total of 56 different individuals have been captured. In 2002, 3 different individuals have been captured and included in the project as well (Figure 1). In Figure 2 the geographic distribution can be seen. Fourteen adult wolverines have been captured (2 males and 12 reproducing females) and equipped with GPS-collars. Four of these were captured several times. In total 45 cubs have been captured at secondary dens (20 males and 22 females) of which 11 have received a VHF implant radio transmitter (6 males and 5 females). All cubs and adults were ID-marked by taking a small DNA tissue sample from their ear.



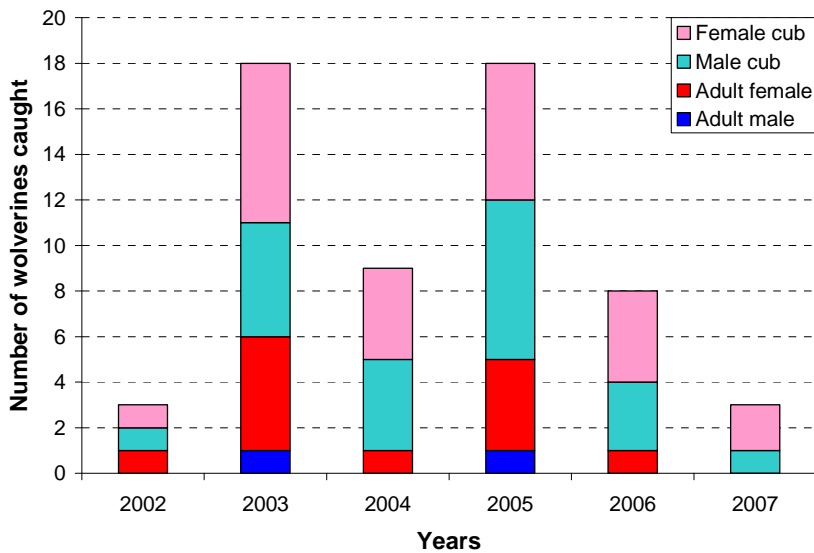


Figure 1. Number of captured individuals over the years.

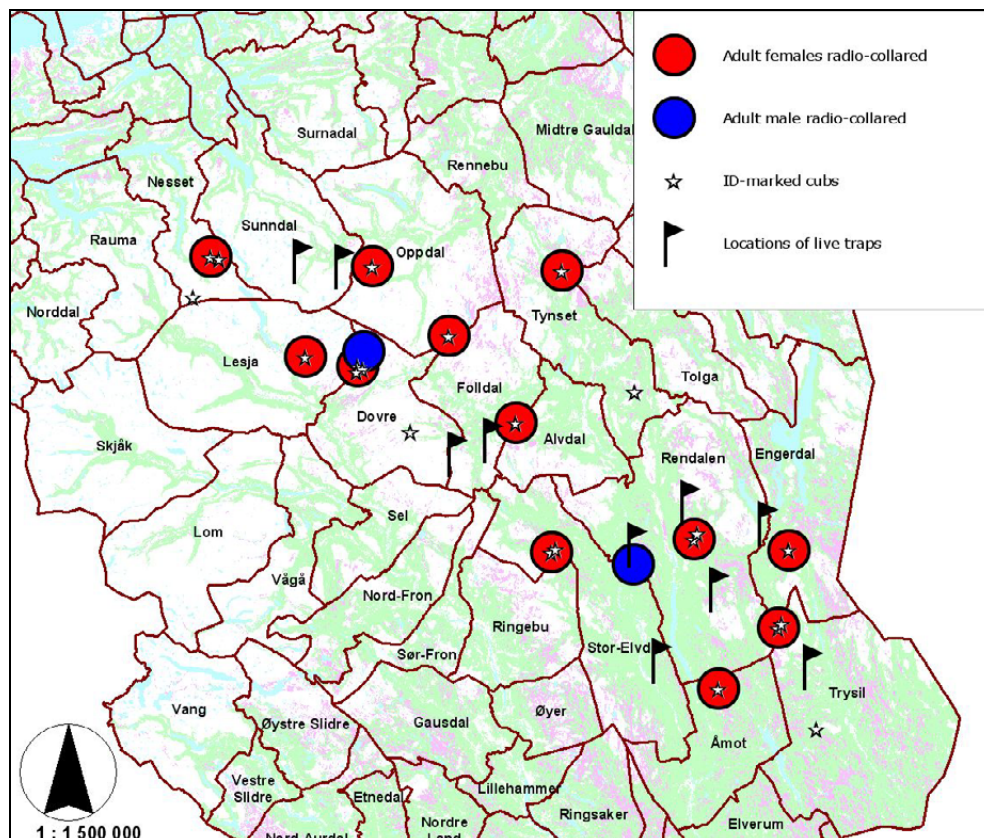


Figure 2. Locations of the capture and instrumentation during the project period.

We have actively followed the status of the animals over the years; however most of the individuals (17 males and 19 females) which are not confirmed dead have an unknown status (Table 1). At the end of the project period 16 of the 59 animals have been confirmed dead (3 males and 13 females). Twelve of these died due to various wolverine control measures: eight were shot during the license hunt during winter (2 males and 6 females), to (1 male and 1 female) were shot following damage control permits, and two (1 adult female and 1 female cub) were killed at their den site as control measure (removal family group). Four additional animals died of other causes (2 females by accident and 2 females most likely killed by wolves).

Table 1. Status of captured wolverines in southern Norway, spring 2008.

ID	Age at capture	Sex	Municipality	Type marking	Status
S14-02 ¹	Cub	M	Dovre	ID/VHF	uncertain
S15-02 ¹	Cub	F	Dovre	ID	died a few days after marking
S16-02 ¹	Adult	F	Dovre	ID/VHF/GPS	alive, DNA March 2006
S17-03	Adult	F	Rendalen	ID/VHF/GPS	uncertain, DNA March 2006
S18-03	Cub	F	Rendalen	ID/VHF	uncertain, DNA March 2007
S19-03	Adult	F	Oppdal	ID/VHF/GPS	uncertain
S20-03	Cub	M	Oppdal	ID/VHF	shot; license hunt 2004/2005
S21-03	Cub	F	Oppdal	ID/VHF	shot; damage control permit 2003
S22-03	Adult	F	Åmot	ID/VHF/GPS	killed by wolves
S23-03	Cub	F	Åmot	ID/VHF	killed by wolves
S24-03	Cub	M	Åmot	ID/VHF	uncertain
S25-03	Cub	M	Åmot	ID	uncertain, DNA April 2006
S26-03	Adult	F	Stor-Elvdal	ID/VHF/GPS	alive, DNA June 2007
S27-03	Cub	F	Stor-Elvdal	ID	accident; put down 2003
S28-03	Cub	M	Stor-Elvdal	ID	uncertain, DNA April 2005
S29-03	Adult	F	Oppdal	ID/VHF/GPS	shot; license hunt 2003/2004
S30-03	Cub	F	Oppdal	ID	uncertain, DNA April 2004
S31-03	Cub	M	Oppdal	ID	shot; damage control permit 2003
S32-03	Cub	F	Dovre	ID	shot; license hunt 2004/2005
S33-03	Cub	F	Dovre	ID	uncertain
S34-03	Adult	M	Stor-Elvdal	ID/VHF/GPS	uncertain, DNA March 2007
S35-04	Cub	M	Rendalen	ID	uncertain, DNA March 2007
S36-04	Cub	F	Rendalen	ID	uncertain, DNA March 2005
S37-04	Cub	F	Ringebu	ID	uncertain, DNA March 2005
S38-04	Cub	M	Ringebu	ID	uncertain, DNA March 2006
S39-04	Adult	F	Folldal	ID/VHF/GPS	shot; license hunt 2004/2005
S40-04	Cub	F	Folldal	ID/VHF	shot; license hunt 2004/2005
S41-04	Cub	M	Folldal	ID/VHF	uncertain, DNA March 2007
S42-04	Cub	F	Dovre	ID/VHF	uncertain
S43-04	Cub	M	Dovre	ID/VHF	uncertain
S44-05	Cub	F	Tynset	ID	uncertain
S45-05	Cub	F	Tynset	ID	uncertain
S46-05	Adult	F	Rendalen	ID/VHF/GPS	alive
S47-05	Cub	F	Rendalen	ID	uncertain
S48-05	Cub	F	Rendalen	ID	uncertain, DNA March 2006
S49-05	Adult	M	Dovre	ID/VHF/GPS	alive, DNA April 2007
S50-05	Cub	M	Dovre	ID/VHF	alive
S51-05	Cub	M	Dovre	ID/VHF	alive, DNA April 2007
S52-05	Adult	F	Nesset	ID/VHF/GPS	alive, DNA March 2006
S53-05	Cub	F	Nesset	ID	shot; license hunt 2005/2006
S54-05	Cub	M	Nesset	ID	uncertain
S55-05	Adult	F	Lesja	ID/VHF/GPS	shot; license hunt 2005/2006
S56-05	Cub	F	Lesja	ID	uncertain
S57-05	Cub	M	Lesja	ID	shot; license hunt 2007/2008
S58-05	Adult	F	Tynset	ID/VHF/GPS	removal family group 2005
S59-05	Cub	F	Tynset	ID	removal family group 2005
S60-05	Cub	M	Nesset	ID	uncertain
S61-05	Cub	M	Nesset	ID	uncertain
S62-06	Adult	F	Engerdal	ID/GPS	uncertain
S63-06	Cub	F	Engerdal	ID	uncertain
S64-06	Cub	M	Engerdal	ID	uncertain
S65-06	Cub	F	Trysil	ID	uncertain
S66-06	Cub	M	Trysil	ID	uncertain
S67-06	Cub	M	Trysil	ID	uncertain
S68-06	Cub	M	Rendalen	ID	uncertain
S69-06	Cub	F	Rendalen	ID	uncertain
S70-07	Cub	F	Nesset	ID	uncertain
S71-07	Cub	F	Nesset	ID	uncertain
S72-07	Cub	M	Nesset	ID	uncertain

¹ captured in 2002

2.3 Data sources and field data

The different studies were based on various data sources depending on the research questions. The three studies on wolverine foraging strategies were based on wolverine scat collection in southern Norway between 2001 and 2004, on 237 km of wolverine tracks in the snow in Østerdalen during two winter seasons 2003–2004 and on documented kills of lambs by wolverines (documented by the staff of SNO) in Norway between 2000 and 2005. The first study on habitat requirements of wolverines in relation to habitat requirements of brown bears, wolves and lynx were based on animal location data of marked individuals in Østerdalen including both GPS data collected between 2002 and 2005 (wolverines) and previously collected VHF data (1990-1995; brown bears and lynx, 1996-2002; wolves). The other three studies on habitat requirements of wolverines were based on VHF data from wolverines in Troms and Dovre (1990-2002), reproductive female activities around their den sites (Troms and Sarek; 1996-2002) and on habitat characteristics of reproductive den sites in southern Norway (2000-2005).

3 Foraging strategies of wolverines

Among carnivores, complex systems of interactions, such as intra-guild competition exist (Creel, Spong & Creel, 2001; Crooks *et al.*, 1999). In an intra-guild context, wolverines have evolved as scavengers utilising remains left by other, more efficient predators such as the wolf, lynx and brown bear, in addition to carcasses of animals which have died from accidents or diseases (Banci, 1994; Landa *et al.*, 1997; Magoun, 1987). In addition, large carnivores, and especially wolverines, are increasingly involved in conflicts with human interests because of their depredation on semi-domestic reindeer throughout the year in Fennoscandia, and on free-ranging domestic sheep during summer in Norway (Landa *et al.*, 2000). In multiple-use landscapes, the sustainability of wolverine 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). Insight into how other, more efficient predators such as the wolf, the wolverine enables to thrive in conjunction with wolves and with outside the mountainous areas with high sheep grazing densities, is crucial for wolverine management in multiple-use landscapes.

3.1 Wolverine diet inside and outside wolf territories

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). Wolf predation increases the availability of carcasses of large prey (Wilmers *et al.*, 2003), especially moose (Sand *et al.*, 2006), which in turn may lead to a diet switch in facultative scavengers like the wolverine.

Using 459 wolverine scats collected during winter-spring 2001-2004 for DNA identity and dietary contents (see Figure 3), we compared diet inside and outside wolf territories while controlling for prey density. We tested the hypothesis that wolverine diet shifted towards moose in the presence of wolves, while taking into account possible differences between male and female wolverines.

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, 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 (Table 2). 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 used the highly available moose carrion and hunted less on small prey within wolf territories.

This 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.

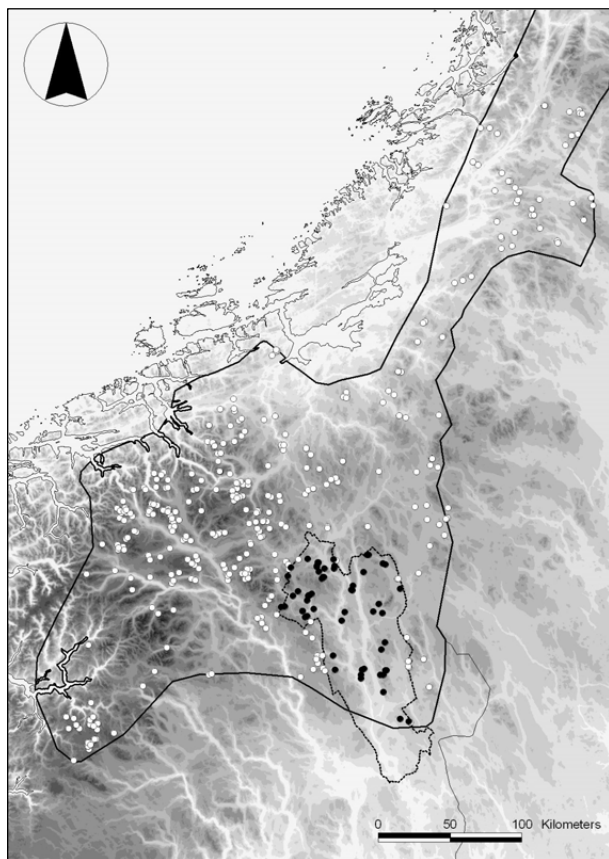


Figure 3. Overview of the wolverine scats analysed within the dietary study in Southern Norway. Scats were collected within wolf territories (dotted border, black circles) and elsewhere (white circles). The solid bordered area delineates wolverine distribution.

Table 2. Percentage of occurrence for the different prey species found within different subsets of wolverine scat samples (after van Dijk et al. 2007). The final row gives the standardized Levin’s niche breadth for the different subsets (after Hurlbert 1978). 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

3.2 Foraging strategies of wolverines within a predator guild

The wolverine has recently recolonized the boreal forests in southern Norway after an absence of approximately 100 years (Flagstad *et al.*, 2004). There is, however, little knowledge about its foraging behaviour in this boreal forest ecosystem and how wolverines co-exist with other carnivores such as the wolf, lynx, brown bear and red fox *Vulpes vulpes*.

We investigated winter foraging behaviour of wolverines in the boreal forest in Østerdalen with regard to wolf, lynx and red fox presence. We followed 55 wolverine tracks in the snow from at least nine individuals (based on DNA identification from scat samples) for a total of 237 km during the winters of 2003-2004. Given that intra-guild interactions (Creel *et al.*, 2001) could result in increased competition for food sources (Creel & Creel, 1996; Linnell & Strand, 2000; Paquet, 1992), and intra-guild predation is a widespread phenomenon in mammalian carnivores (Linnell *et al.*, 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 (Banci, 1994; Hornocker & Hash, 1981; Magoun & Copeland, 1998).

We documented 19 moose and four bird carcasses, and recorded 16 unsuccessful hunting attempts on small prey. 18 of the 19 moose carcasses were over two weeks old and consisted only of some hide and bones. Moose carcasses were apparently preferred or abundant enough that scavenging or hunting other prey was either less likely or not energy efficient.

Wolverines did not follow guild species trails directly to carcasses. 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, we did not find any evidence that the probability that wolverines encountered guild species trails increased when approaching carcasses, which implies that either wolverines did not use guild species trails to locate carcasses or that they even avoided other guild species trails when approaching carcasses. While wolverines were more active at higher elevations the probability of encountering a wolf was higher at lower elevations (Figure 4), suggesting a spatial separation between wolverines and wolves. Although wolverines seem to depend on wolf for carrion during winter, they did not use wolf trails to find carcasses. This may indicate that wolverines reduce risk of intra-guild predation by avoiding direct confrontation with wolves.

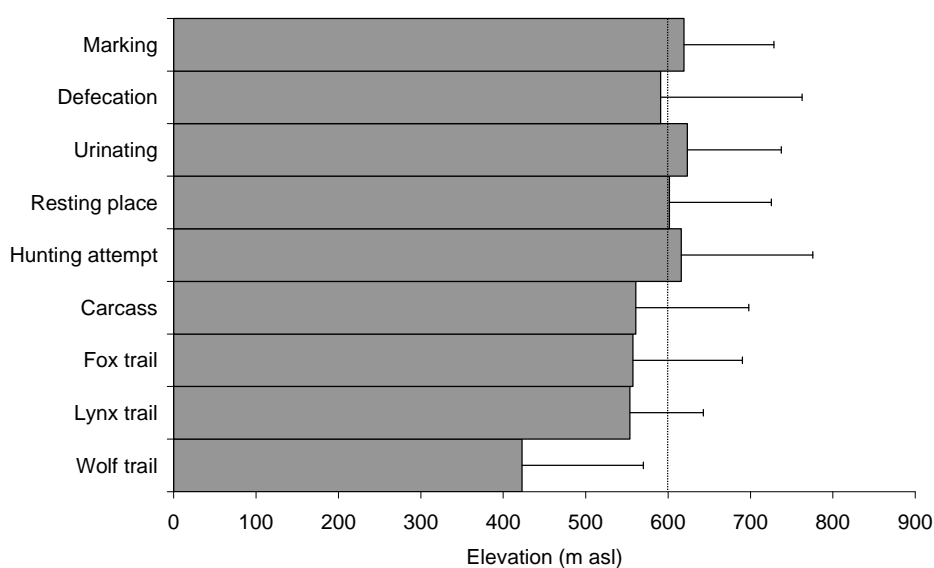


Figure 4. Average elevation (+ SD) of each observation along wolverine tracks in southeastern Norway. The dotted vertical line indicates average elevation of the wolverine tracks.

The importance of scavenging from prey killed by other guild species together with the spatial separation between wolverines and wolves, 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 (§ 4.1). However, we have to keep in mind that wolf, lynx and wolverine populations in Østerdalen are heavily exploited by humans. Also the recolonization of wolverines following wolves in this area occurred recently. These two aspects likely reduce the magnitude of intra-guild relationships between wolverine, lynx and wolf as is seen today.

3.3 Wolverine predation on domestic sheep

In Norway wolverines are involved in conflicts with human interests because of their predation on free-ranging domestic sheep during summer (Landa *et al.*, 2000). 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.

We analysed the spatio-temporal variation in lamb losses with use of the by the staff of SNO documented kills of lambs by wolverines (2001-2004) (Figure 5). Within the statistical modelling procedure reproductive events, removed wolverines (i.e., killed during licence hunt, predator-control or by removal of females with cubs), lamb availability and habitat were included as possible explanatory variables. The increase of depredation losses during the development of the sheep-grazing season was analyzed using information (bite marks and hoarding behaviour) recorded on the registration forms of carcass autopsies.

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. 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 or other males (since breeding season overlaps with maternal care) 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 that differences in sheep losses among grazing areas were probably related to local variation in wolverine density.

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. 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. Because wolverines can roam over long distances the potential for other wolverines re-establishing home ranges in an area where another one has been removed is high.

The increase of depredation losses during the development of the sheep-grazing season was most apparent in alpine shrub land (i.e., forest/alpine tundra ecotone); with a typical depredation increase during the latter portion of the grazing season (Figure 6). Sheep begin the grazing season at lower elevations and move to higher elevations as the summer 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, 2007). 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 (§ 4.3). 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 revealed that wolverine cubs become nutritionally independent in August (§ 4.4). Seasonal depredation patterns coincide with cub independence (Figure 7);

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 training prey to perfect their hunting skills before the onset of winter. However analyzing the information from carcass autopsies did not reveal any specific age class that was responsible for the increased depredation during the latter portions of the grazing season.

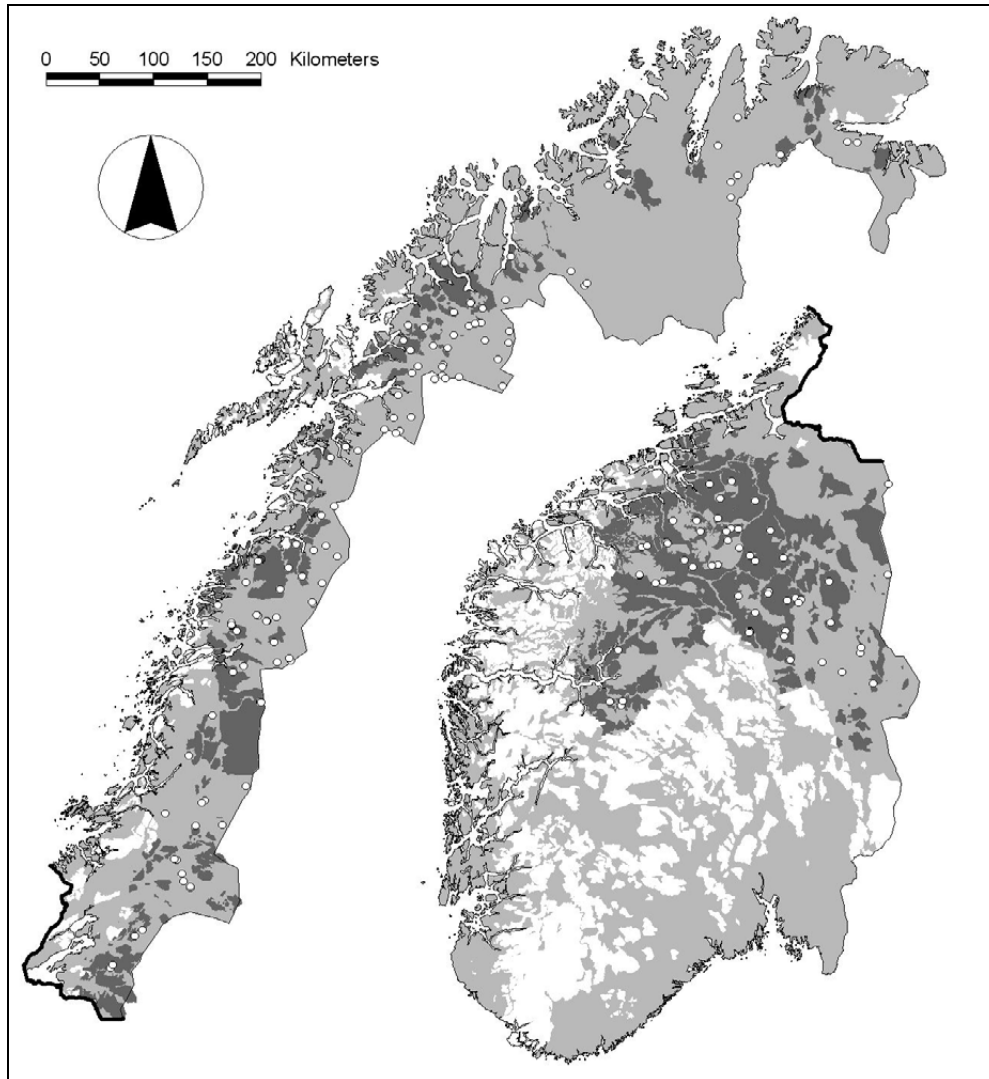


Figure 5. Registered sheep grazing areas (dark grey polygons) in northern (on the left) and southern Norway (on the right) within the wolverine distribution. White polygons were the grazing areas outside the wolverine distribution, and not included in the analyses. The white dots represent wolverine reproductions between 2000 and 2005.

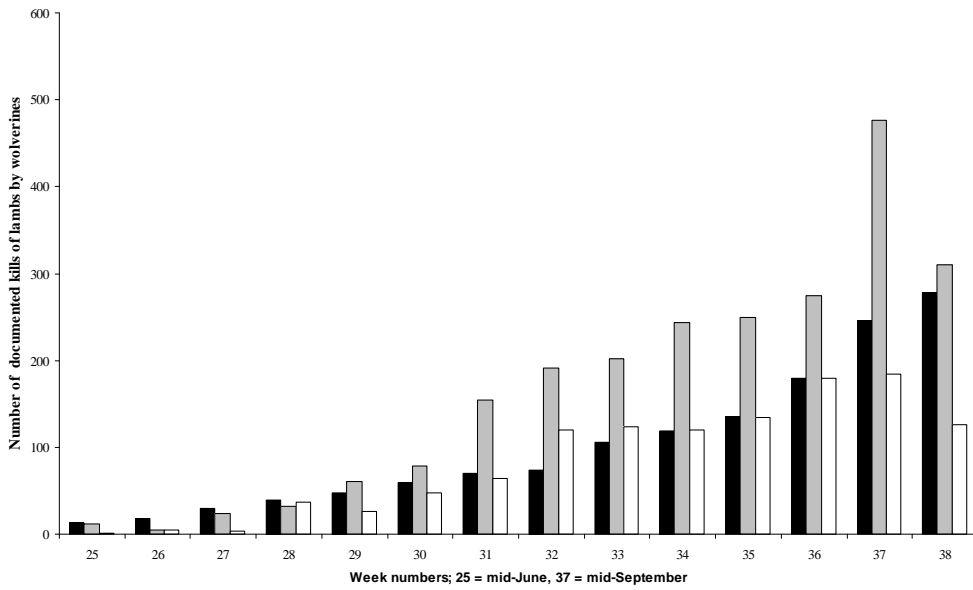


Figure 6. Number of documented kills of lambs by wolverines found in forest (black), alpine shrub land (grey), or alpine tundra (white) during the development of the grazing season.

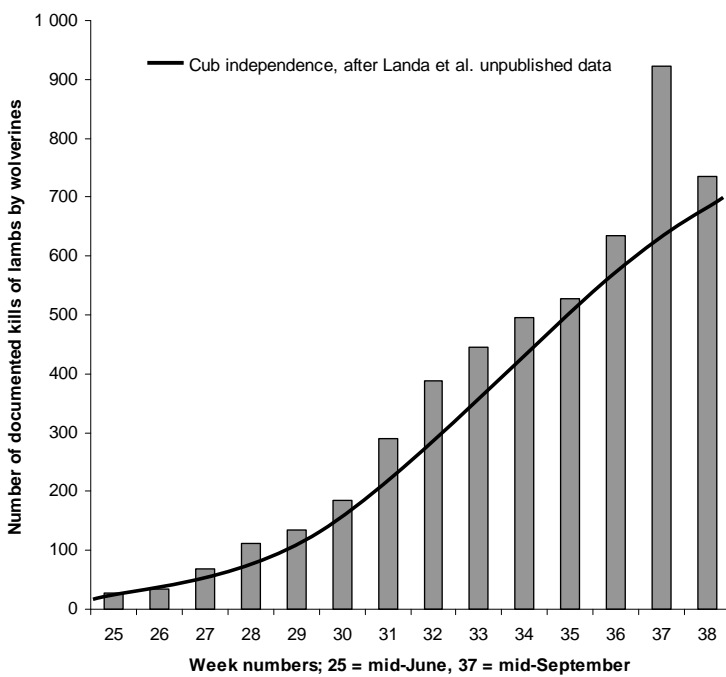


Figure 7. Number of documented kills of lambs by wolverines and the degree of wolverine cub independence, as measured by the increasing distance between females and their cubs (after Landa et al. unpublished data), during the development of the grazing season.

3.4 Lamb-ewe behaviour and their vulnerability to predation

In Norway domestic sheep range unattended in mountainous areas during the summer season. Wolverines re-established in the alpine regions of southern Norway during recent decades and are viewed as a substantial predator on lambs (Landa *et al.*, 1999; Landa *et al.*, 1998a; Warren & Mysterud, 2001; Aanes, Swenson & Linnell, 1996). Reducing predation on sheep by wolverines would not only reduce the economic loss to farmers but also promote the acceptance of wolverines in their summer ranges. In wild ungulates, (de)predation on males generally is higher, which is thought to be a result of higher level of locomotor activity and an increased distance from their mother (Jackson, White & Knowlton, 1972; Mathisen *et al.*, 2002; Schwede, Heindrichs & Wemmer, 1992; Aanes & Andersen, 1996). Other studies on sheep have shown that male lambs did move larger distances from the ewe compared to female lambs (Melting, Eggen & Kvam, 1998; Warren & Mysterud, 1995).

In this behavioural study we hypothesized that male lambs would be more prone to wolverine predation, because of higher locomotor activity, lower behavioural ewe–lamb synchrony and larger ewe–lamb distance. We studied ewe and lamb behavioural patterns, synchrony and ewe–lamb distance on a summer range in Knutshøi, south-central Norway.

Although no differences were found in ewe–lamb distance or locomotor activity in gender, female lambs synchronized their behaviour more with their mother than males. Only for female lambs, increased synchrony resulted in closer ewe–lamb distances. Overall losses to wolverines based on long-term data indicate that male lambs are more prone to predation than females later in the season. These sex-specific behavioural differences in lambs affect the spatial and social relationships between ewe and lamb, and are likely to increase with age eventually leading to sexual segregation (Bon & Campan, 1996). Male lambs can therefore be expected to be more prone to wolverine predation towards the end of the season, when lambs become independent from the ewe.

4 Spatial ecology of wolverines

Within their geographic range, wolverines occupy a variety of habitats. General characteristics of wolverines are their large area requirements, low densities and remoteness from human development, which make them particularly vulnerable to landscape changes (Landa *et al.*, 2000; Sunquist *et al.*, 2001). Also, compared to the other northern large carnivores, wolverines are more sensitive to anthropogenic effects (Carroll, Noss & RPaquet, 2001; Rowland *et al.*, 2003) and more selective about habitat quality (Banci & Harestad, 1988; Weaver, Paquet & Ruggiero, 1996), especially for reproducing females (Heinemeyer, Aber & Doak, 2001; Magoun *et al.*, 1998). Given the extensive habitat needs of wolverines, their perceived susceptibility to human disturbance and the continuing encroachment of human activity on wilderness areas, provision of adequate habitat where there is no potential for conflict could be difficult (Landa, 1997). If conservation and management are to be successful, knowledge on multiple-scale habitat requirements and their adaptability to changing environments is of critical importance to minimise conflicts and maintain or restore viable populations (Landa *et al.*, 1998b). The results from the following studies will shed light on the spatial processes wolverines are facing in the multiple-use landscapes of Scandinavia.

4.1 Habitat preference of the large carnivore community

The re-establishment of large carnivores in Norway has led to increased conflicts and the adoption of regional zoning (Linnell *et al.*, 2005; Swenson & Andrén, 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. 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. We studied differentiation in habitat and kill sites within the large-carnivore community in south-eastern Norway.

For this, we compared habitat selection of the brown bear, Eurasian lynx, wolf and wolverine, based on radio-tracking data (1988-2005; Figure 8a). Differences in choice of kill sites were explored using locations of documented predator-killed sheep (Figure 8a). 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 projected probability of occurrence maps we estimated continuous patches of habitat within the study area.

Although bears, lynx and wolves had overlapping distributions (Figure 8b), we found a clear differentiation for all four species in both 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 (Figure 9). Some degree of sympatry was possible in over 40% of the study area, although only 1.5% could hold all four large carnivores together (Figure 8c). The wolverine both had a high amount of small patches (<10 km²) and the smallest average patch size >1000 km² (Figure 10a). Both the overlap of three species and of the forest-dwelling species had a relatively low amount of small patches (<10 km²) and large average patch sizes >1000 km² (Figure 10b).

Within an intra-guild community setting, sympatry of the wolverine with the three forest-dwelling carnivore species, the lynx, wolf and brown bear, appears to depend on the availability of mountain ranges as a spatial refuge (§ 4.2) and the presence of wolves to provide scavenging opportunities (§ 3.2, 3.3). This result fits well with the perception that the wolverine is a carnivore of remote alpine regions (Carroll *et al.*, 2001; Rowland *et al.*, 2003). Despite their similar potential distribution patterns, the three forest-dwelling species also had clear differences in choice of habitat and kill sites. It is likely that high prey densities, low large carnivore densities and decreased dietary overlap have led to a situation with reduced exploitative exclusion (Heithaus, 2001; Holt & Polis, 1997). In a broader regional context our study area encom-

passes 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. Our estimates of available patches for large carnivores inside the entire study area may render insight into the minimum area required for viable populations, and scale of regional zoning (Mech, 1995). Large carnivores are known to be vulnerable to anthropogenic disturbance (§ 4.2; Nellemann *et al.*, 2007). Our modelling indicates that wolverines were most sensitive to fragmentation of habitat, given the high amount of small disjointed patches. For the three forest-dwelling species a continuous geographical unit could be delimited in the south of the study area (Figure 8c). The spatial extent of regional planning depends on the scale at which population processes are occurring. 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 live-stock/game conflicts, and fear (Linnell *et al.*, 2002; Linnell *et al.*, 2005; Swenson *et al.*, 1995). Successful regional zoning of all four carnivores may therefore rely on establishing zones spanning an elevational gradient. Zoning of all four species into this region may thus enhance the conservation of an intact guild of large carnivores in the boreal forest ecosystem. On the other hand, sympatry of all four species may well increase conflict levels and resistance to carnivore conservation locally (Linnell *et al.*, 2005; Wabakken, 2001).

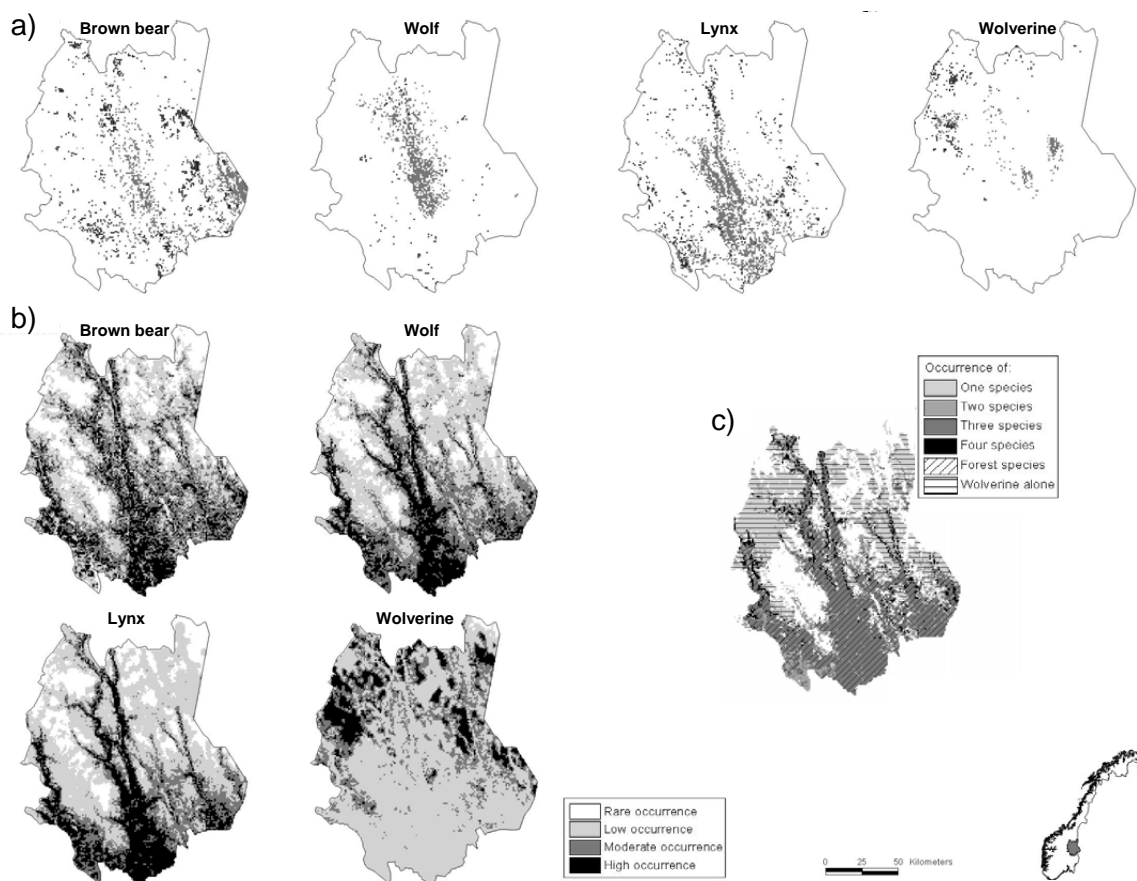


Figure 8. a) Presence maps for four large carnivore species within the study area in south-eastern Norway (see corner). Presence pixels from radio-tracking data are given in grey; locations of sheep killed by each carnivore species are given as black dots. b) Occurrence maps for each species; probability distributions were based on species-specific resource selection function models (Figure 9). c) Possible sympatry based on the overlap of moderate- and high-occurrence classes for each species.

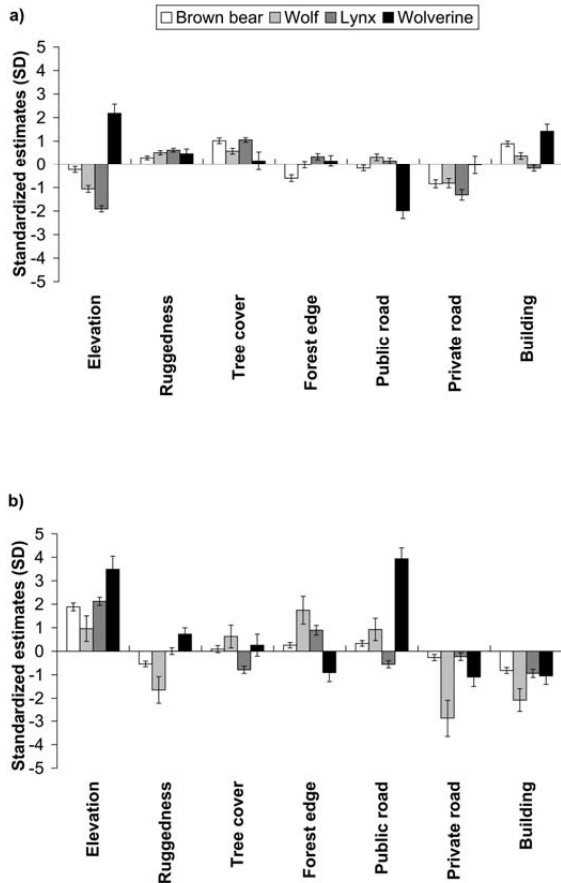


Figure 9. Standardized estimates (\pm SD) of the resource selection functions for a) habitat selection relative to available habitat within the study area, and b) choice of kill sites relative to selected habitat. Positive bars indicate selection for and negative bars indicate avoidance of habitat features. The last four covariates are distance measures.

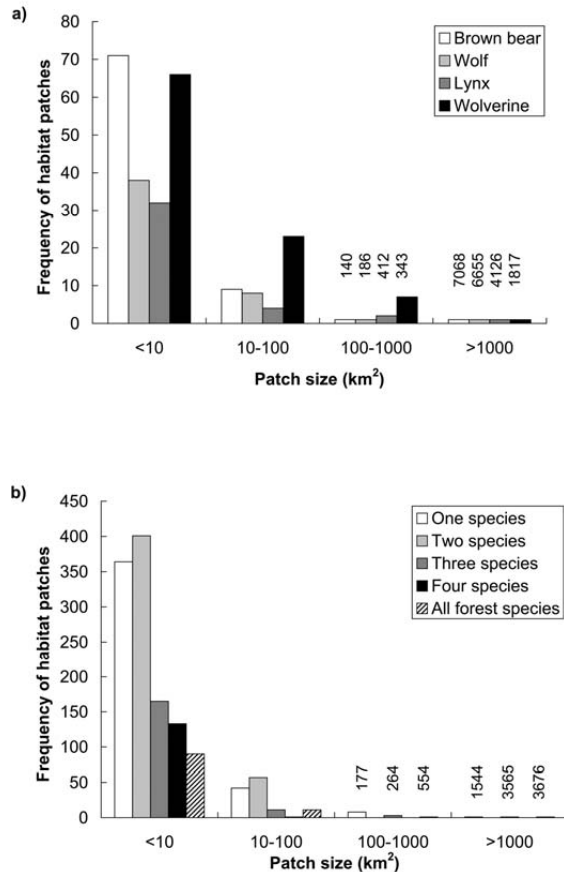


Figure 10. Size distribution of habitat patches for a) four large carnivore species identified using resource selection functions and b) degree of overlap in south-eastern Norway. For the highest two categories the average patch size is given.

4.2 Impact of infrastructure

Although wolves may provide wolverines with scavenging opportunities, further wolverine recovery in forest ecosystems might be difficult, given the concentrated human development in forested areas at lower elevations and the continuing encroachment of human activity on wilderness areas (Landa *et al.*, 2000). Nowadays wolverines in Scandinavia are mainly found in remote alpine areas, and we investigated whether human development through presence of infrastructure has relegated them to these areas.

We analysed wolverine habitat selection and the impact of infrastructure; based on individuals radio-marked with VHF collars in Snøhetta (1990-1995) and Troms (1996-2002) using compositional analysis.

We found that wolverines in Norway located their home ranges in relatively undeveloped high alpine areas (i.e., alpine tundra and rock/ice; Figure 11). The selection for alpine areas is consistent with previous studies on home range use and altitude selection by wolverines. We found that habitat selectivity in developed habitats was low, indicating that infrastructure and not habitat was the primary factor for home range location. Also, wolverines were more selec-

tive about habitat quality in undeveloped areas when establishing their home range. Within their home ranges however, wolverines used alpine shrub land and forest, irrespective of human development.

Increased human development and activity in once remote areas may thus cause reduced ability of wolverines to perform their daily activities unimpeded, making the habitat less optimal or causing wolverines to avoid the disturbed area (Landa *et al.*, 2000; Landa & Skogland, 1995). Wild and semi-domestic reindeer constitutes wolverines' most important source of winter food, and can be found in mountainous areas (Landa *et al.*, 1997; Magoun, 1987). Reindeer is one of the ungulate species most sensitive to habitat fragmentation and human disturbance (Nellemann *et al.*, 2003; Vistnes *et al.*, 2001). The sympatric distribution of wolverines with wild and semi-domestic reindeer may therefore indicate that wolverines are vulnerable to indirect loss of habitat; a result also found in modelling studies in the USA (Carroll *et al.*, 2001; Rowland *et al.*, 2003). Although wolverines have been shown to travel through developed areas and transportation corridors (Landa *et al.*, 1998b; Vangen *et al.*, 2001), they apparently locate their home ranges away from human disturbance (undeveloped habitat), and use habitat which provides them with enough shelter and food (alpine shrub land and forest).

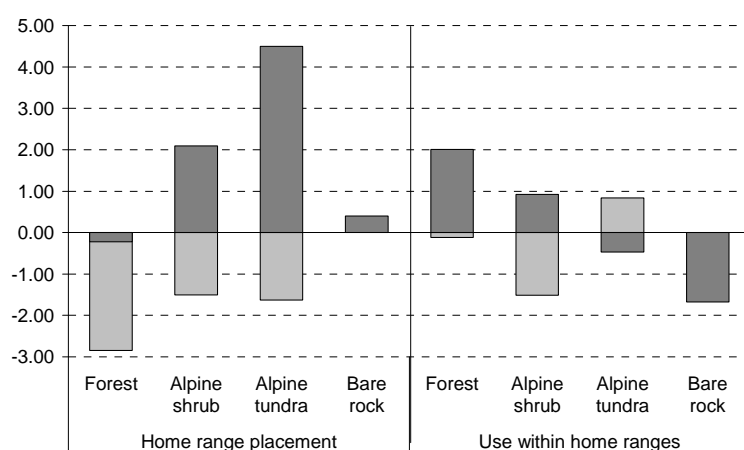


Figure 11. Selection ratios for undeveloped (dark grey) and developed (light grey) habitat. Negative values indicate avoidance, whereas positive values indicate selection.

4.3 Movement patterns in space and time

Conservation of carnivores in an increasingly changing environment (Crooks, 2002; Noss *et al.*, 1996; Sunquist *et al.*, 2001; Woodroffe & Ginsberg, 1998) is much enhanced by understanding the decision-making processes underlying habitat patch choice. Foraging theory may give us insight into spatio-temporal search patterns and the consequent foraging decisions that carnivores make in heterogeneous and fluctuating environments. Especially for central place foragers, such as the wolverine, the nature and strength of the trade-off between central-place foraging and optimal foraging are likely to influence both spatio-temporal movement patterns and patch choice (Orians & Pearson, 1979).

We investigated the spatio-temporal ranging behaviour of seven reproductive female wolverines in south-central Norway, based on GPS data collected in 2002-2005. The study was conducted using autoregressive models and discrete choice models, which incorporated individual preferences. Travel speed, home range use and selection for elevation were analysed in relation to spatial and temporal covariates (time-of-day and Julian date). We assessed six models which captured possible foraging strategies in wolverines.

Although individual foraging strategies differed, overall spatio-temporal ranging behaviour best fit the central-place foraging model with seasonal trade-off. The next best model also indicated a diminishing daily movement pattern (Figure 12). Over the summer, wolverines increasingly preferred lower-lying, clustered locations. The daily activity pattern of wolverines clearly showed an increase in activity during the night (see also § 4.4). Their daily pattern showed a preference for lower-lying, less clustered locations at night. Higher, peripheral locations were used mainly for the purpose of transportation from patch to patch; given their higher travel speed in the home range periphery.

The wolverines under study deployed a foraging strategy more attuned to changing their spatial patterns over the summer than their daily activity patterns. They increasingly utilized the profitable forest-alpine tundra ecotone (Grytnes, 2003) for foraging. Different prey species actively use this ecotone (rodents: Virtanen, Parviainen & Henttonen, 2002; Kalela *et al.*, 1971; ptarmigan: Andersen, Pedersen & Steen, 1986; Gruys, 1993; mountain hare: Angerbjörn & Flux, 1995; domestic sheep: Mysterud, Iversen & Austrheim, 2007; reindeer: Mårell, 2006), thus support higher prey densities and ultimately results in a higher species abundance (Kark & van Rensburg, 2006; Ries *et al.*, 2004). Reproducing female wolverines are thus faced with a continuous, but diminishing, trade-off between providing food and shelter for their offspring throughout the summer. They cope with this trade-off by selecting higher terrain at first, when cubs are placed at rendezvous sites (c.f. Magoun *et al.*, 1998), and moving downhill as cubs grow more mobile and independent. Incorporating spatially and temporally explicit activity patterns and home range use in discrete choice resource selection models thus enhances the biological meaning of behavioural choices animals make along their path (e.g. Rhodes *et al.*, 2005; Sunde & Redpath, 2006).

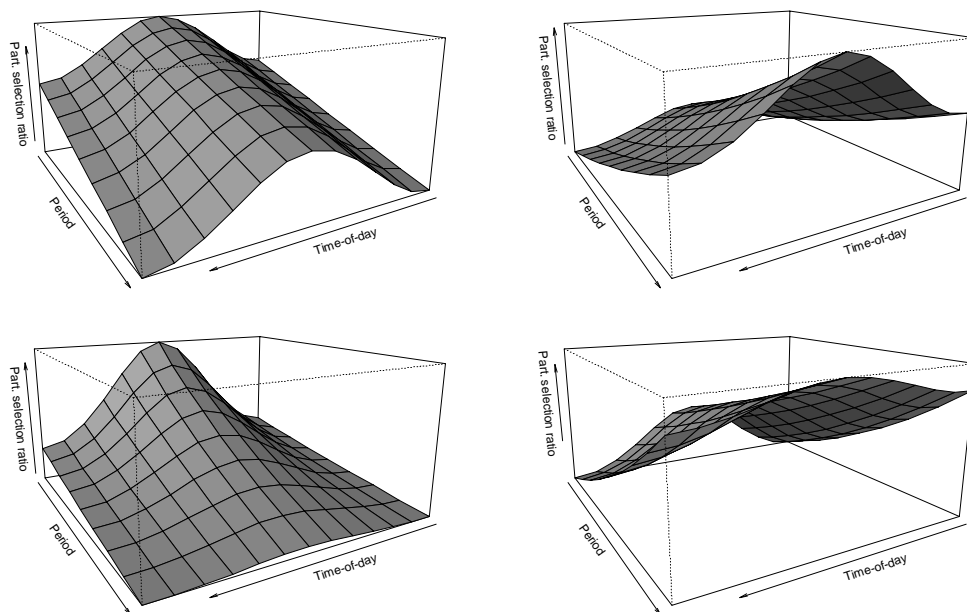


Figure 12. Temporal decomposition of the partial selection strength (z-axis) for elevation (left-hand panels, in m a.s.l.) and spatial location (right-hand panels) for 'Central-place foraging with seasonal trade-off' (best model; upper panels) and 'Daily trade-off between central-place foraging and optimal foraging with seasonal trade-off' (next best model; lower panels).

4.4 Maternal care in wolverines

Successful reproduction is essential for population survival. In exploited and controlled carnivore populations, as in Norway, decrease in population densities can reduce reproductive rates (Miller, 1993), increase infanticide (Swenson *et al.*, 1997) and influence dispersal (Frank & Woodroffe, 2001). Therefore knowledge on the reproductive biology of carnivores is of the utmost importance. In this study we studied maternal care in female wolverines from the den to cub independence. In coping with the trade-off placed upon reproducing females, they are expected to employ specific spacing strategies and maternal care. The adoption of a denning strategy followed by a more nomadic life style should be expected to allow the cubs to become nearly full-grown and reach independence before the onset of winter.

We monitored radio-marked females and their cubs at reproductive den sites with activity sensor systems (Troms, northern Norway; Sarek, Sweden; Snøhetta, southern Norway), and followed their movements intensively throughout the rearing period (Troms, northern Norway: 1996-2000).

In the, mainly altricial, parturition and weaning period (mid-March – mid-May), female wolverines relied on food caches and spent most of their time together with the cubs. During this period they had a mainly nocturnal activity pattern (Figure 13 – top). When cubs become larger, the female became more active outside the denning area and was away for longer time periods (Figure 13 – bottom). Over 33% of reindeer body parts equipped with radio-transmitters were moved by wolverines. The minimum number of reindeer individuals cached at wolverine (natal) den sites, counted by body part remains was 1.87 ± 0.5 SE. The denning area was abandoned mid-May. Over the rearing period, the intervening distances between mother and offspring increased significantly and by the beginning of September, cubs were nearly full-grown and nutritionally independent from their mother (Figure 14). Break-up of sibling pairs took place at the end of September. Over the rearing period depredation on domestic sheep had a high positive correlation with proportion of cubs separated from their mother. Predation on semi-domestic reindeer decreased both with time the female spent outside the denning areas and with proportion of cubs separated from their mother.

Wolverine cubs are likely to be most vulnerable to predation when they are left unattended in the den (March-April, Magoun *et al.*, 1998), when they have just left the den site (May-July, Persson *et al.*, 2003) and when becoming independent (August-September, Vangen *et al.*, 2001). Raising altricial cubs to weaning dictates brief foraging trips for the female during the denning period and is consistent with Haglund (1966), who suggested that food caching is especially important in the vicinity of natal dens to reduce the time spent foraging. Also, parturition in Norway was shown to correspond closely with the period when reindeer were most vulnerable (Bevanger, 1992; Haglund, 1966). After the den abandonment cubs are placed at rendezvous sites when their mother hunts and they are still too young to follow her very far. When the risk of (intra-specific) predation is high for cubs which are left unattended at the den or rendezvous site, the choice of the female to stay away for longer periods might be driven by food depletion. The time spent at rendezvous sites decreases gradually as the cubs get older and more mobile, and are able to follow their mother for extended periods (Magoun, 1985). The cubs' ability to accompany the mother more and more puts less energetic costs on the mother, and simultaneously optimizes growth, foraging skills, and independence in the cubs. Insight into the reproductive biology of wolverines, especially maternal care and activity patterns of family groups, provides valuable information for management authorities to avoid unnecessary disturbance of denning areas (see also § 4.5), minimize depredation-conflicts (see also § 3.3), and maintain a sustainable population of wolverines.

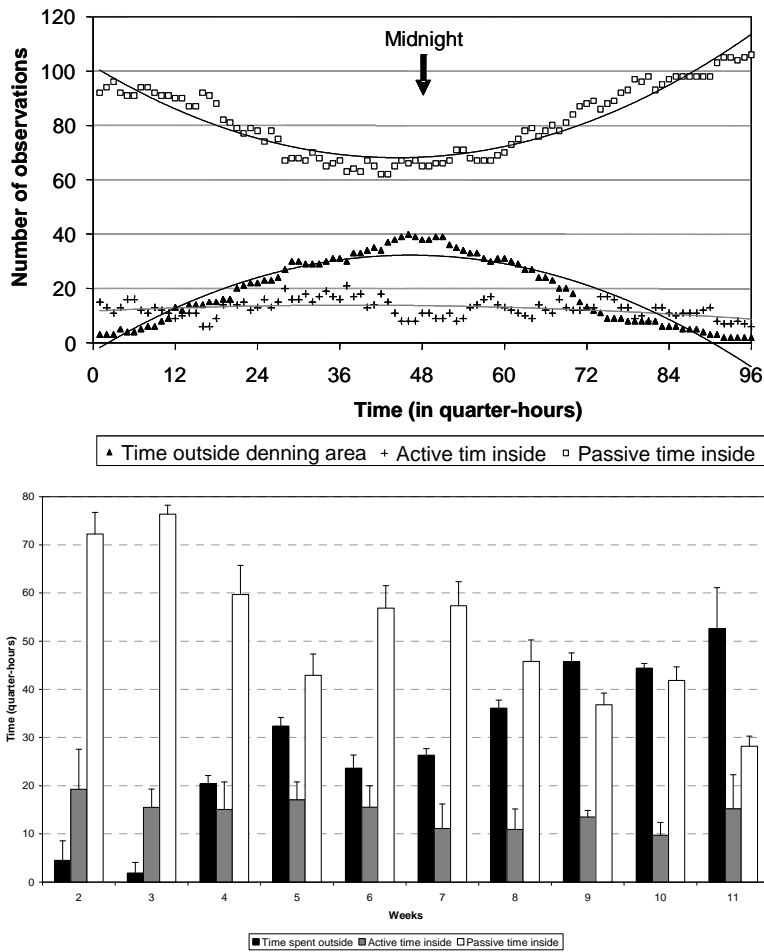


Figure 13. Daily activity pattern of reproducing female wolverines (top) and activity pattern over the denning period (bottom).

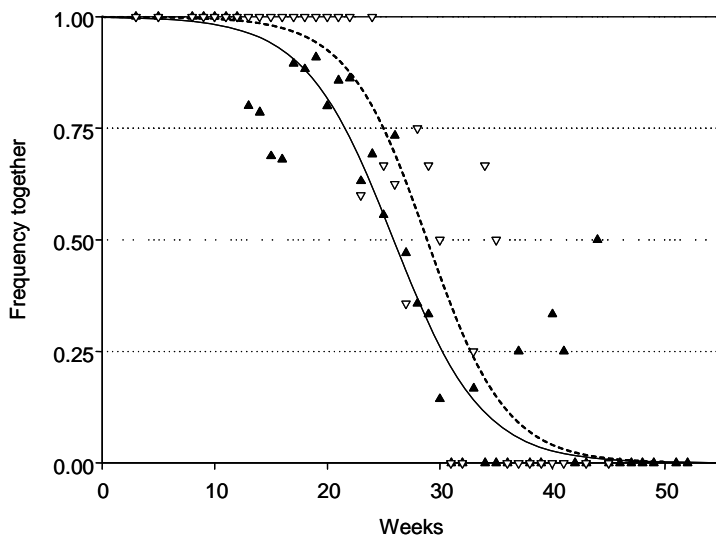


Figure 14. Observed proportion of females together with their cubs (black triangles, solid line) and cubs together among themselves (white triangles, dashed line) over weeks from March 1st.

4.5 Den site selection

Reproductive female wolverines are thought to be particularly sensitive to human disturbance during the natal denning period (Heinemeyer *et al.*, 2001; Landa *et al.*, 2000; Magoun *et al.*, 1998). Successful reproduction, and thereby population viability, is likely to be enhanced by choice of suitable den sites.

We investigated which topographic features were selected for 50 natal den sites by female wolverines in southern Norway (2000-2006), at three spatial scales (landscape, home-range and site-specific scale). We further assessed reproductive frequency, based on denning localities registered in 1992-2005, and related it to topographic features.

Natal den sites were generally placed at rocky sites, often with shrub or woody dwarf (heather, dwarf shrubs, berries) vegetation (Figure 15). At the site-specific scale, den sites were associated with steep, rugged terrain with bare rock (Figure 16). At the home-range and landscape scale, den sites were placed in rugged terrain at 1,000 meters above sea level and away from infrastructure (private roads and public roads, respectively). Reproductive frequency, measured as the ratio number of reproductive events by number of years monitored, was 0.50 ± 0.03 (SE). Re-use of den sites was higher in denning localities found in rugged lower-lying terrain away from private roads.

Our results are associated with characteristic wolverine den sites dug out in deep snow, but also indicate an avoidance of infrastructure. At all three spatial scales, the overall ruggedness or steepness of the terrain appeared to be an important feature for den sites. Steep and rugged terrain enables wolverines to dig out den sites in snowdrifts (Banci, 1994; Magoun *et al.*, 1998; Myrberget, 1968; Pulliainen, 1968). It is also possible that steep and rugged terrain, especially when placed farther from human infrastructure, is perceived as providing security from humans or other potentially dangerous carnivores. This appears to be a general pattern for wolverines to prefer steep slopes, ravines or boulder fields (Banci, 1994; Magoun *et al.*, 1998; Pulliainen, 1968). The avoidance of infrastructure at both scales of wolverine den site selection corroborates well with previous authors who have expressed their concern that wolverines may be especially sensitive to disturbance during the natal denning period (COSEWIC, 2003; Heinemeyer *et al.*, 2001; Magoun *et al.*, 1998; Weaver *et al.*, 1996). It has been hypothesised that differences in reproductive frequency are likely to be due to differences in habitat quality of the various denning localities (Landa *et al.*, 1997). Wolverine are known to have low reproductive rates as compared to similar sized carnivore species. Our estimate of reproductive frequency from monitoring of denning localities was similar to reproductive rates of radio-collared wolverines in Scandinavia (Persson *et al.*, 2006). However, it is important to bare in mind that we have only examined areas that wolverines have used for reproduction at least once, indicating that all of them are suitable to some degree. There are clearly many areas that are not suitable for wolverines and where wolverines have never settled. Reproductive frequency was influenced by topographic features of den sites and distance to infrastructure. This indicates that the distribution of den sites, and possibly successful reproduction, may be partly influenced by direct disturbance or a higher risk of human-caused mortality associated with infrastructure (Landa *et al.*, 2000; Thurber *et al.*, 1994). Recurrent use of specific topographic features may provide valuable information for directing monitoring efforts (Landa *et al.*, 1998c), protecting denning localities from unnecessary human disturbance (COSEWIC, 2003; Heinemeyer *et al.*, 2001; Magoun *et al.*, 1998), and augmenting recovery of endangered wolverine populations (e.g., Fortin *et al.*, 2005).

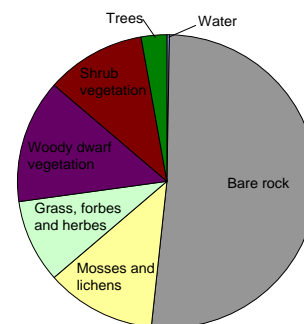


Figure 15. Vegetation characteristic in a 10-m radius surrounding natal den sites in southern Norway.

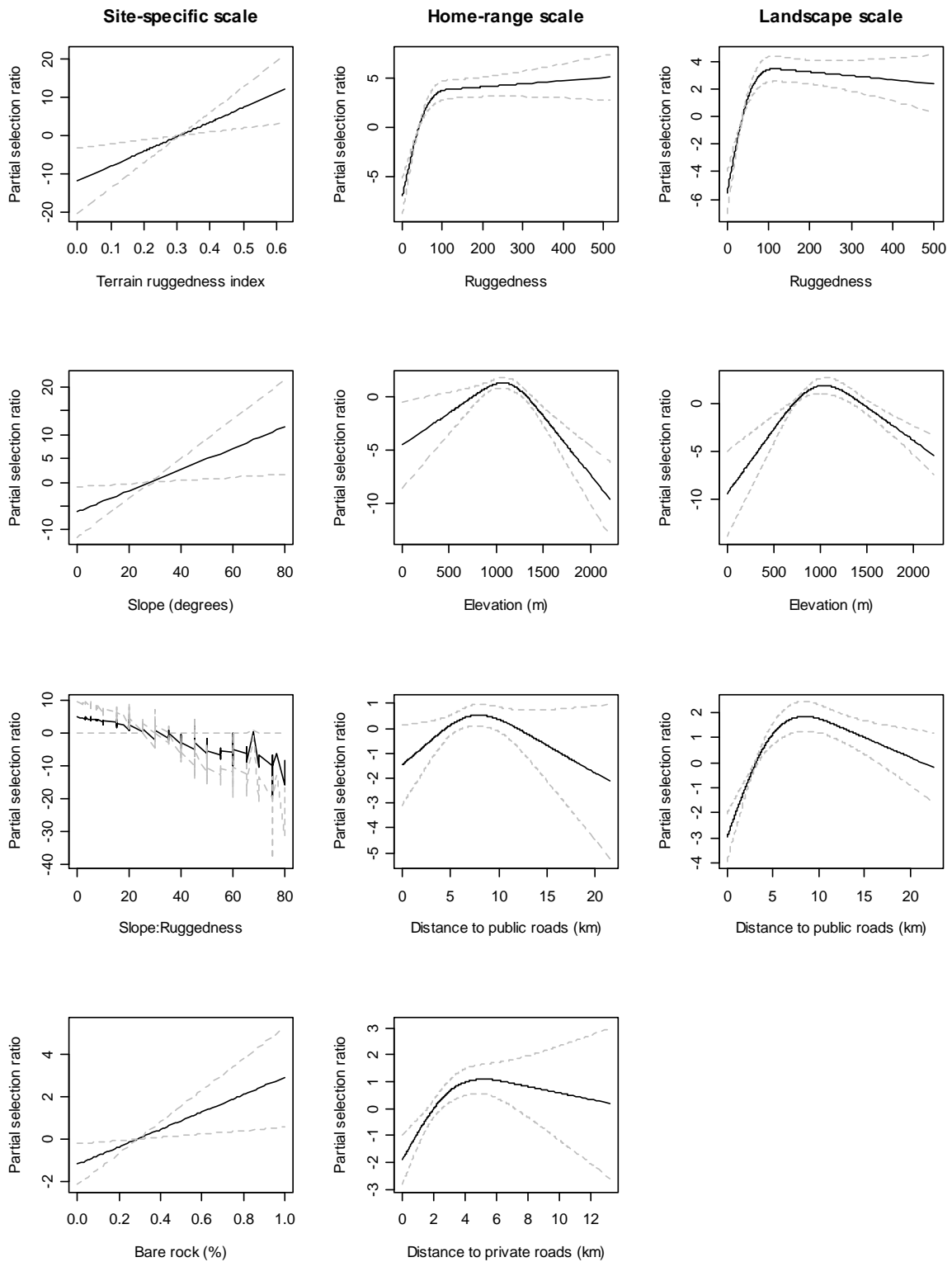


Figure 16. Partial selection ratios for den site selection of wolverines in southern Norway as a function of different non-linear covariates for the site-specific, home-range and landscape scale. Ratios above zero indicate selection for, and below zero selection against the covariate.

5 Management implications

Conserving large carnivores in landscapes that are also used by humans (i.e., multiple-use landscapes) 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. Still, the Scandinavian wolverine population is subdivided in several genetically distinct sub-populations (Flagstad *et al.*, 2004). The wolverine is endangered according to the Norwegian Red List (Kålås, Viken & Bakken, 2006). Given the large areas of continuous habitat that are required by large carnivores such as the wolverine, 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 their spatial requirements, inter-specific relationships among carnivores, while aiming to minimize livestock depredation conflicts.

Conservation and management of the wolverine can become successful when sufficient emphasis is put on understanding the effects of both spatial and temporal changes in the use and management of our natural environment. Wolverines occupy large home ranges which make them potentially more vulnerable than other species to habitat fragmentation resulting from human infrastructural development and habitat conversion. Our studies indicate that wolverine distribution may be partly influenced by direct disturbance or higher risk of human-caused mortality associated with infrastructure (§ 4.2). Their sympatric distribution with wild and semi-domestic reindeer, which are known to avoid areas with anthropogenic disturbance and areas with higher risks of predation (Nellemann *et al.*, 2003; Vistnes *et al.*, 2001), may indicate that wolverines are vulnerable to indirect loss of habitat. Increased human development (e.g., houses, cabins, settlements and roads) and activity (e.g., recreation and husbandry) in once remote areas may thus cause reduced ability of wolverines to perform their daily activities unimpeded, making the habitat less optimal or causing wolverines to avoid the disturbed area. Although wolverines have been shown to travel through developed areas and transportation corridors (Landa *et al.*, 1998b; Vangen *et al.*, 2001), they apparently locate their home ranges away from human disturbance (undeveloped habitat), and use habitat which may provide them with enough shelter (alpine shrub land and forest).

Also in less densely populated countries like Norway (Norway has Western Europe's lowest human population density), wilderness areas are embedded in multi-use landscapes with varying degrees of development. Therefore mitigation of fragmentation and isolation of the declining natural areas will form important measures in conserving species that are especially sensitive to habitat changes and human disturbance. Now that wilderness areas have become more developed as a result of increased infrastructure and human mobility, the direct and indirect effect of human activities on sensitive species, like the wolverine, should be better understood to enable proper and holistic management for future conservation. Consolidation of wolverine populations at a viable level can only be maintained when infrastructural development of wilderness areas is minimized, and placement of infrastructure and human activities are carefully zoned.

In exploited and controlled carnivore populations, as in Norway, decrease in population densities can reduce reproductive rates, increase infanticide and influence dispersal. Therefore knowledge on the reproductive and spatial biology of wolverines is important. Especially during the natal denning period (February – May) for reproductive females, wolverines are thought to be selective about habitat quality and particularly sensitive to human disturbance (Heinemeyer *et al.*, 2001; Magoun *et al.*, 1998). During this period, females with cubs employ central place strategies constraining their movements to areas close to the den (§ 4.3). Importance of den sites in wolverine ecology involves both provision of shelter for cubs and safety from predators during the infant period (§ 4.5).

Wolverine den sites can be described as being located in steep, rugged and rocky terrain, facing north to north-west, relatively far from human activity, and just above the treeline (§ 4.5). These features are consistent with selection for suitable snowdrifts as these are often associated with steep and rugged terrain (Lee & Niptanatiak, 1996; Magoun *et al.*, 1998). It is also possible that steep and rugged terrain, especially when placed farther from human infrastructure, is perceived as providing security from humans or other potentially dangerous carnivores. Overall, dens were generally located relatively far from human infrastructure, which is difficult considering the almost complete lack of true wilderness areas in modern Norway. Given a recurrent use of denning localities and preference of specific topographic characteristics of den sites, it would be recommended to emphasise within your wolverine management plan on the areas that wolverines have selected themselves as being suitable. This further includes direct monitoring efforts which are based on localizing den sites (Landa *et al.*, 1998c), and providing valuable information for protecting known denning localities from unnecessary human disturbance during the natal denning period. Also, identification of “typical” den sites within potentially suitable wolverine habitat augments the chances for successful recovery or reintroduction of wolverines to previously inhabited landscapes (Fortin *et al.*, 2005) by establishing recovery zones or delineating reintroduction sites.

The natural recovery of carnivore populations has led to increased conflict in Norway (Landa *et al.* 2000). The main causes of the conflict are their depredation on semi-domestic reindeer throughout the year in Fennoscandia, and on free-ranging domestic sheep during summer, primarily in Norway (Landa *et al.*, 2000). Although most predation on reindeer is caused by wolverines and lynx, all large carnivores in Norway kill free-ranging sheep (Swenson *et al.*, 2005). This has led to the adoption of a geographically differentiated management policy (i.e., zoning of large carnivores) aimed at conserving viable populations of large carnivores, while minimizing the potential for conflicts (Linnell *et al.*, 2005). The present population goals for large carnivores in Norway are specified for eight management regions. The large-carnivore region of Hedmark County, in which the major part of our studies on the role wolverines have within the large carnivore community (§ 3.1, §3.2, §4.1) was situated, is the only region that has populations of all four large carnivore species. When planning the future distribution of large carnivores, it was therefore important to consider details of their potential habitat tolerances, and the strength of differentiation among the four species.

Although sympatry of the three forest species was possible in over one-third of the study area, only 1.5% was suitable for all four species (§ 4.1). Successful regional zoning of all four carnivores may therefore rely on establishing zones spanning an elevational gradient. Zoning of all four species may enhance the conservation of an intact guild of large carnivores in the boreal forest ecosystem. On the other hand, fostering sympatry of all four species may well increase conflict levels and resistance to carnivore conservation locally (Linnell *et al.*, 2005; Wabakken, 2001). These conflicts may be reduced by discouraging extensive sheep husbandry (Milner *et al.*, 2005; Zimmermann, Wabakken & Dötterer, 2003), 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 *et al.*, 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 provide guidance to managers attempting to elaborate on regional-scale zoning management to facilitate recovery of large carnivores in Scandinavia.

Within the predator guild, the wolverine has evolved as a scavenger of prey killed by more effective predators like the wolf (§ 3.1). The observed spatial and temporal separation between wolverines and wolves suggests that maintaining a wolverine population in the presence of other guild species is ecologically feasible within the boreal ecosystem (§ 3.2). Although wolves provide wolverines with scavenging opportunities, further wolverine recovery in forest ecosystems might be difficult given the reproductive den site requirements (§ 4.5), the concentrated human development in forested areas at lower elevations, and the continuing encroachment of human activity on wilderness areas. In a broader regional context this area en-

compasses 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 the seven other management regions in Norway. The spatial extent of regional planning depends on the scale at which population processes are occurring.

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. Since then wolverine recovery in Norway has occurred, but also sheep stock numbers have increased while herding and livestock traditions had been lost. 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. In 2003 the Norwegian government adopted a new large carnivore management policy 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 several studies on large carnivore livestock depredation in Norway (e.g. Landa *et al.* 1999; Odden *et al.* 2002) argue that depredation-control measures will only be effective if eradication or severely reduction in population numbers is implemented as management goal. 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 also likely to be affected periodically. Reducing the wolverine population might therefore have not the desired effect of reducing conflict levels or enhancing the level of acceptance for wolverines, especially not in those areas that cover these 39 reproductions. Successful conservation of wolverines can therefore only be achieved by seeking a balance between biological processes, management practices and local social acceptance. Combining these three levels an effective measure to minimise the wolverine depredation is therefore to focus on mitigation measures and prevention such as for example the practise of systematically rounding-up sheep earlier in grazing areas with wolverine reproduction.

6 Publications

The scientific results of the studies will be published in referee journals and NINA-reports. An important part of the project was to disseminate the findings the different studies to government officials, organisations and individuals involved in wolverine management in a number of articles in popular scientific and management related journals and also by maintaining a continuous dialogue on results from these studies relevant to management practices. A broad public support and acceptance on a community level was sought by organising local public meetings prior to and after conclusion of the separate field-related studies. Finally, for general information on wolverines, updates on project activities and progress, and salient results web-based information aimed at the general public and regular project newsletters were emitted.

6.1 Scientific publications

- Dijk, J. van, Hauge, K., May, R., Landa, A. & Andersen, R. (2007) An evaluation of scat-analysis methods to assess wolverine *Gulo gulo* diet. – *Wildlife Biology*, 13(2), 62-67.
- Dijk, J. van, Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H. & Landa, A. (2008) Diet shift of a facultative scavenger, the wolverine, following the recolonization of wolves. – *Journal of Animal Ecology*, in press.
- Dijk, J. van, Andersen, T., May, R., Andersen, R., Andersen, R. & Landa, A. (2008) Foraging strategies of wolverines within a predator guild. – *Canadian Journal of Zoology*, in press.
- Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P. & Ellegren, H. (2004) Colonization history and non-invasive monitoring of a re-established wolverine (*Gulo gulo*) population. – *Conservation Biology*, 18(3), 676-88.
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6.3 Popular publications, presentations and media

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- Andersen, R. (2003) *Forskinga på jerv dei siste åra med spesiell vekt på Sør-Norge*. Presentation: R.i.m. Romsdal, Sunndalsøra.
- Andersen, R. (2003) *Orientering om jervprosjektet i Oppdal 2003*. Presentation: k.o.v.i.O. Beitelag, Oppdal.
- Andersen, R. (2006) *Jerv-Sau*. Presentation: Norges Naturvernforbund, Hamar.
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- Andersen, R. & Dijk, J. van (2004). *Forskning på jerv i område Alvdal 2004 og sau tapt*. Presentation: F. Beitelagene, Fjellopsyn, Alvdal.
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- Landa, A., May, R., Dijk, J. van & Andersen, R. (2003) *Sau og jerv i Knutshøyområdet*. Presentation: Beitelag, Follidal.

- May, R. (2002) Veelvraten in Noorwegen, onbekend maakt onbeschermd. - *Zoogdier* 13: 3-5. [i nederlands: Jerver i Norge, ukjent betyr uvernet.]
- May, R. (2004) *Oversikt og aktiviteter Jervprosjektet 2004 - Dovrefjell*. Presentation: Dovrefjell-rådet, Dovrefjell.
- Moen, T.O. (2003) Knallstart for Jerveprosjekt. - *Villmarksliv* 6: 16.
- Odden, J. (2006) *Overvåking av jerv*. Presentation: SNO, Snåsa.
- Odden, J. (2006) *Nasjonalt overvåkingsprogram for store rovdyr - overvåking av gaupe og jerv*. Presentation: Rovviltnemnda i Region 2, Drammen.

6.4 Theses

PhD theses

- Dijk, J. van (2008) *Foraging strategies of wolverines in a multiple-use landscape*. PhD thesis. NTNU/NINA, Trondheim, Norway, 190 pp.
- May, R. (2007) *Spatial Ecology of Wolverines in Scandinavia*. PhD thesis. NTNU/NINA, Trondheim, Norway, 200 pp.

MSc theses

- Andersen, T. (2003) *The wolverines (Gulo gulo) diet, hunting behaviour and intra-guild relations during the winter season in the boreal forests of southern Norway*. – University of Bergen, Institute of Biology, Bergen, Norway.
- Forland, J.M. (2004) *Sex-specific differences in lamb behaviour and predation vulnerability*. – The Agricultural University of Norway, Department of Ecology and Natural Resource Management, Ås, Norway.
- Gorini, L. (2006) *Multiscale analyses of the factors influencing den site selection in wolverines, Gulo gulo, in Norway*. – University of Rome "La Sapienza", Faculty of Mathematical, Physical and Natural Sciences, Rome, Italy.
- Gustavsen, L. (2006) *The diet of a facultative scavenger, the wolverine Gulo gulo, after recolonization of wolf Canis lupus in southern Norway*. – University of Oslo, Norway.
- Østereng, G. (2004) *Habitat selection and wolverine depredation-risk in free-ranging sheep at an alpine pasture*. – The Agricultural University of Norway, Department of Ecology and Natural Resource Management, Ås, Norway.

6.5 Scientific presentations and posters

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- Brøseth, H., Bø, T., Franzén, R. & Andersen, R. (2005) *Monitoring wolverine natal dens in Scandinavia*. Presentation: 1st International Symposium on Wolverine Research and Management, Jokkmokk, Sweden.
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- Dijk, J., van, Brøseth, H., Landa, A., Andersen, R. & May, R. (2005) *Status and distribution of wolverines in Norway*. Presentation: 1st International Symposium on Wolverine Research and Management, Jokkmokk, Sweden.
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- Gustavsen, L., Dijk, J. van, Landa, A., May, R., Andersen, R. & Andersen, R. (2005) *The effect of intra-guild species on wolverine prey availability and diet*. Presentation: 1st International Symposium on Wolverine Research and Management, Jokkmokk, Sweden.
- Hedmark, E., Persson, J., Segerström, P. & Landa, A. (2005) *Paternity analysis in Scandinavian wolverines*. Presentation: 1st International Symposium on Wolverine Research and Management, Jokkmokk, Sweden.
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- May, R. (2005) *Towards an IUCN Action Plan for the global conservation of the wolverine*. Presentation: 1st International Symposium on Wolverine Research and Management/Wolverine Workshop, Jokkmokk, Sweden.
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- May, R. (2007) *Spatial Ecology of Wolverines in Scandinavia*. Presentation: NTNU, Trondheim.
- May, R., Gorini, L., Dijk, J. van, Landa, A., & Andersen, R. (2006) *Wolverine den site selection at different spatial scales*. Presentation: 1st European Conference on Conservation Biology, Eger, Hungary.
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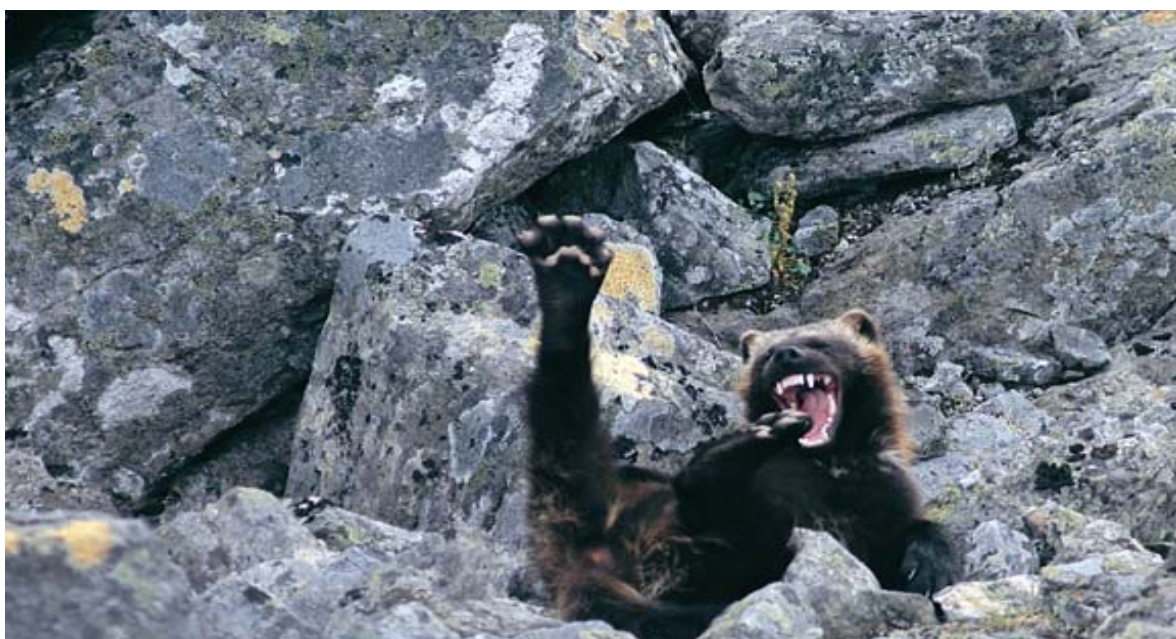
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