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

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Summary

1. The re-establishment of large carnivores in Norway has led to increased conflicts and the adoption of regional zoning for these predators. When planning the future distribution of large carnivores, it is important to consider details of their potential habitat tolerances and strength of interspecific differentiation. We studied differentiation in habitat and kill sites within the large-carnivore community of south-eastern Norway.

2. We compared habitat selection of the brown bear Ursus arctos L., Eurasian lynx Lynx lynx L., wolf Canis lupus L. and wolverine Gulo gulo L., based on radio-tracking data. Differences in kill site locations were explored using locations of documented predator-killed sheep Ovis aries L. 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.

3. Although bears, lynx, wolves and wolverines had overlapping distributions, 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. Some degree of sympatry was possible in over 40% of the study area, although only 1·5% could hold all four large carnivores together.

4. Synthesis and applications. A geographically differentiated management policy has been adopted in Norway, aimed at conserving viable populations of large carnivores while minimizing the potential for conflicts. Sympatry of all four carnivores will be most successful if regional zones are established of adequate size spanning an elevational gradient. High prey densities, low carnivore densities, low dietary overlap and scavenging opportunities have most probably led to reduced competitive exclusion. Although regional sympathy enhances the conservation of an intact guild of large carnivores, it may well increase conflict levels and resistance to carnivore conservation locally.

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

Introduction

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

Apart from direct competition for prey, possible sympathy of multiple carnivore species also depends on intra-guild competition and interference. Intra-guild competition is fiercer...
Habitat differentiation in a large-carnivore guild

STUDY AREA
Norway is the country in mainland Europe with the lowest human population density (c. 12 km\(^{-2}\)) and with large continuous areas of semi-natural landscapes. Despite the low human density, wilderness areas have declined dramatically in the last century through resource extraction (i.e. livestock grazing, hunting, timber logging), infrastructural development (i.e. roads, recreational cabins and hydropower plants), and recreation. Our study area (18 374 km\(^2\)) was located in south-eastern Norway. It consists of 10 municipalities in the northern parts of Hedmark County and three bordering municipalities in Oppland County (see corner Fig. 1), and was centred on lake Storsjøen (latitude 61°27′, longitude 11°18′). The river Glomma and the adjacent national highway RV3 run from north to south in the centre of the study area. The landscape consists of boreal forests interspersed with low mountain ranges. Areas above tree line, at 900–1000 m above sea level, are mainly found in the west and north of the study area. Infrastructure is mainly found in the west and east of the study area, and in the valley bottoms. All four large-carnivore species exist within the study area and were estimated by the national large-carnivore monitoring programme at 14–17 wolves (three to four packs or scent-marking pairs), 20–30 wolverines and 31–37 lynx (Broseth & Andersen 2004; Broseth, Odden & Linnell 2004; Wabakken et al. 2004). The total number of bears was estimated at nine to 13 for southeast Norway (Ostlandet) (Swenson et al. 2003). The populations of all four species are in a natural re-colonizing stage, with the bear population in particular being dominated by males. Bears and lynx were already present before the start of this study (1988) and have expanded their range from the (north)east and from the (south)east, respectively. Wolves re-colonized the study area in 1998 from the (south)east; wolverines followed the year after from the northeast and west. At present, all four species occur throughout the study area. The average winter densities of potential large prey species are 0·9 km\(^{-2}\) and 0·8 km\(^{-2}\) for moose Alces alces L. and roe deer Capreolus capreolus L., respectively (Solberg et al. 2003). However, roe deer are distributed less evenly over the area than moose. Other potential ungulate prey species are red deer Cervus elaphus L. and wild reindeer. Moreover, semi-domestic reindeer are herded in the north-eastern two municipalities of the study area. Potential small prey are tetraonids and other bird species, medium-sized and small rodents and insectivores, as well as medium-sized and small carnivores. Throughout the study area, with disjoint distribution and at highly variable densities, free-ranging, and mostly unattended domestic sheep and cattle Bos taurus L. graze in the forests and low mountain ranges during the summer (June–September) (Zimmermann, Wabakken & Dötterer 2003).

STUDY DESIGN AND SPATIAL SCALE
The scale (i.e. grain/resolution and domain/extent) of investigation of the differentiation in habitat tolerances among guild members is important, as ecological processes can occur at different spatio-temporal scales, which influence the strength of habitat preferences (Boyce 2006). Our spatially, but not temporally, overlapping data sets (Table 1) on the large-carnivore guild in one specific region of Norway best fit a landscape approach. To address differentiation among wide-ranging large-carnivore species, the resolution need not be very fine; a coarser grain will reduce intra-specific spatial heterogeneity at finer resolutions leaving the inter-specific
differences under study. However, the extent should be large enough to encompass the regional dynamics of the large-carnivore community in multiple-use landscapes. We therefore chose to study patterns of use on the landscape using a grain of $1 \times 1$ km resource units (pixels), and investigated habitat differentiation within the large-carnivore guild by comparing selection of geographical ranges among the species within the study area (first order selection, Johnson 1980).

Table 1. Sampling statistics of the radio-tracked large carnivores and predator-killed sheep in south-eastern Norway

|                        | Brown bear | Wolf | Lynx   | Wolverine |
|------------------------|------------|------|--------|-----------|
| **Statistics habitat** |            |      |        |           |
| Collection period      | 1988–2004  | 2001–2005 | 1995–2002 | 2003–2004 |
| Collection methods     | VHF, GPS   | GPS  | VHF, GPS | GPS       |
| No. of individuals     | 20         | 4*   | 16      | 4         |
| Adult females          | 5          | 2    | 10      | 3         |
| Adult males            | 15         | 2    | 6       | 1         |
| Individuals per year   | $4.9 \pm 1.4$ | $2.6 \pm 0.9$ | $7.6 \pm 4.6$ | $3.5 \pm 0.7$ |
| Total radio fixes      | 2194       | 2780 | 3681   | 453       |
| No. of radio fixes per individual | $110 \pm 139$ | $498 \pm 305$ | $230 \pm 144$ | $227 \pm 88$ |
| No. of habitat pixels  | 1169       | 874  | 1761   | 265       |
| **Statistics kill sites** |          |      |        |           |
| No. of sheep carcasses | 1558       | 416  | 861    | 364       |
| No. of kill site pixels | 760       | 102  | 462    | 218       |

*Two alpha pairs of two packs.
DATA SETS
The study was based on radio-tracking adult individuals within research projects on large carnivores (Table 1). Only locations more than 24 h apart were used in order to reduce autocorrelation (Otis & White 1999) and standardize between GPS and VHF data (i.e. several positions per day vs. up to one position per day, respectively). As the data were collected during different time periods, this study renders insight into spatial but not necessarily temporal sympathy of the four large carnivores.

Location of kill sites was assessed using locations of documented predator-killed sheep falling within the boundaries of the study area from the period 1994–2004 (Fig. 1a). To receive compensation for losses suffered by predators, it is economically important to the owners of free-ranging sheep to intensively search for carcasses throughout the summer grazing season (~100 days yr⁻¹). Carcasses are examined by trained personnel of the State Nature Inspectorate, who record the location and determine the species of the predator, based on well-documented species-specific kill patterns through necropsy (Landau 1999). Although the locations of sheep kills found are likely to be biased towards ease of human detection, this can be expected to be irrespective of carnivore species.

MODELLING AND STATISTICAL ANALYSES
All statistics were performed in R 2.5-1 (R Development Core Team 2007), the geographical analyses were performed in ArcView 3.3 and Spatial Analyst extension (ESRI Inc., Redlands, CA, USA). For each species, we transformed the set of radio-tracking locations and killed sheep into presence maps, where each 1 × 1 km pixel indicated whether or not it included one or more locations (Fig. 1). This large scale minimizes unwanted spatial autocorrelation and pseudo-replication effects. We expected a pseudo-replication effect for the members of the two wolf packs while travelling together, and for animals that were tracked over several years. Also, large carnivores, especially bears and wolves, often kill several sheep during one attack. Here we assumed that the individuals used in this study represented the resource selection of the species. Intra-specific variation was found to be insignificant compared to inter-specific variation (see Supplementary Material Appendix S1).

We modelled each species’ habitat selection relative to availability on a landscape scale, and each species’ location of kill sites relative to its habitat used (i.e. presence pixels), using logistic regression to estimate coefficients in exponential resource selection functions (Manly et al. 2002):

\[ w(x) = \exp(\beta_i + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + \ldots + \beta_n \cdot X_n) \]  

with \( \beta_i \) as the model coefficient of the \( i \)th of \( n \) habitat covariates, \( X \). Availability for habitat selection was considered to be the same for all species, and was based on a ‘presence’ map generated from a data set of 2500 points randomly spread throughout the study area following the same procedure as mentioned above (rendering 2311 availability pixels). Because the focus of this study was to elucidate habitat differentiation among large carnivores, we present the full models only. To evaluate predictive success of the resource selection function models we used the k-fold cross-validation procedures as proposed by Boyce et al. (2002). Cross-validated Spearman-rank correlations were calculated between 10 resource selection function bin ranks and area-adjusted frequencies for five model ‘test-training’ sets.

The resource selection functions for habitat selection were for each cross-validation set projected spatially on each 1 × 1 km cell across the study area to generate maps of the relative probability of occurrence for each species. For ease of interpretation, we classified the relative probabilities of occurrence into four broad classes: rare– (<−10), low– (−10−μ), moderate– (μ−10) and high– (>10) occurrence habitats. To gain better insight into the scale of our study area vs. necessary scales for regional zoning, we calculated the degree of overlap among species for each cross-validation set based on the distribution of moderate- and high-occurrence habitats for each species (i.e. pixels with relative probability > μ). Finally, we calculated the distribution of patch sizes for each species and degree of overlap, based on occurrence maps produced from the averages over the set of five cross-validation maps. Continuous patches were identified using the Patch Analyst 2.2 extension (Rempel 2000), after smoothening the occurrence maps using a 3 × 3 moving window majority filter.

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

\[ \beta'_i = \frac{\hat{\beta}_i - \mu}{\sigma} \]  

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

\[ D_{jk} = \left( \sum_{i=1}^{n} (\beta'_i - \beta'_j)^2 \right)^{1/2} \]  

We incorporated the uncertainty from the resource selection functions by calculating the average multivariate distances from 1000 iterated random draws from a distribution with mean \( \bar{\beta} \) and standard error \( S' \). We used a linear stretch to scale the multivariate distances between −1 and +1 for totally differentiated and identical selection, respectively.

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\[
D_x = 1 - 2 \cdot \frac{D_a - D_{na}}{D_{na} - D_{na}}
\]

eqn 4

Finally, we performed multinomial logistic regression (Hosmer \\
& Lemeshow 2000) on the combined presence data over all species
(separately for habitat and kill sites) to investigate each species’
degree of differentiation in habitat use (or location of kill sites) relative
to habitat (or kill sites) used by the other species, and determine
which covariates they differed, and how strongly. The species were
taken as a categorical dependent variable (1 = bear, 2 = wolf, 3 = lynx,
4 = wolverine). By taking each species as a reference category in an
iterative way, each unique species combination could be compared.

Results

HABITAT USE AND LOCATION OF KILL SITES

All four habitat models had good predictive performance,
given the significant Spearman-rank correlations across the
five cross-validation sets (bear: \( r = 0.980 \pm 0.010 \) (SD),
\( P < 0.001 \); wolf: \( r = 0.950 \pm 0.026 \), \( P < 0.001 \); lynx: \( r = 0.979 \pm
0.014 \); \( P < 0.001 \); wolverine: \( r = 0.859 \pm 0.097 \), \( P < 0.001 \)).
The models explained 13–14% of the deviance for bears,
wolves and wolverines, and 40% for lynx (Nagelkerke’s \( R^2 \) of
0.139, 0.129, 0.142 and 0.402, respectively). The resource
selection functions for bears, wolves and lynx indicated that
the presence of these species was generally associated with
rugged, forested areas at lower elevations, and relatively close
to private roads (Fig. 2a, Supplementary Material Table S1).
Of these species, lynx preferred the lowest elevations, the
densest forests, and kept closest to infrastructure. Wolverines,
on the other hand, selected rugged terrain at higher elevations
and away from buildings but closer to public roads. They did
not show any selection for tree cover or private roads.

The kill site models for bears, wolves and lynx had good
predictive performance and explained 16–22% of the deviance
(bear: \( r = 0.919 \pm 0.048 \) (SD), \( P < 0.001 \), Nagelkerke’s \( R^2 \) =
0.201; wolf: \( r = 0.804 \pm 0.081 \), \( P < 0.001 \), \( R^2 = 0.163 \); lynx:
\( r = 0.932 \pm 0.018 \); \( P < 0.001 \), \( R^2 = 0.215 \)). The kill site model
for wolverines had a lower, but significant, Spearman-rank
 correlation and explained over 50% of the deviance (wolverine:
\( r = 0.601 \pm 0.159 \) (SD), \( P < 0.05 \), Nagelkerke’s \( R^2 = 0.570 \)).
Sheep kill sites were for all four species found at higher
elevations and closer to private roads and buildings compared
to their selected habitat (Fig. 2b, Supplementary Material
Table S1). The three forest-dwelling species killed sheep in less
rugged terrain and farther from forest edges; opposite effects
were found for the wolverine. All species, except lynx, killed
sheep farther from public roads.

PATTERNS OF INTRA-GUILD DISTRIBUTION

A clear distinction can be seen between the distributions of
wolverines vs. the three forest-dwelling carnivore species
(Fig. 1b). Whereas wolverine presence was most probable in
the more mountainous northwest of the study area, the presence
of the other three species was more distributed in the south
and along the Glomma Valley running from north to
south in the centre of the study area. Using a minimum
threshold of moderate occurrence, 7490 km² ± 87 (SD) of the
study area was defined as suitable for bears, and 7126 ± 124,
5214 ± 64 and 5418 km² ± 117 were classified as suitable for
wolves, lynx and wolverines, respectively. The mean patch
size for bear, wolf, lynx and wolverines were 93 ± 780 (SD),
149 ± 959, 133 ± 664 and 54 ± 210 km², respectively. The
wolverine both had a high amount of small patches (< 10 km²)
and the smallest average patch size >1000 km² (Fig. 3a).

We calculated the degree of overlap among species and
patch sizes based on the distribution of moderate- and high-
ocurrence habitats in the occurrence maps for each species
(Fig. 1c). Using a minimum threshold of moderate occurrence,
4893 km² ± 141 (SD) of the study area could hold only one
species, whereas 2612 ± 50, 4671 ± 72 and 280 ± 38 km²
were classified as suitable for two, three and four species,
respectively. In total, 4496 km² ± 47 (SD) of the study area
could hold all three forest species. Again, the clear distinction
between sympathy of the three forest-dwelling species and
the wolverines is clear (Fig. 1c), with a 60–99% overlap between
bears, wolves and lynx and a 5–29% overlap with wolverines
(Table 2). The mean patch sizes for overlap of one, two, three,
four species and overlap of the three forest species were
12 ± 80 (SD), 5 ± 8, 28 ± 269, 2 ± 1 and 47 ± 365 km², respectively.
Both the overlap of three species and of the forest-dwelling
Table 2. Proportional degree of overlap (± SD) in distribution between species based on the distribution of occurrence for each species (pixels with a probability higher than the mean), averaged over five cross-validation sets

| Species distribution | Proportional overlap with distribution of |
|----------------------|-----------------------------------------|
|                      | Brown bear | Wolf | Lynx | Wolverine |
| Brown bear           |            |      |      |           |
| Wolf                 |            |      |      |           |
| Lynx                 |            |      |      |           |
| Wolverine            |            |      |      |           |

Table 3. Strength of differentiation in habitat use and location of kill sites between species as measured by the multivariate distances between the standardized partial regression coefficients, given in Fig. 2. Negative mean values indicate differentiation and positive values similar use/location. When the 95% CI includes zero; neither could be determined. Significant results are given in bold

| Species pairs | Mean       | SD        | 95% CI       |
|---------------|------------|-----------|--------------|
| Habitat use   |            |           |              |
| brown bear    | 0.561      | 0.112     | 0.341–0.781  |
| wolf          | 0.114      | 0.076     | −0.034–0.263 |
| lynx          | −0.281     | 0.117     | −0.511–0.051 |
| wolf          | 0.577      | 0.116     | 0.349–0.804  |
| lynx          | −0.513     | 0.104     | −0.717–0.309 |
| Kill sites    |            |           |              |
| brown bear    | −0.181     | 0.176     | −0.526–0.163 |
| wolf          | 0.595      | 0.098     | 0.403–0.786  |
| lynx          | −0.329     | 0.112     | −0.549–0.110 |
| wolf          | −0.303     | 0.156     | −0.608–0.002 |
| lynx          | −0.627     | 0.132     | −0.886–0.368 |
| Wolverine     | −0.512     | 0.102     | −0.712–0.313 |

Although no differentiation was found for bears–wolves and wolves–lynx, bears and lynx killed sheep in similar habitat (Table 3).

Multinomial logistic regression indicated a clear differentiation in use of habitat covariates among all four species (Nagelkerke’s $R^2 = 0.318$, Fig. 4a). The strongest differentiation in preference was found for elevation. Lynx were found at the lowest elevations, followed in rising elevation by wolves, bears and wolverines (Fig. 4a, Supplementary Material Table S1). The bear was found in less rugged terrain and closer to forest edges than the other three species. Also, a clear effect in differentiation was found for tree cover and infrastructure. The lynx preferred pixels with a higher percentage of tree cover, and closer to private roads and buildings than the bear and wolf. The wolverine was found in more open areas far from private roads and buildings. The wolf and wolverine also differentiated from bear and lynx in their proximity to public roads.

Multinomial logistic regression on the locations of predator-killed sheep indicated a clear differentiation in kill sites among species (Nagelkerke’s $R^2 = 0.485$, Fig. 4b, Supplementary Material Table S1). As for the differentiation in habitat, elevation of kill sites had a similar strong differentiating

Fig. 3. Size distribution of habitat patches for (a) four large-carnivore species identified using resource selection functions (Fig. 1b) and (b) degree of overlap in south-eastern Norway (Fig. 1c). For the highest two categories the average patch size is given.

DIFFERENTIATION IN HABITAT AND KILL SITES

Overall, wolverines differed in their habitat use compared to the three forest-dwelling carnivore species (Table 3). Bears–wolves and wolves–lynx selected similar habitat, but no differentiation was found between bears and lynx. The overall differentiation in location of kill sites showed a clear difference for wolverines compared to the three forest-dwelling species.
effect; except in the case of wolf–lynx kill sites. For these two species, ruggedness and distance to public roads at kill sites differed most. Lynx and wolverines killed sheep in more rugged terrain than bears and wolves. Wolverines killed sheep in more open areas, whereas bears chose more forested sites closer to forest edges. Lynx stayed closer to public roads and buildings than the other species. Wolves killed sheep closer to private roads than bears and wolverines.

Discussion
The results from this study indicate that the three forest-dwelling large-carnivore species, the lynx, wolf and bear, had relatively similar habitat preferences. All three species selected rugged, forested areas at lower elevations. In contrast, the wolverine selected open, rugged terrain at higher elevations and killed sheep in similar terrain, but farther from infrastructure. This result fits well with the perception that the wolverine is a carnivore of remote alpine regions (May et al. 2006; Copeland et al. 2007). Wolverines overlapped most with bears and least with lynx (cf. Carroll, Noss & Paquet 2001). Within the study area, sympatry of wolverines with the three forest-dwelling carnivores appears to depend on the availability of mountain ranges as a spatial refuge. Wolverines in our study area, however, depend highly on moose carcasses in their diet both from hunting leftovers and wolf-kills (van Dijk, Gustavsen, Mysterud, May, Flagstad, Broseth, Andersen, Andersen, Steen & Landa 2008). The wolf is likely to be least affected by intra-guild aggression; rather it may instigate it (i.e. intra-guild predator, Palomares & Caro 1999). Additionally, wolves may facilitate wolverines with scavenging opportunities (Landa et al. 1997; Wilmers et al. 2003), which may enhance sympatry (Landa & Skogland 1995).

Despite their similar potential distribution patterns, the three forest-dwelling species had clear differences in habitat and kill sites. Bears preferred less rugged and higher elevation terrain than wolves and lynx, and chose more forested kill sites closer to forest edges. Although both wolves and bears feed on moose (Sand et al. 2005; Swenson et al. 2007), aggressive exploitative competition is not likely to be of significance because of the omnivorous diet of bears (Dahle et al. 1998) and low densities of both bears and wolves in the study area.
Bears may also benefit to some extent from the presence of other predators through increased scavenging opportunities (MacNulty, Varley & Smith 2001; Wilmers et al. 2003). Our study showed that wolves and lynx differed least in habitat use. However, lynx used denser forests at lower elevations and killed sheep in more rugged terrain than wolves, which may reflect differences in hunting techniques (i.e. stalking vs. chase hunt), different habitat preference during hunting and avoidance of intra-guild predation. Also, lynx prey mainly on roe deer and small game (Odden, Linnell & Andersen 2006) in our study area.

In this study, we modelled carnivore selection for habitat and location of kill sites. Although resource selection in carnivores will also depend on local differences in wild ungulate densities and probability of encounters (Hebblewhite, Merrill & McDonald 2005), no such fine-scale prey data were available. As expected, kill sites were biased towards higher-lying, more open areas closer to private roads and buildings, indicative of sheep grazing preferences and ease of human detection. Kill sites may however be biased by specific sex or age groups of large carnivores (e.g. lynx males: Odden et al. 2006; wolverine females: Landa et al. 1997; young dispersers of all species). Also, most bear kill sites were found in the lower occurrence classes, which is likely to be due to the bears’ non-territorial behaviour. Still, understanding differentiation in kill sites among species provides important information for future management of depredation conflicts. Overall, elevation had the strongest differentiating effect both on selection of habitat and location of kill sites in all four large carnivores. The presence of guild members may well have resulted in elevational shifts in their respective distributions to avoid aggressive interactions. It is likely, however, that high prey densities, low large-carnivore densities (due to management actions) and low dietary overlap have led to a situation with reduced competitive exclusion (cf. Heithaus 2001).

In a broader regional context, our study area encompasses similar habitat/land use compositions and prey densities as that found in large stretches of southern Norway and central Sweden, and has a carnivore management regime comparable to other regions in Norway. The spatial extent of regional planning depends on the scale at which population processes are occurring. Our estimates 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 (cf. Mech 1995). Large carnivores are known to be vulnerable to anthropogenic disturbance (e.g. May et al. 2006; Nelleman 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 (see Fig. 1c).

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

Although sympatry of two or more species was possible in over 40% of the study area, only 1-5% was suitable for all four species together. Sympatry of all three forest carnivores was possible in one-quarter of the study area. Successful regional zoning of all four carnivores may therefore rely on establishing zones of adequate size 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 (Wabakken 2001). On the other hand, fostering sympatry of all four species may well increase conflict levels and resistance to carnivore conservation locally (Wabakken 2001; Linnell et al. 2005). These conflicts may be reduced by discouraging extensive sheep husbandry (Zimmermann et al. 2003; Milner et al. 2005), employing effective preventive and mitigation measures required for adequate compensation schemes, promoting different lifestyles and livelihood (e.g. ecotourism and outdoor recreation), and also allowing for limited control (Linnell et al. 2005; Swenson & Andrén 2005). However, the social context (non-material nature) of many of the large-carnivore conflicts in Norway should never be forgotten (Skogen 2003). Our study results may provide guidance to managers attempting to design regional-scale zoning to facilitate recovery of large carnivores in Scandinavia.

Acknowledgements

This was a collaborative study of the Scandinavian Brown Bear Research Project, Scandinavian Lynx Project (SCANDLYNX), Scandinavian Wolf Project (SKANDULV) and the Norwegian Wolverine Project. These projects have been financed by the Norwegian Research Council, Norwegian Directorate for Nature Management, Swedish Environmental Protection Agency, Norwegian counties, WWF-Sweden, Norwegian Institute for Nature Research, and Hedmark University College. The writing of this manuscript was made possible by a specific donation from Alertis, Fund for Bear and Nature Conservation, the Netherlands. We would furthermore like to thank the field coordinators R. Andersen, S. Brunberg and T. Stromseth, and hundreds of field trackers, volunteers and students for all the data they collected within the different carnivore projects. The comments of M. Hebblewhite and two anonymous referees greatly improved earlier versions of this manuscript.

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Received 16 April 2007; accepted 28 June 2008
Handling Editor: Mark Hebblewhite

Supplementary material
The following supplementary material is available for this article:

Appendix S1. Intra- vs. inter-specific differences among four large-carnivore species

Table S1. Statistics for the radio-telemetry data and locations of predator-killed sheep

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01527.x
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