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

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

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

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

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

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

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

Material and methods

Study areas

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

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

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

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

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

Radio-tracking and home ranges

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

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

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

Definition of habitat availability

Frequently, habitat availability is defined by selecting arbitrary study area boundaries (Aebischer et al. 1993b, McClean et al. 1998). Following animals at different sites or in different years complicates the definition of available habitat. To avoid this problem we defined a general region of probable wolverine movement for both study areas (Schadt et al. 2002). The area available to the wolverines is represented by the 100% MCP polygon drawn around all independent tracking points. To include the area possibly available to 'boundary individuals', the MCP was enlarged by the upper limit of the one-tailed 95% confidence interval of the mean activity radius (mean activity radius + t *SE) over the tracked wolverine population. Activity radii were calculated as the mean linear distance between each independent tracking point and the geographical centre (arithmetic mean) of each individual's multi-annual home range. The buffers were 13.5 km (10.2 + 1.812*1.8; N = 11) in south-central Norway and 7.4 km (6.5 + 1.689*0.5; N = 36) in Troms. The study areas therefore encompassed a total of 10,839 km^2 in south-central Norway and 10,652 km^2 in Troms.

Background maps

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

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

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

Compositional analysis

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

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

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

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

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

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

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

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

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

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

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

Results

Home range location

South-central Norway

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

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

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

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

Troms

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

Use within home ranges

South-central Norway

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

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

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

Troms

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

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

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

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

Habitat differentiation by age of female wolverines in Troms

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

Discussion

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

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

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

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

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

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References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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