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Predicting occurrence of wolf territories in Scandinavia

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Abstract

We used logistic regression to compare a set of habitat features inside known Scandinavian wolf *Canis lupus* territories with the same habitat features in areas outside known territories, but still close enough to be available for wolf colonization. In addition, we analysed changes in habitat variables over time within wolf territories. Wolf territories had lower densities of roads, built-up areas and open land than areas outside wolf territories, but there was no difference in the density of the wolves' main prey, elk *Alces alces*. The logistic regression model classified 79% of Scandinavia outside the reindeer husbandry area as suitable wolf habitat, that is with a probability of wolf occurrence >0.5. The proportion of built-up areas within the wolf territory decreased as the 'borders' of the wolf territory changed over time. Our model had a reasonably high predictive power, with correct classification in 90% (18 of 20) of the observed wolf territories in the study area. Polygons, randomly distributed outside the observed wolf territories, were correctly classified as not being occupied by wolves in 85% of the cases (17 of 20). This allows a more effective use of resources to, for example, prevent wolf depredation on livestock and dogs.

Introduction

A major difficulty in the management of any species is the ability to distinguish correctly between suitable and unsuitable habitats (Shriner, Simmons & Farnsworth, 2002). Identifying variables that are both readily available over large areas and correlated with species occurrence is essential to effective management (Simberloff, 1988). The usefulness of a habitat suitability model increases but the accuracy decreases as the predictions of the model become more general and thus applicable across a range of ecological contexts (Rodriguez & Andrén, 1999). The disadvantage of reduced accuracy should be weighed against the potential of a model to be generally applied.

Many countries in Europe as well as states in the USA have wolf *Canis lupus* populations that are growing in numbers and expanding in range (Boitani, 2003). In a region like Scandinavia, with a small but growing wolf population, management decisions crucial for wolf conservation are made in the early stages of wolf recolonization. Knowledge, models and predictions from other parts of the world will thus be more influential in a phase when management decisions have the greatest potential to affect conservation success. It is valuable for managers not only to gain insight on factors affecting conservation efforts, and models predicting effects in other parts of the world, but also to obtain data on to what extent the knowledge, models and predictions may or may not be applied in regions or countries other than where they were produced.

In contrast, prey density has often been an insignificant variable in habitat suitability modelling, probably because wild prey density has been high enough in most of the studied areas (Thiel, 1985; Mech *et al*., 1988; Thurber *et al*., 1994; Fritts & Carbyn, 1995; Mladenoff *et al*., 1995; Harrison & Chapin, 1998; Mladenoff, Sickley & Wydewen, 1999). Several studies of wolf colonization and habitat use in North America have shown that human-related mortality and disturbance were the major factors affecting wolf distribution (Thiel, 1985; Mech *et al*., 1988; Thurber *et al*., 1994; Fritts & Carbyn, 1995; Mladenoff *et al*., 1995, 1999; Harrison & Chapin, 1998). In Italy, however, where livestock may have been the only prey over large areas, abundance of wild prey may have been a significant factor for wolf colonization (Massolo & Meriggi, 1998).

In Scandinavia (Norway and Sweden), the wolf population declined strongly throughout the 19th and 20th centuries leaving an estimated less than 10 individuals at the time of protection, 1966 in Sweden and 1972 in Norway (Haglund, 1968). During the 1970s and 1980s, there was an increasing number of wolf observations in the south-central part of Scandinavia (Wabakken *et al*., 2001). In 1983 the first wolf reproduction, after the protection, was confirmed. Since 1983 there have been annual wolf reproductions in the south-central part of Scandinavia with a yearly increase in the wolf population of about 20% during the 1990s (Wabakken *et al.*, 2001). In 2003, the number of reproducing wolf pairs in Scandinavia was 11, and the total wolf population in spring 2004 was 101–120 individuals (Aronson *et al.*, 2004).

Depredation by wolves has been estimated to 300–600 sheep and 15–20 dogs annually (Directorate for Nature Management, 2004; Swedish Wildlife Damage Centre, 2004). In the area of the present distribution of wolves, depredation on dogs is one of the main causes of conflicts with humans. Another important source of conflict is human fear of wolves. An attitude survey showed that more than 30% of Scandinavians expressed a fear of having wolves in the area where they live (Dahle, 1987; Ericsson & Heberlein, 2003), whereas depredation on sheep and competition for game such as elk *Alces alces* and roe deer *Capreolus capreolus* was less important (Ericsson & Heberlein, 2003).

Wolf depredation on livestock and dogs has resulted in governmental programmes for compensating damage and subsidizing preventive measures. Livestock owners are compensated by the government for all livestock killed by wolves. Compensation is generally well above market value for killed or injured livestock. Subsidies for preventive measures (mainly electrical fencing) are offered to all sheep owners in wolf territories.

The aims of this study were to test the predictive power of a wolf habitat model from Wisconsin (Mladenoff *et al.*, 1995, 1999) on Scandinavian conditions and to use field data in a geographical information survey (GIS) to explore which habitat variables are the most important predictors of wolf territory occurrence in Scandinavia. As part of this, we were also interested in knowing how the proportion of important habitat variables changes as wolf territory borders change between years.

Methods

Study area

The study area was located in south-central Scandinavia between latitude 54°N and 75°N and longitude 27° and 14°E, defined by a minimum convex polygon (MCP) covering all known Scandinavian wolf territories from 1997 to 2001 (Fig. 1). The total area was 83 000 km^2 with an altitude range between 50 and 1000 m a.s.l. This area has, for Scandinavia, a continental climate with average temperatures of 15 °C in July and about −7 °C in January (Swedish Meteorological and Hydrological Institute). From December to March the ground is generally covered with snow of varying depth (20–50 cm). Boreal coniferous forests cover most of the area, which is dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, and sometimes mixed with birch *Betula pendula* and *Betula pubescens*, aspen *Populus tremula* and alder *Alnus incana* and *Alnus glutinosa*. The area is characterized by intensive forestry with clear-cuts and areas of young forest. Intensive forestry has led to high densities of forest roads. Human population density varies greatly, but averages <1 person km^{-2} (Wabakken *et al.*, 2001). Potential prey species in the area are elk, roe deer, red deer *Cervus elaphus*, badger *Meles meles*, beaver *Castor fiber*, mountain hare *Lepus timidus*, capercaillie

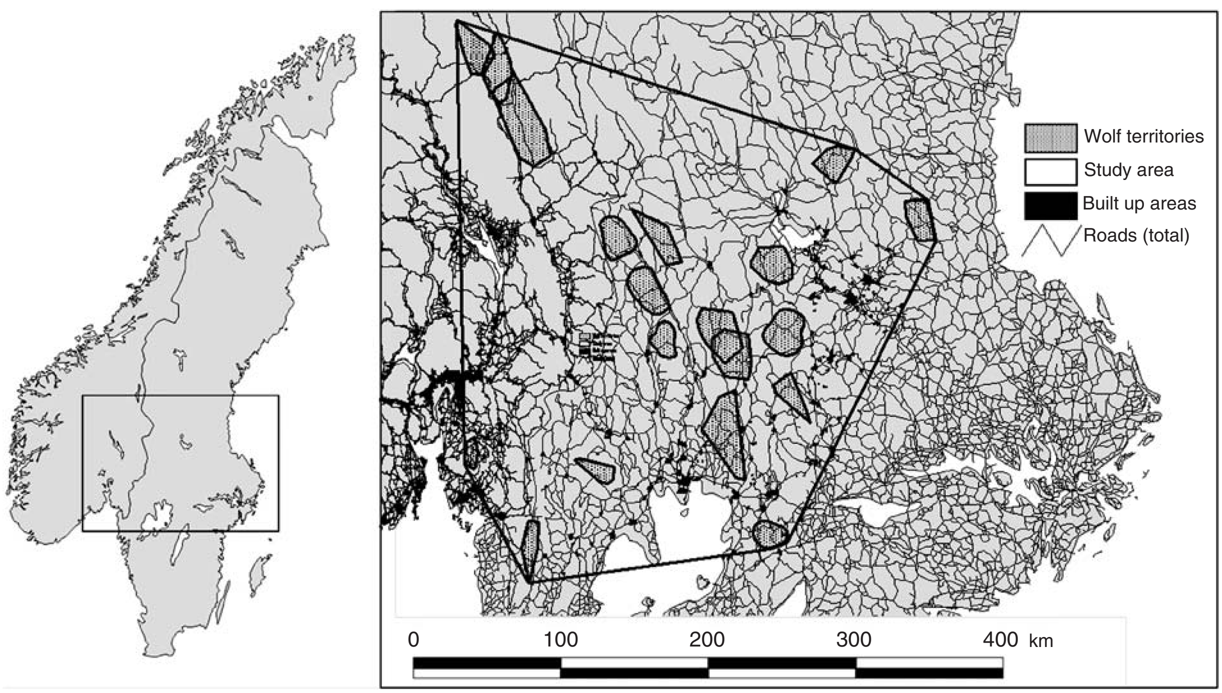

Figure 1 The Scandinavian peninsula with our study area (box). Wolf *Canis lupus* territories, roads and built-up areas are plotted on the map.

Tetrao urogallus and black grouse *Tetrao tetrix* (Olsson *et al*., 1997). Other large and medium-sized predators in the study area are lynx *Lynx lynx*, brown bear *Ursus arctos* and red fox *Vulpes vulpes*.

At present there are no wolf territories in the reindeer husbandry area, which is the northern 30% of Scandinavia. Because there are so many differences in, for example, prey species and prey densities as well as in human land use in the reindeer husbandry area, compared with the rest of Scandinavia, we chose not to extrapolate our results to that part of Scandinavia.

Wolf territories

For eight territories without radio-collared wolves, territory boundaries were defined from observations of wolf scent markings found during snow tracking; the different packs were distinguished by simultaneous snow tracking and DNA from scats. For each of the 12 territories with radio-collared wolves, the territory was defined as an MCP on 90% of uncorrelated fixes (>3 days in between). The mean MCP size of the Scandinavian wolf territories was 1000 km^2 (range: 300–2000 km^2). There were no significant differences in the average territory size between those of radio-collared wolves and the eight territories without radio-collared wolves. (Mann–Whitney U, $n_1=12$, $n_2=8$, $Z=-1.60$, $P=0.11$). An ArcView extension was constructed to redistribute the 20 observed wolf territory polygons randomly over the study area. The polygons were allowed to rotate but could not be placed closer than 10 km to an observed wolf territory, in order to minimize effects from potential errors made in determining territory borders (Mladenoff *et al*., 1995). The county administration boards are responsible for finding all new wolf territories and determine their approximate size and distribution. Each county administration board has field personnel driving transects with a car and snowmobile during winter. In summer, wolf observations and DNA from scats are used for finding newly formed territories. Given the limited size and distribution of the Scandinavian wolf population and the high density of local roads, it is very unlikely that new wolf territories are formed without being detected. Thus, the randomly distributed polygons can be regarded as true absences. To assess changes in the proportion of habitat variables in wolf territories, over time (as the MCP of wolf territories often changes somewhat between years), habitat composition in the first year of occupation was compared with the latest year of wolf occupation in territories. The range between first and latest years compared was from 1 to 3 years. For this comparison to be made, there had to be at least 25 independent telemetry fixes from the territories' first and last years, respectively.

As a coarse measure of wolf mortality in the different territories, we used the number of wolf individuals in each territory during the first winter after reproduction. The number of wolves in each territory was the minimum number of wolves documented in the respective territory each season, mainly based on snow tracking, but direct observations made by field personnel were also used (Aronson *et al*., 1999, 2000, 2001, 2002). A lower proportion of a habitat variable in wolf territories compared with areas outside wolf territories may be due to either avoidance by wolves or the habitat variable being positively correlated with wolf mortality. We therefore tested the degree of correlation between the different habitat variables and the number of wolves in winter after the first reproduction.

Habitat variables

The choice of habitat variables in this study was based on earlier studies, mainly from North America, as one of our objectives was to assess the predictive power of a Wisconsin habitat model in Scandinavia. The mean number of elk shot per 10 km^2 (i.e. elk hunting bag) in the respective hunting districts for the years 1998, 1999 and 2000 was used as an index of elk density in each hunting district (County Administrative Boards, unpubl. data). Cederlund & Markgren (1987) (Ericsson & Wallin, 1999) showed that elk hunting bag was highly correlated to elk densities in Sweden. As wolf territories often overlap more than one hunting district, elk hunting bag data from each overlapping district were weighted in relation to their proportion of the total wolf territory area.

We divided land types into three different categories: forested land, open land and built-up areas. We only used the latter two in the analysis because whatever is left is forest. Data for open land and built-up areas (proportion of wolf territory) were obtained from the governmental land mapping offices in Sweden and Norway at a scale of 1:100 000. The open land consisted almost exclusively of agricultural land, but a small proportion consisted of gravel pits, golf courses, etc. The definition of built-up areas was that used by Statistics Sweden (2000), where a built-up area is an area with >200 inhabitants and <200 m between the buildings. Roads (km road per km^2 wolf territory) were divided into three different categories: national roads, regional roads and local roads. National and regional roads are always paved whereas local roads most often are not. Traffic intensity, expressed as the average number of vehicles per day, was >1000 for national roads, >500 for regional roads and <500 for local roads (Swedish National Road administration database 2006). For the GIS analysis, ArcView 3.2 was used.

Test of a habitat model from Wisconsin

We tested the logistic regression model from northern Wisconsin [$\text{logit}(p)=-6.5988+14.6189*\text{road density}$; Mladenoff *et al*., 1995, 1999] on our data on wolf territory distribution in Scandinavia. The estimated road density from northern Wisconsin was based on roads used by cars, but excluding unimproved forest roads or trails. To correct for possible differences in the classification of roads between Wisconsin and Scandinavia, we used the combination of national and regional roads as well as the total road density (national, regional and local roads). If the model returned a

$P > 0.5$ for a wolf territory, it was considered a correct prediction; if the model returned a $P < 0.5$ for a random polygon, it was considered a correct prediction.

Logistic regression analysis

The difference between wolf territories and randomly distributed polygons was analysed using logistic regression. Variables that added significantly ($P < 0.05$) to the model were included in the model (forward stepwise selection). We restricted the number of variables in the model to two, because of the small sample size (total $n = 40$). The probability cut-off was set to the value where receiver operation characteristics (ROC) plots indicated the highest proportion of correct predictions (Pearce *et al.*, 2002).

Results

Test of the model from Wisconsin

Using a cut-off at $P = 0.50$, the model from Wisconsin predicted wolf territories to be more likely to occur in areas with road densities less than 0.45 km km^{-2}. The model correctly predicted $n = 20$ of 20 Scandinavian wolf territories, but only one random polygon was correctly predicted. The mean probability of a wolf territory was 0.97 ($\pm$0.0078SE) for the Scandinavian wolf territories and 0.89 ($\pm$0.047SE; Mann–Whitney, $nZ = -4.53$, $P < 0.001$) for the random polygons when using the total road density (national, regional and local road) as an estimate of road density.

Habitat variables in Scandinavia

All land and road variables we tested were lower (and thus forest cover was higher) within wolf territories compared with the randomly distributed polygons (Table 1), but elk hunting bag levels were similar. The proportion of open land within the wolf territory was the single best variable describing the occurrence of wolf territories, followed by local road density, total road density and built-up areas (Table 2). However, several of the variables were intercorrelated, particularly those describing human activity, such as open land, regional and local roads (Table 3). In a multiple logistic regression, only local road density added significantly to open land (Table 4). We selected the model with open land and local road density: Logit(p) = 6.22–47.69*open land −25.09*local road density (log likelihood ratio test $G = 33.66$, d.f. = 2, $P < 0.001$).

The ROC plot suggested a probability threshold of 0.5. The model correctly classified 85.0% (17 of 20) of the observed randomly distributed polygons as not being occupied by wolves and 90.0% (18 of 20) of the observed wolf territories, when tested with a jackknife procedure and using 0.5 as a cut-off, which gives a total correct classification rate of 87.5% (35 of 40; Fig. 2). The model predicted that 79% of Scandinavia outside the reindeer husbandry area had a probability of more than 0.50 of having a wolf territory (Fig. 3). This corresponds to an area of 660 000 km^2.

Habitat changes within wolf territories over time

There was a significant decline in the proportion of built-up areas over the years within wolf territories (Wilcoxon sign rank test, $Z = 2.54$, $n = 10$, $P = 0.018$). No significant

Table 1 Mean and range, within brackets, for the different habitat variables in Scandinavian wolf *Canis lupus* territories and randomly distributed polygons

Variable	Wolf territories	Random polygons
National road density (km km^{-2})	0.004 (0–0.05)	0.02 (0–0.11)
Regional road density (km km^{-2})	0.03 (0–0.25)	0.072 (0–0.49)
Local road density (km km^{-2})	0.10 (0.006–0.19)	0.2 (0.03–0.30)
Total road density (km km^{-2})	0.15 (0.03–0.34)	0.31 (0.14–0.65)
Built-up area (proportion)	0.0006 (0–0.005)	0.02 (0–0.08)
Open land (proportion)	0.07 (0.0007–0.11)	0.12 (0.02–0.58)
Forest land (proportion)	0.98 (0.91–0.99)	0.87 (0.41–0.99)
Elk hunting bag (n/10 km^2)	3.97 (1.36–6.24)	3.84 (2.60–4.47)

Table 2 Logistic regression models with a single variable predicting the probability of a wolf *Canis lupus* territory in an area

Variable	Regression coefficient	SE	P value	Log likelihood	AUC value
Open land	−53.53	16.09	0.001	−14.12	0.93
Local roads	−27.61	9.93	0.005	−14.23	0.88
Total road density	−20.29	6.99	0.004	−14.39	0.87
Built-up area density	−495.65	253.35	0.050	−14.21	0.84
National roads	−50.48	24.16	0.037	−18.18	0.76
Elk hunting bag	+0.79	0.54	0.14	−20.94	0.66
Regional roads	−5.87	10.04	0.558	−22.00	0.59

Twenty observed wolf territories were compared with 20 randomly distributed polygons.

Table 3 Correlation matrix (Pearson r) between the habitat variables used in the analysis

Variable	Proportion of open land	Proportion of built-up area	National roads	Regional roads	Local roads	Total roads
Proportion built-up area	0.10					
National road density	0.12	0.15				
Regional road density	0.32	0.20	−0.21			
Local road density	0.41	0.23	0.41	0.08		
Total road density	0.41	0.29	0.52	0.35	0.92	
Elk hunting bag	−0.05	−0.13	−0.08	−0.08	−0.25	−0.18

Table 4 Performance of different logistic regression models for predicting the presence of wolf *Canis lupus* territories in Scandinavia

Model no.	Variable(s)	Log likelihood	AICc value	ΔAICc value	AUC value	P value	Partial P value
1	Open land + local roads + built-up areas	−8.73	24.96		0.99	<0.001	0.01 0.04 0.10
2	Open land + local roads	−10.89	26.48	1.52	0.95	<0.001	<0.001 0.01
3	Open land	−14.12	30.46	3.98	0.92	<0.001	

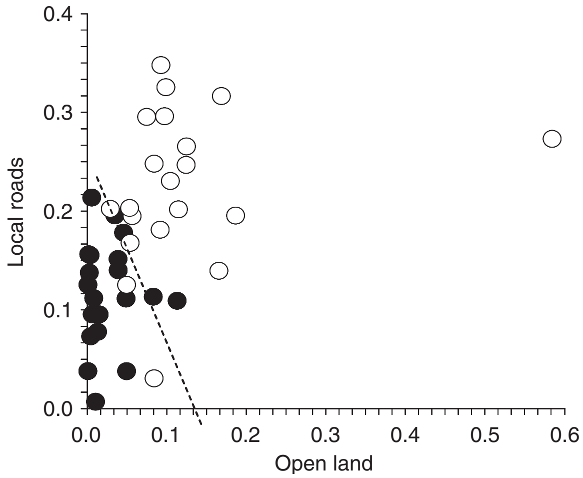

Figure 2 Wolf *Canis lupus* territories (●) and randomly distributed polygons (○) in relation to the proportion of open land and local road density (km km^{-2}) within the territories. The line indicates the cut-off of P=0.50 according to the habitat model (Table 4).

change over the years could be found for open land (Wilcoxon sign rank test, $Z=1.82$, $n=8$, $P=0.20$) and local road density (Wilcoxon sign rank test, $Z=0.66$, $n=10$, $P=0.50$). Data on elk hunting bags were not available for this analysis.

Habitat variables and average number of wolves in each territory

The number of wolves in the territory in the first year after reproduction showed a tendency to be negatively correlated to the proportion of built-up areas (Spearman rank, $r_s=-0.40$, $n=19$, $P=0.09$). However, the number of wolves in the territory in the first year after reproduction was not significantly correlated with the density of local roads (Spearman rank, $r_s=0.23$, $n=19$, $P=0.34$), national roads ($r_s=-0.06$, $n=19$, $P=0.80$), regional roads ($r_s=-0.08$, $n=19$, $P=0.74$), open grounds ($r_s=-0.16$, $n=19$, $P=0.61$) or elk hunting bags ($r_s=-0.43$, $n=19$, $P=0.07$).

Discussion

The model developed in northern Wisconsin (Mladenoff *et al.*, 1995, 1999) for predicting the occurrence of a wolf territory in an area was a good predictor for the presence but not the absence of wolf territories in Scandinavia. The main reason for this seems to be that the Wisconsin model underestimates the negative effects of roads on wolf occurrence in Scandinavia, as it predicts both observed wolf territories and random polygons without wolves as suitable wolf habitat with a high likelihood of colonization. This is probably due to road densities in Wisconsin non-pack areas being about three times higher than in Scandinavian

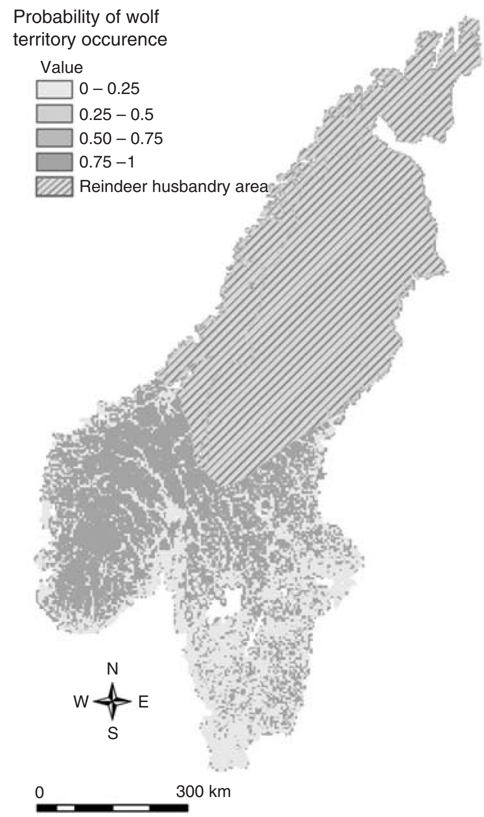

Figure 3 Map over Scandinavia with the probability of wolf *Canis lupus* occurrence in four different classes according to the model: logit (p)=6.22–47.69*open land−25.09*local road density (log likelihood ratio test G=33.66, d.f.=2, P<0.001. The northern part of Scandinavia, the reindeer husbandry area is not predicted as terrain and management of wolves and prey is very different from south-central Scandinavia.

non-pack areas, while road densities within wolf territories in Scandinavia and Wisconsin differ much less. In Wisconsin, 14 wolf territories with a mean size of 166 km^2 covered 4% of the study area. In Scandinavia, the 20 territories with a mean size of 1000 km^2 covered 24% of the study area. The difference between the two models is thus not likely due to Wisconsin wolves being more forced to colonize low-quality (secondary) habitat.

However, the model by Mladenoff *et al.* (1995, 1999) gave a significantly higher probability of wolf occurrence for wolf territories than for the random polygons in Scandinavia. This result implies that a model for a wolf population in another setting may still indicate potential areas for wolf colonization.

Because elk is the main prey of wolves in our study area (Olsson *et al.*, 1997; Sand *et al.*, in press), elk density was initially considered a potentially important variable. However, elk density showed no significant effect on the probability of wolf occurrence in this study. This is probably because elk density was generally high within the study area. The elk density was on average higher than 1 elk km^{-2}, which is above the density of prey where wolves respond numerically (Fuller, 1989; Messier, 1994; Peterson *et al.*, 1998).

In the stepwise logistic regression analysis on Scandinavian data, the proportion of open land and the density of local roads were two significant variables explaining the difference between real wolf territories and random polygons (Table 4). The variables describing roads, built-up areas and open land are mainly indicators of the intensity of human activity. The variables most important for the probability of wolf territory occurrence are clearly those associated with human activity. Wolves either avoid areas with a high degree of human activity or suffer from higher mortality in those areas compared with areas with low human activity.

Open land is probably a better indicator of human activity than both roads and built-up areas as it can also indicate the magnitude of human activity in an area as well as the spatial distribution of this activity. Other studies have shown that roads merely seem to serve as indicators of human-related mortality, either through direct mortality from car collisions or through indirect mortality as legal killing of problem individuals, illegal killing (poaching or poisoning) and diseases (Thiel, 1985; Mech *et al.*, 1988; Mladenoff *et al.*, 1995).

The proportion of built-up areas within wolf territories significantly decreased as the territory-specific boundaries changed over the years. During the same period, the proportion of open land and roads in the territories did not change significantly. A plausible explanation for this is that although built-up areas may fall within the constructed MCP during the first year of colonization, wolves generally avoid built-up areas once they know where they are found.

There was no significant correlation between density of local roads and pack size. Built-up areas, though, showed a tendency to be correlated with pack size in winter. Mortality is probably the most likely explanation as to why there are fewer individuals in wolf packs living in territories with relatively high proportions of built-up areas compared with wolf packs in the same region of Scandinavia, but with lower proportions of built-up areas. Direct mortality from car and train collisions was of minor importance, accounting for *c.* 6% of the mortality among 32 dead or assumed dead radio-collared Scandinavian wolves between 1998 and 2003 (Linder-Olsen, 2003). Diseases (mainly scabies) and legally killed wolves constituted 19 and 3%, respectively, of the total mortality in the same study (Linder-Olsen, 2003). Preliminary data from radio-collared wolves confirm that illegal killing is one of the largest sources of mortality among Scandinavian wolves (O. Liberg, pers. comm.). This has also been shown to be true for wolves and other large carnivores in other countries (Thiel, 1985; Mech *et al.*, 1988; Mladenoff *et al.*, 1995; Mace & Waller, 1996; Sunde, Snorre & Kvam, 1998; Andrén *et al.*, 2006). Areas that wolves prefer to colonize may not necessarily be suitable for colonization as various mortality factors may be high in these areas (Delibes, Gaona & Ferreras, 2001). In territories with higher proportions of built-up areas, there is a higher potential for human impact and combined with high densities of local roads there is also a vector for realizing this potential.

The present management goal for wolves is 20 annual reproductions in Sweden and three annual reproductions in Norway. With a mean territory size of 1000 km^2 (Johansson, 2002), the 660 000 km^2 predicted to have a probability of wolf colonization higher than 0.5 is large enough to encompass about 600 wolf packs. Loss of suitable habitat will thus not be the main problem facing wolf management in Scandinavia.

Our results predict a lower likelihood of wolf territory occurrence in areas with a large proportion of open land and built-up areas, as well as relatively high densities of roads. These variables may serve as indicators of human activity, and human activity may affect both habitat preference by wolves and probability of wolf mortality. The model in this study has high predictive power, but because it does not take into account any 'human dimension' variables, it is an indirect description of a suitable wolf habitat in Scandinavia. If human attitudes towards wolves become more positive, variables indicating human activity may not be useful predictors of wolf territory occurrence as degree of human activity will then be weakly correlated with wolf mortality. The same problem will probably affect most habitat suitability models, not only when dealing with large and controversial animals, but certainly also for common species. Incorporation of a human dimension in terms of public attitudes in habitat suitability models may prove to be an important factor in future research concerning habitat preference and suitability.

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