Diversity and Distributions, (Diversity Distrib.) (2004) **10**, 225–233

BIODIVERSITY RESEARCH

Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland

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ABSTRACT

Based on data collected during the National Wolf Census in 2000–01, we analysed the main habitat factors influencing the distribution and abundance of the wolf, *Canis lupus*, in northern Poland. The study region forms the western border of the continuous Eastern European range of wolves, although attempts at westward dispersal have been observed. Using Geographic Information System techniques, we measured nine habitat variables and three parameters related to wolf occurrence in 134 circular sample plots (radius 7 km, area 154 km^2 each). We compared 72 plots where wolves were recorded and 62 plots with no signs of wolf presence. Wolf plots were characterized by significantly higher forest cover, less fragmentation of forests, lower density of villages, towns, motorways, and railways than wolf-free plots. We found a positive correlation between the sum of wolf observations in plots and forest cover. The number of domestic animals killed by wolves was higher in areas with higher indices of wolf abundance and lower forest area. In multiple regression analysis, four independent variables explained 59% of the variation in wolf distribution and abundance in northern Poland: straight-line distance to continuous range of wolves in Eastern Europe; forest cover; forest fragmentation; and length of major motorways. We conclude that protection of wolves in Poland (since 1998) may not be an adequate conservation measure, especially because of the increasing density of highways and express motorways. Existing forest corridors should be protected and new ones should be restored to ensure long-term conservation of wolves and allow range expansion into Western Europe.

Keywords

***Canis lupus*, dispersal barriers, forest cover, habitat selection, landscape analysis, large predator, Poland, road density, wolf.**

INTRODUCTION

The natural range of wolf (*Canis lupus*) distribution in Europe used to cover most of the continent, but today it is restricted mainly to its eastern and south-eastern portions (Okarma, 1993, 1997). The present distribution of the wolf is a consequence of the past extermination programmes, as well as the contemporary barriers to dispersal and lack of suitable habitats (Mech, 1995; Mladenoff *et al*., 1995; Linnell *et al*., 2001; Singleton *et al*., 2002). The western border of wolves' continuous continental range is located in Poland. The eastern part of the country is permanently inhabited by a viable wolf population, whereas the western part has been colonized by some packs or individuals, which however, usually are not able to persist longer than a few years (Wolsan *et al*., 1992; Jędrzejewski *et al*., 2002), despite the fact that the wolf has been protected in Poland since 1998. This situation indicates a need to study habitat preference of wolves, and determine variables affecting wolf distribution.

Studies in North America, based on Geographic Information System (GIS) methods, showed that wolves most often occurred in forests with at least some coniferous stands and strongly avoided agricultural land (Conway, 1996). Furthermore, territories of wolf packs (interior 80% radio locations) examined in Wisconsin, USA, were consistently characterized by low density of roads (mean 0.23 km/km^2) and humans (mean 1.5 person/km^2; Mladenoff *et al*., 1995). GIS methods were also used to aid wolf recovery planning (Mladenoff & Sickley, 1998; Mladenoff *et al*., 1999), and to study habitat preferences and distributions of other large carnivores such as black bears *Ursus americanus* (Mitchel *et al*., 2002) and cougars *Puma concolor* (Riley & Malecki, 2001).

In this paper, we present the results of a GIS analysis of habitat variables associated with wolf occurrence in northern Poland.

The aims of our study were to determine: (1) the main habitat factors that influence the distribution and numbers of wolves; (2) anthropogenic barriers to wolf dispersal; (3) habitat features related to wolf damage to livestock.

STUDY AREA

The study region was the northern part of Poland including the provinces of Pomerania, Wielkopolska, Masovia, Masurian Lakeland, Warmia and Podlasia. The area extends from 52° N on the south, to the Baltic Sea coast or to the state border on the north (Fig. 1). Furthermore, we use the division into the north-eastern part of Poland (east of 19°30′ E) and the north-western part (west of 19°30′ E). The total area covers about 160,000 km^2. The lowland landscape of northern Poland was shaped by glaciers (mainly by the Riss, 310,000–130,000 yr BP, and the Würm glaciations, 70,000–10,000 yr BP). It is mostly a plain with some belts of frontal and moraine hills. The elevation ranges from −2 to 392 m a.s.l. The forest cover of the study area (31%) is somewhat higher than the average for Poland (28%; Statistical Yearbook of the Republic of Poland, 1999). Most of the forests are composed of young commercial stands (about 60% of stands are < 60 years old, 30% are between 61 and 100 years, and 10% are > 100 years old). The dominant tree species is the Scots pine, *Pinus sylvestris* (about 80% of forest area). A few stands are composed of Norway spruce, *Picea abies* (4%), and deciduous species such as oak, *Quercus robur*; ash, *Fraxinus excelsior*; maple, *Acer platanoides*; birch, *Betula pendula*; beech, *Fagus sylvatica*; hornbeam, *Carpinus betulus*; and black alder, *Alnus glutinosa* (Forestry Statistical Yearbook, 1998). Numerous postglacial lakes (especially in Masuria and Pomerania) and some of the largest as well as the best preserved woodlands (Białowieża Primeval Forest, Knyszyn, Pisz, and Tuchola Forests) are located in northern Poland. The main rivers are the Vistula, Odra, Bug, Warta, Narew, and Biebrza. Apart from several big cities (Gdańsk, Poznań, Szczecin, Olsztyn, and Białystok), the human population in the region is not dense, on average 87 person/km^2, whereas the national mean amounts to 124 person/km^2. Also, the density of roads is lower:

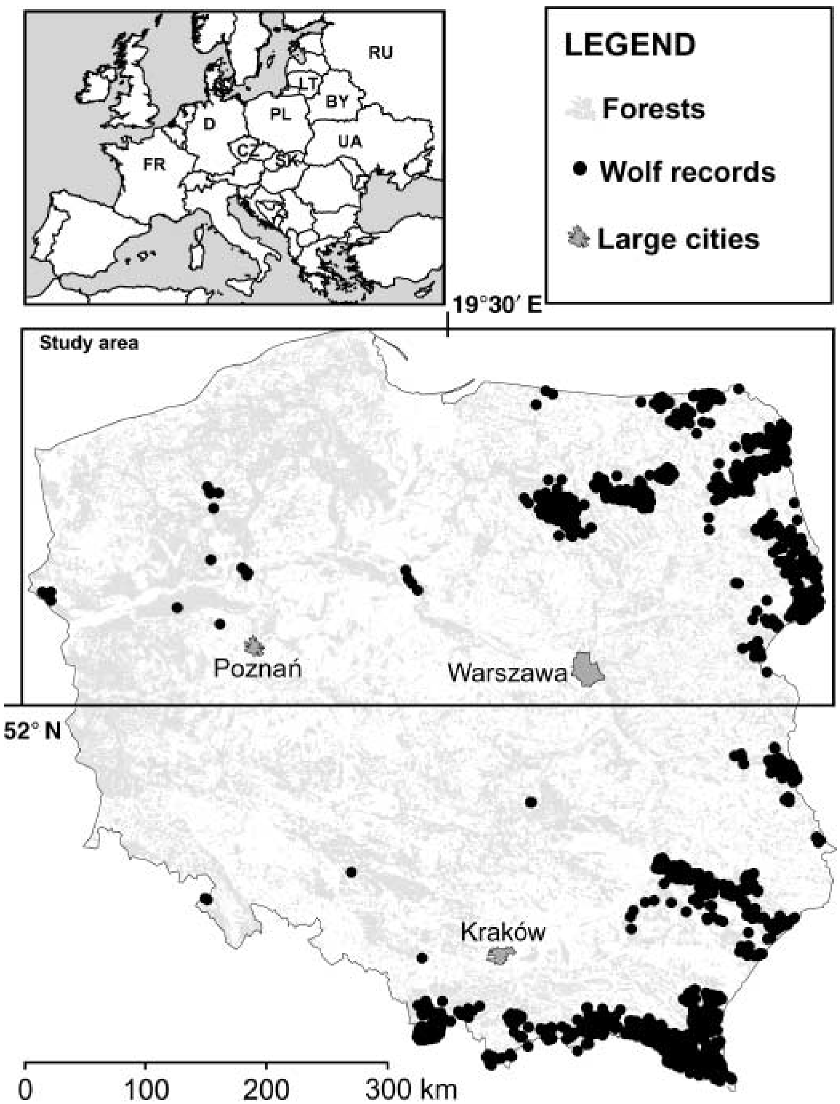

Figure 1 Distribution of wolves (*Canis lupus*) in Poland, from National Wolf Census data in 2000–01 (after Jędrzejewski *et al.*, 2002) and the area for wolf habitat analysis (northern Poland).

62 km of paved motorways per 100 km^2 in northern Poland compared to 78 km/100 km^2 in the whole country (Statistical Yearbook of the Republic of Poland, 1999). Mean road traffic averages 6300 vehicles/day on the national motorways and 2000 vehicles/day on regional motorways (the respective means in whole country: 7000 and 2400); (General Directorate of Motorways & Highways; http://www.gddkia.gov.pl).

Since biogeographical and landscape conditions in southern Poland (large regions with hills, the Carpathian Mts., no lakelands, dense technological infrastructure and urbanization) are very different from those in northern part of the country, the factors shaping wolf distribution south of 52° N will be analysed separately.

METHODS

The data on wolf distribution in the region were obtained during the National Wolf Census carried out in Poland in 2000–01 (Jędrzejewski *et al*., 2002). The census was conducted by the services of Polish State Forestry and National Parks, under the supervision of the Mammal Research Institute, Polish Academy of Sciences, in Białowieża (MRI PAS). Year round, the forest and national park personnel recorded wolf tracks, kills, dens, and other observations. Once or twice during the winter, the mapping of fresh wolf tracks and trails was performed by driving the forest roads after a new snowfall. Also, interviews with local people and hunters were conducted. All data were sent to MRI PAS where they were analysed in the program MapInfo 5.5 (MapInfo Corporation, 1999). One of the results was the map of all wolf records in Poland (Fig. 1).

For habitat analysis, we randomly selected 134 circular sample plots of 14-km diameter each (area 154 km^2). The plots with wolves (72) were selected only in areas where the animals occur. The rest were randomly chosen in the whole study area excluding the biggest cities. The plots did not overlap and their diameter was based on empirical values of the nearest neighbour distance for active breeding dens of wolves recorded during the census in whole Poland (mean 13.7 km, SE = 0.7, range 7.3–20 km, $n = 24$) (Jędrzejewski *et al*., 2002). The size of the sample plot was equivalent to 75% of the average wolves' territory studied by radio tracking in eastern Poland (Jędrzejewska & Jędrzejewski, 1998). In total, the sample plots covered 20,617 km^2 (nearly 13% of northern Poland) and included 72 plots with wolf occurrence recorded (60 in NE Poland and 12 in NW part of the country) and 62 plots with no signs of wolf presence (32 in NE Poland and 30 in the NW part). As indices of wolf abundance, we used: (1) a total number of wolf records (all observations summed) in a sample plot, and (2) the maximum number of wolves in a pack recorded in a plot.

For all sample plots, we analysed the following parameters: (1) percent forest cover, (2) forest fragmentation (number of forest patches > 1 ha, which were separated by open areas), (3) river length (we did not include streams and waterways), (4) length of main (national and international) motorways, (5) length of secondary (regional) roads (the other two categories: district roads and communal roads were not included), (6) length of railways, (7) lake area (lakes > 10 ha included), (8) number of villages (usually < 1000 inhabitants), (9) number of towns (usually > 1000 inhabitants), (10) number of domestic animals killed by wolves, and (11) the shortest straight-line distance to the eastern border of Poland, as a proxy of the distance to continuous range of wolves in Eastern Europe. The variables 1 and 2 were obtained from a database granted to us by the General Directorate of Polish State Forests (Ministry of Environment, Warsaw). The variables 3–9 were measured or counted on the numerical maps prepared by the IMAGIS Company. Data on livestock killed by wolves during 1999–2001 were obtained from the Nature Conservation Offices of the Warmia-Masuria, Masovia, and Podlasia Voivodships. The data originated from farmers' reports on cases of wolf depredation on livestock.

Information on abundance of wolf prey (red deer, *Cervus elaphus*; roe deer, *Capreolus capreolus*; moose, *Alces alces*; wild boar, *Sus scrofa*) was available in the form of official statistics from game inventories in forestry districts. Since we were not able to assess the reliability of the data, we did not use them for quantitative analysis. Nonetheless, even if treated with due caution as qualitative indices, the official statistics suggest that wild ungulates are numerous in forests of northern Poland and are not likely to seriously affect the distribution of wolves in woodlands (W. Jędrzejewski, M. Niedziałkowska, S. Nowak, unpubl. data). No data on wild ungulates are available for nonforest habitats.

RESULTS

The number of wolf records in sample plots with wolves ranged from 1 to 112 (mean 20.3), and the pack size varied from 1 to 9, on average 4.1 (Table 1). Number of wolf records and pack size within sample plots were significantly correlated ($r = 0.717$, $n = 64$, $P < 0.005$). Therefore, we assumed that both these variables were reliable indices of wolf abundance. The number of wolf records in a plot declined with the increasing distance from the eastern border of Poland ($Y = 2.896 - 0.003X$, $R^2 = 0.178$, $n = 134$, $P < 0.0005$). Also, wolf packs were getting smaller from east to west, with the growing distance from wolf contiguous range in Eastern Europe ($Y = 4.949 - 0.005X$, $R^2 = 0.19$, $P < 0.0005$).

Sample plots with wolves were characterized by significantly higher percent forest cover (mean 50.5%) than plots with no wolves (32.9%; Table 1). Also, we found a positive relationship between the number of wolf records in a plot and its forest cover (Fig. 2). Forests were more fragmented in plots with no wolves (Table 1). Significantly fewer villages and towns were found in wolf plots than in the sample plots without wolves (Table 1). Moreover, the number of villages and the number of wolf records in a plot were negatively correlated (Fig. 2). Since forest cover and density of human settlements were mutually negatively correlated in all plots (see Fig. 2), the wolves' preference for woodlands generally coincided with their avoidance of villages and towns. However, in the regions with dense forest cover, wolves were sometimes able to tolerate towns nearby. For example, in NE Poland, we recorded wolves' presence at a distance < 5 km from the small towns Moryń and Mieszkowice (with the population

Table 1 Habitat characteristics of sample plots with wolves ($n = 72$) and those with no wolves ($n = 62$) recorded in northern Poland. Sample plots were circles of diameter 14 km. Comparison of wolf and wolf-free plots was done with Kruskal–Wallis nonparametric ANOVA, ns — nonsignificant

Parameter (n, km, or km^2 per plot)	Plots with wolf records: Mean ± SE	(min–max)	Wolf-free plots: Mean ± SE	(min–max)	Statistical significance of difference
Sum of wolf observations	20.3 ± 2.7	(1–112)	0	—	—
Maximum pack size	4.1 ± 0.3	(1–9)	0	—	—
Livestock killed by wolves	1.6 ± 0.4	(0–21)	0	—	—
Forest cover (%)	50.5 ± 2.8	(11–94)	32.9 ± 2.5	(2–94)	< 0.0001
Number of villages	4.6 ± 0.2	(0–11)	6.6 ± 0.3	(1–11)	< 0.0001
Length of main motorways (km)	2.7 ± 0.6	(0–17)	6.0 ± 1.0	(0–32)	0.003
Length of railway (km)	6.4 ± 0.9	(0–22)	10.1 ± 1.2	(0–34)	0.02
Forest fragmentation (n forest patches)	17.7 ± 0.9	(3–43)	20.2 ± 1.0	(4–40)	0.04
Number of towns	0.3 ± 0.1	(0–2)	0.5 ± 0.1	(0–3)	0.05
Lake area (km^2)	3.4 ± 0.8	(0–34)	1.6 ± 0.4	(0–14)	ns
Length of secondary roads (km)	12.3 ± 1.0	(0–42)	12.9 ± 1.4	(0–40)	ns
Length of rivers (km)	11.8 ± 1.0	(0–34)	11.9 ± 1.4	(0–40)	ns

Table 2 The mean (± SE) values of habitat variables and indices of wolf abundance in sample plots with and without wolves in the north-eastern and the north-western Poland. Number of sample plots in parentheses. Comparison of wolf and wolf-free plots (in each region separately) was done by Kruskal–Wallis nonparametric ANOVA. P — Statistical significance, ns — nonsignificant

Parameter	Sample plots in NE Poland: With wolves (60)	No wolves (32)	P	Sample plots in NW Poland: With wolves (12)	No wolves (30)	P
Straight-line distance to the eastern border of Poland (km)	87 ± 8.5	155 ± 10.6	< 0.0005	487 ± 24.6	450 ± 13.8	ns
Sum of wolf observations	23.6 ± 3.1	—	—	3.9 ± 1.3	—	—
Maximum pack size	4.6 ± 0.3	—	—	2.2 ± 0.4	—	—
Forest cover (%)	48.7 ± 3.1	26.0 ± 2.1	< 0.0005	60.0 ± 6.7	40.2 ± 4.4	0.02
Length of main motorways (km)	2.9 ± 0.7	5.8 ± 1.2	0.03	1.5 ± 1.1	6.2 ± 1.6	ns (0.07)
Length of railway (km)	6.2 ± 0.9	7.0 ± 1.3	ns	7.7 ± 2.2	13.5 ± 1.8	ns (0.1)

of 5000 each) and < 3 km from a larger town Pisz (population 20,000).

Wolves strongly avoided the main motorways. In wolf plots, the average length of such major roads was less than half of that in plots without wolves (2.7 vs. 6.0 km; Table 1). Similarly, wolves avoided areas with a dense net of railway lines (Table 1). Secondary roads, lakes, and rivers did not have any influence on wolf distribution.

The average number of farm animals (mainly cattle) killed by wolves in a sample plot was 1.6, but large variation among plots was recorded (Table 1). In a multiple regression analysis, two factors, percent forest cover (F), and the sum of all wolf records in a plot (W) explained 35% of the observed variation in wolf depredation on livestock ($Y = 3.224 + 0.099W - 0.072F$, $R^2 = 0.345$, $n = 72$, $P < 0.0005$). The number of farm animals killed by wolves was positively correlated with the index of wolf abundance, and negatively related to forest cover. Semipartial correlation squared (sr^2 after Tabachnick & Fidell, 1983) showed that the numbers of wolves were more important ($sr^2 = 0.302$) than shortage of forest cover ($sr^2 = 0.172$).

We also compared habitat characteristics and wolf preferences in NE Poland, where relatively high-density population of wolves inhabited most of the large woodlands, with NW Poland, where extensive forests were either uninhabited or inhabited by few wolves only (see Fig. 1). In the north-west, the average wolf pack was more than two times smaller (Mann–Whitney test, $U = 518$, $P < 0.0005$), and the sum of wolf observations in a plot was significantly smaller than in the north-east ($U = 577.5$, $P = 0.001$; Table 2). Although overall forest cover in the whole north-western part was greater (34%) than that in the north-eastern part (29%), wolves were equally selective towards more forested areas, and tended to avoid major motorways in both regions (Table 2). There was a significant difference in the density of railway between the analysed regions, with the network of railway lines in the north-west twice as dense as that in the north-east (Mann–Whitney test, $U = 1283$, $P = 0.001$). In NW Poland, wolves had a

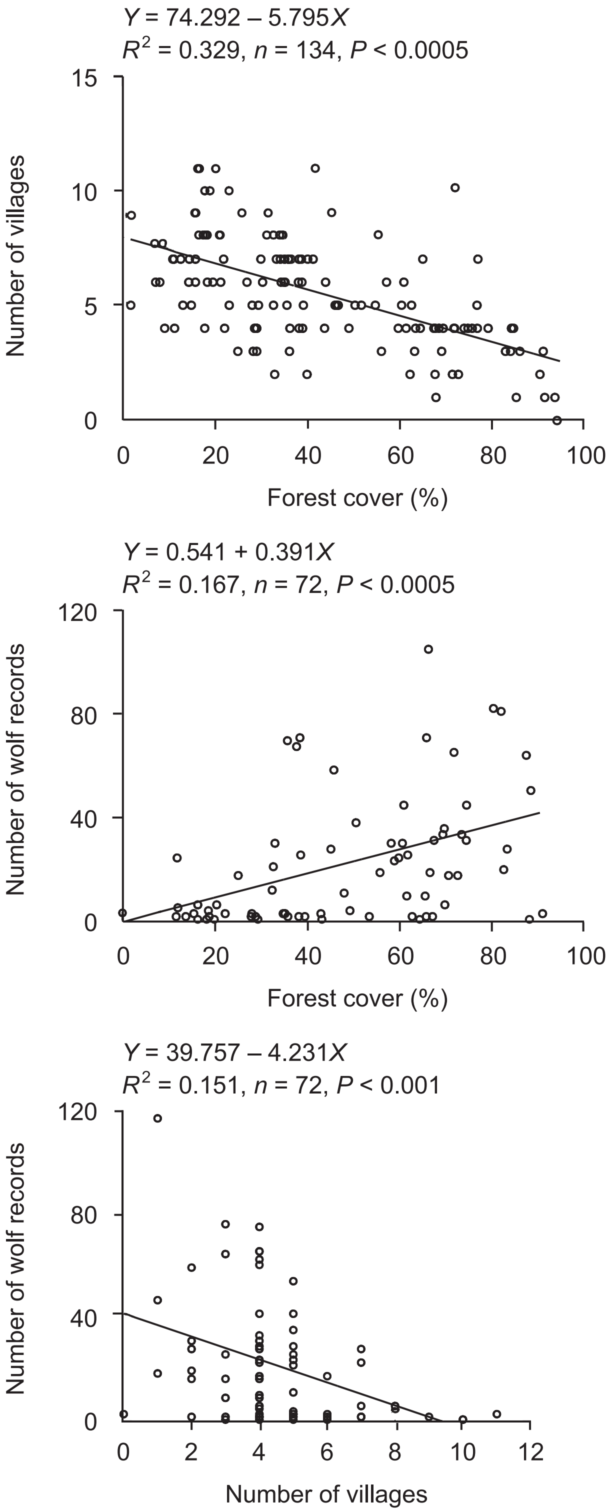

Figure 2 Relationship between two habitat variables, and between wolf abundance and each variable in 134 circular sample plots (154 km^2 plot, 72 with wolves and 62 without wolves). Upper graph: Relationship between forest cover and number of villages. Middle graph: Relationship between index of wolf abundance (sum of wolf observations per occupied plots) and percent forest cover. Lower graph: Relationship between index of wolf abundance (as above) and number of villages per plot.

tendency to avoid areas with high density of railway. In north-east, such avoidance was not detected, as the railways were rare in that part (Table 2).

Based on the results of habitat analysis, we conducted a multiple regression analysis to explain the variation in indices of wolf abundance in northern Poland. Four independent variables showed strong and significant relationship with the log-transformed sum of wolf observations in a sample plot: percent forest cover, distance to the state border, forest fragmentation, and length of main motorways. Since several models including various sets of these variables were statistically significant, we tested the group of 6 models with the AIC (Akaike's Information Criterion; Anderson *et al.*, 2000). The best model (Akaike's weight $\omega_i = 0.853$) included four variables: straight-line distance to the eastern border of Poland (*B*), forest cover (*F*), length of major motorways (*MR*), and forest fragmentation (*FP*, number of forest patches) (Table 3). The four factors explained 59% of the observed variation in the log-transformed sum of wolf observations in sample plots: $W = 1.838 - 0.005B + 0.029F - 0.034MR - 0.032FP$, $R^2 = 0.586$, $P < 0.0005$, $n = 134$ sample plots; $W = \text{Ln}$ (Sum of wolf observations in a sample plot + 1).

In order to estimate the role of each independent variable in explaining the whole variation, we calculated semipartial correlations squared (sr^2). The most important factor was the distance to the eastern border, as a proxy of a distance to continuous East-European range of wolves ($sr^2 = 0.302$, $P < 0.0005$; negative correlation). The second most important factor was forest cover ($sr^2 = 0.180$, $P < 0.0005$; positive correlation). Major roads and forest fragmentation ($sr^2 = 0.022$ for each of the two variables, $P = 0.01$) had smaller influence and were negatively correlated with wolf abundance.

On the basis of the multiple regression equation, we constructed a simple graphic model to predict relative wolf numbers in northern Poland along the east–west gradient at two levels of forest cover (80 and 30%), two levels of forest fragmentation (1

Table 3 Multi-model inference based on regression models on effects of percent forest cover (*F*), forest fragmentation (*FP*, number of forest patches), the minimum straight-line distance to the state border (*B*, a proxy of a distance to the continuous wolf range in Eastern Europe), and the length of main motorways (*MR*) on the index of wolf abundance (*W*, ln [sum of wolf observations + 1]) in 134 sample plots in northern Poland. R^2 — coefficient of linear or multiple regression in each model, AIC — Akaike's Information Criterion, ω_i — Akaike's weight. Each of the six models tested was significant at $P < 0.0005$

Model	k	R^2	AIC_i	ω_i
$W = f(F + B + FP + MR)$	5	0.586	−0.563	0.853
$W = f(F + B + MR)$	4	0.564	4.430	0.070
$W = f(F + B + FP)$	4	0.564	4.443	0.070
$W = f(F + B)$	3	0.542	9.023	0.007
$W = f(F)$	2	0.248	73.368	0.000
$W = f(B)$	2	0.243	74.344	0.000

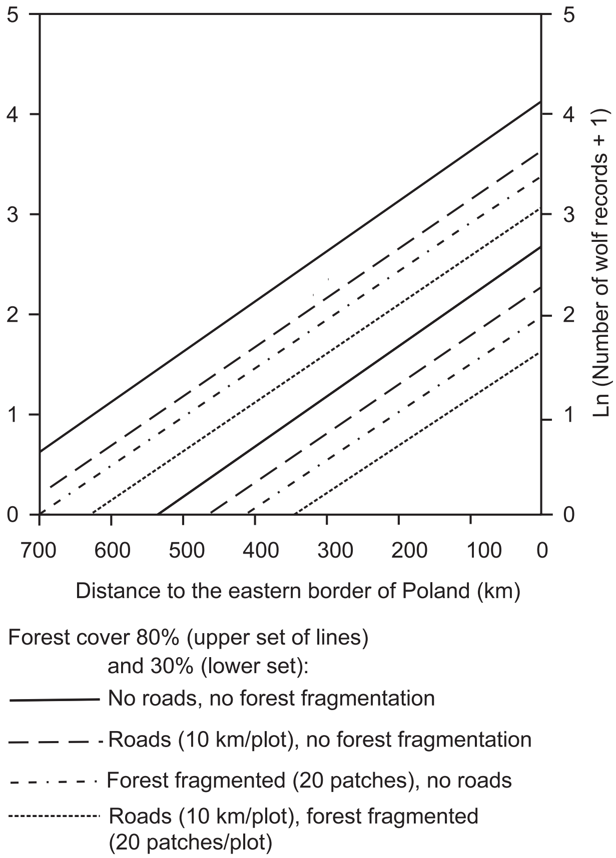

Figure 3 Graphical model, based on empirical data and multiple regression analysis (see text) predicting relative abundance of wolves along the east–west gradient in northern Poland in optimal habitats (80% area covered by forests) and unfavourable habitats (30% forest cover). In each case, 4 levels of anthropogenic barriers to wolf dispersal were modelled (from upper to lower lines): (1) no barriers, (2) high density of main motorways (10 km per 154-km^2 sample plot), (3) forest fragmentation (forest in 20 patches separated by open areas), (4) high density of roads and forest fragmentation. Distance to the eastern border of Poland approximates the distance to continuous East European range of wolves.

and 20 forest patches per sample plot) and two densities of the main motorways (0 and 10 km per plot) (Fig. 3). With the growing distance from their continuous East European range, wolves are less likely to occur even in the best habitats (dense forest cover, no anthropogenic barriers to dispersal). Main motorways and forest fragmentation reduce the wolves' chances to spread west, and the model shows that these two anthropogenic barriers have rather strong effect, if they occur together (Fig. 3).

DISCUSSION

As the western border of wolf range in the lowlands of Europe is now located in north-eastern Poland (Okarma, 1993, 1997), the westward expansion of the species depends on its protection, favourable environmental conditions, and habitat barriers to dispersal. In this study, we found that forest cover was the most important habitat variable influencing wolf distribution and numbers. Wolves live in all types of forests. Research conducted in the Białowieża Primeval Forest (E Poland) by Jędrzejewska & Jędrzejewski (1998) did not reveal wolves' preferences for a particular forest association. In north-western Poland, wolves were even recorded in commercial monocultures of pine (Bereszyński, 2000). Mikusiński & Angelstam (2003) have documented wolves' preference for woodlands by comparing of large-scale coarse data of geographical occurrence of wolves with the remote sensing forest maps in boreal and temperate zones of Europe. Wolves most frequently occurred in UTM grid cells (50 × 50 km) with forest cover of 50–80%. Woodlands ensure prey resources (wild ungulates) and safe den sites to wolves. Nonetheless, wolves are ecologically tolerant animals. In northern Poland, the minimal forest cover in plots inhabited by wolves was 11%. Wolf packs in Wisconsin, USA, occupied areas that averaged > 90% forest cover (Mladenoff *et al.*, 1995). In regions with no large forest tracts but abundant prey, they occupied mosaic habitats of forests and agricultural areas (Ryabov, 1987). In Russia, Ryabov (1987) reported cases of a female wolf bringing up her pups in sunflower and corn crops or even in an open area 250 m away from an animal farm.

Presence of wolves in a mosaic agricultural-forest environment increases the risk of damage to livestock. Domestic animals fell as prey to wolves, because they were more easily available for the predators than the wild ungulates (Ciucci & Boitani, 1998; Sidorovich *et al.*, 2003). Cattle and sheep are the main components of wolf diet in Italy, where the density of wild ungulates (represented mainly by wild boar) is low (Meriggi *et al.*, 1991; Meriggi & Lovari, 1996). Depredation by wolves also depends on the number of grazing animals, location of pastures, and the awareness of the danger connected with the wolf presence in the area (Mech, 1995; Okarma, 1995; Ciucci & Boitani, 1998).

Apart from forest area and fragmentation of forests, other natural environmental features such as lakes and rivers had little influence on the distribution and number of wolves in northern Poland; unlike Wisconsin, USA, where wolves showed a negative relationship with proportional geographical area covered by water (Mladenoff *et al.*, 1995). Haight *et al.* (1998) and Harrison & Chapin (1998) reported that rivers and lakes can be barriers for the wolves' movements. However, in North America, a radio-located wolf crossed three big rivers during a three-month move (Van Camp & Gluckie, 1979). Frozen rivers and lakes are often used by wolves to travel faster (Mech, 1994; Musiani *et al.*, 1998). In northern Poland, wolves had to cross the lower Vistula River to reach the western part of the country. Recent records of wolves in East Germany (Ansorge *et al.*, 2003), indicate that they had successfully travelled across the Nysa Łużycka River. Both the Odra and the Vistula freeze in very cold winters (e.g. 1979/1980, 1995/1996), which can facilitate wolves' dispersal.

The negative relationship between human and carnivore density is not clear and has been discussed by many authors (e.g. Woodroffe, 2000; Linnell *et al.*, 2001; Chapron *et al.*, 2003). We found that dense networks of settlements and motorways limited wolf distribution. In the Białowieża Forest, Poland, wolves avoided human-made structures such as settlements and roads

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(Theuerkauf *et al*., 2003). In the United States, wolves preferred areas with < 1.5 person/km^2 and < 0.25 km of roads per 1 km^2 (Conway, 1996). However, as the population grew, wolves occupied suboptimal habitats as well (Mech *et al*., 1988; Mech, 1995; Mladenoff *et al*., 1999). In Italy, where forest cover is sparse, in winter wolves were often observed near villages, settlements and towns, where they searched for food in garbage dumps (Boitani, 1982; Meriggi *et al*., 1991; Ciucci *et al*., 1997). In Minnesota, USA, wolves lived and reared their pups within 90 km of the large metropolitan area of Minneapolis/St. Paul (Mech, 1995).

Roads and railways may be barriers to wolf dispersal and a cause of direct mortality from vehicle collisions or poaching. In northern Poland, the maximum density of main and secondary roads (combined) recorded in a sample plot with wolves was 0.38 km/km^2. In the USA, the density of roads in areas inhabited by wolves was as high as 1.4 km/km^2 (Merrill, 2000), although the earlier studies suggested that wolves rarely occur in areas, where density of roads exceeded 0.6 km/km^2 (Mech *et al*., 1988). In the regions with 0.7 km of roads per 1 km^2, over 50% of known mortality of wolves was caused by humans (Mech *et al*., 1988). In northern Poland, the density of motorways is still low and there are no modern highways. However, there are plans to build a system of highways and express motorways in the near future. Although some observations suggest that wolves can adapt to traffic of motor vehicles (Thiel *et al*., 1998), generally highways are mechanic, acoustic, chemical, thermal, and luminous barriers that cause serious fragmentation of habitat and populations of large predators (Hędrzak & Brzuski, 1999; Kerley *et al*., 2002; Singleton *et al*., 2002). To mitigate the negative influence of highways, wildlife travel corridors should be developed in areas of traditional travel routes of large mammals (Woess *et al*., 2002). The secondary roads are less important barriers for wolves' dispersal. They can even be used by predators to move easier and faster (Ryabov, 1987; Thurber *et al*., 1994; Musiani *et al*., 1998). In the USA, wolves were observed many times standing on such roads or crossing them (Thiel *et al.,* 1998).

Because we have not detected any important differences in habitat characteristics between NE and NW Poland, it seems that the limiting factors for wolf colonization to western Poland are the long distance from the continuous wolf range and numerous dispersal barriers. The distance by itself (up to 640 km between the eastern- and westernmost sample plots) is not a complete barrier for wolves. In North America, a radio-tagged wolf travelled a straight-line distance of over 670 km within 81 days (Van Camp & Gluckie, 1979). The distance combined with dispersal barriers (main motorways) and low availability of good habitats (small area and highly fragmented forest) cause wolf numbers in western Poland to be low and unstable, despite protection since 1998. Even relatively short distance of 25 km (comparable to wolves' daily routes; see Jędrzejewski *et al*., 2001) between habitats favourable to wolves can be a problem for the predators, if there are travel barriers such as roads and intensively used areas with high density of human population (Wydeven *et al*., 1998). The species can exist in a metapopulation, but must be able to move between its parts (Fritts & Carbyn, 1995; Haight *et al*., 1998). To enable and promote wolf dispersal from eastern to western part of Poland and Germany, the existing forest corridors should be protected and new ones, especially in central Poland, should be planned and restored.

ACKNOWLEDGEMENTS

We thank the Directorate General of the State Forests (Drs Konrad Tomaszewski, Janusz Dawidziuk, and Ryszard Kapuściński), all the Regional Directorates of State Forests, the Department of Nature Conservation of the Ministry of Environment (Dr Jan Wróbel), and the Board of Polish National Parks (Dr Arkadiusz Nowicki) for their help and support. We are grateful to the personnel of the forest districts and national parks for their cooperation during the National Wolf Census. The study was financed by the Directorate General of the State Forests (Poland), Euronatur (Germany), and the budget of the Mammal Research Institute PAS in Białowieża. We thank Drs Adrian P. Wydeven, Guillaume Chapron and an anonymous referee for their comments on the earlier version.

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