Acta Theriologica 50 (3): 417–428, 2005.
PL ISSN 0001–7051

Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland

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Jędrzejewski W., Niedziałkowska M., Mysłajek R. W., Nowak S. and Jędrzejewska B. 2005. Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. Acta Theriologica 50: 417–428.

Using data from the National Wolf Census, carried out in Poland in 2000–2001, and GIS techniques we analysed habitat selection by wolves *Canis lupus* Linnaeus, 1758 in uplands and mountains of southern Poland. We compared ten habitat variables and two parameters related to wolf abundance in 52 circular plots (154 km^2 each) with recorded wolves and 97 randomly selected plots with no signs of wolf presence. Wolf plots were characterized by higher elevation and closer location to the state border than wolf-free plots. Furthermore, wolf plots had higher forest cover, but smaller number of villages and towns and shorter railways and roads than plots without wolves. The best model explaining wolf distribution included forest cover, number of villages, length of roads and railway lines. Compared to northern Poland, the southern part of the country offers worse habitats for wolves due to significantly denser network of settlements and transportation routes.

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Key words: wolf distribution, *Canis lupus*, habitat variables, forest cover, road density, GIS techniques, landscape analysis

Introduction

After centuries of persecution, wolves *Canis lupus* Linnaeus, 1758 have survived mainly in the wild and remote areas of high importance for nature and biodiversity conservation (Promberger *et al.* 2000). In Europe, areas suitable for the wolf are located mostly in the montane regions (Masolo and Meriggi 1998, Glenz *et al.* 2001, Salvatori *et al.* 2002a, b, Ciucci *et al.* 2003). In such regions, climatic and geomorphologic conditions are less appropriate for economic development, so human disturbance is relatively low and abundance of prey and forest cover is usually high (Promberger *et al.* 2000). The largest continuous wolf population in Central Europe occurs in the Carpathian Mountains and embraces parts of Romania, Ukraine, Slovakia, and Poland (Salvatori *et al.* 2002a, b). From the Carpathian population wolves migrate to Hungary (Farago 1992) and Czech

Republic (Boitani 2003). In Croatia, a small population of wolves inhabits only the mountainous regions of Gorski Kotar and Lika (Frkovic and Huber 1992), from which they disperse to Slovenia (Adamic 1992) and Hungary (Farago 1992). In Italy, wolves occur in the Apennine Mts. and the Alps (Corsi *et al.* 1999, Glenz *et al.* 2001, Boitani 2003). Wolves, which are now re-colonizing the southern and western Europe, expand their range from Italy to France and Switzerland through Alps even to Eastern Pyrenees (Masolo and Meriggi 1998, Glenz *et al.* 2001, Boitani 2003). In the Iberian Peninsula, a large part of the wolves' population also inhabits montane areas (Vila *et al.* 1992, Promberger 1992).

Therefore, mountains are important refuges for wolves in the contemporary European landscapes. There were few studies conducted on habitats suitable for wolves in mountains of southern and western Europe (Masolo and Meriggi 1998, Glenz *et al.* 2001, Salvatori *et al.* 2002a), but little is known about wolves' habitat preferences in central and eastern Europe, especially in the Carpathian Mountains. In this paper, we report on factors influencing wolf distribution in uplands and mountains of southern Poland. Based on GIS analysis of habitat variables associated with wolf occurrence, we aimed at determining the main habitat characteristics important for wolves' existence and the anthropogenic barriers to their dispersal. Finally, using the earlier published data on wolves in northern Poland (Jędrzejewski *et al.* 2004), we compared habitat suitability of lowland and montane parts of the country for the wolf population.

Study area

The study region was the southern part of Poland (49°–52° N, 14°–24° E), which covers about 152 000 km^2 (Fig. 1). It is mostly lowland below 300 m a.s.l. Uplands (300–500 m a.s.l.) cover 12% of the area and mountains (500–2499 m a.s.l.) – about 6%. The mountains extend along the southern border of the country and include the Carpathians and the Sudety. The central part of the region includes the Świętokrzyskie Mountains (max altitude 612 m a.s.l.). The lowland landscape has been shaped by glaciers (mainly by the Riss, 310 000 to 130 000 years BP, and the Würm glaciations, 70 000 to 10 000 years BP).

The forest cover of the study area (27%) is similar to the average for whole Poland (28%; Central Statistical Office, 2002). Most of the forests are composed of young commercial stands (about 60% of stands are <60 years old, 30% are between 61–100 years, and 10% are >100 years old). The dominant tree species is the Scots pine *Pinus sylvestris* (about 70% of forest area). A few stands are composed of Norway spruce *Picea abies* (5%), beech *Fagus silvatica* (6%), fir *Abies alba* (5%) and deciduous species such as oak *Quercus robur*, ash *Fraxinus excelsior*, maple *Acer platanoides*, birch *Betula pendula* and *B. verrucosa*, hornbeam *Carpinus betulus,* and black alder *Alnus glutinosa* (Central Statistical Office, 2000). The main rivers are the Vistula and Odra with their numerous tributaries. The human population within the region is dense, on average 143 persons/km^2, whereas the national mean amounts to 124 persons/km^2. However, 62% of the population live in towns, especially in big urban agglomerations such as Wrocław, Łódź, Katowice, Kraków, Opole, Rzeszów, and Kielce. The density of roads is higher: 1.12 km of paved motorways per km^2 in southern Poland compared to 0.78 km/km^2 in the whole country (Central Statistical Office, 2002). The average traffic was 7500 vehicles per day on the national motorways and 2600 vehicles/day on regional motorways; these figures are higher than the respective means for the whole country: 7000 and 2400 vehicles/day (data from General Directorate of Motorways and Highways).

Material and methods

The data on wolf distribution in the southern Poland were obtained during the National Wolf Census carried out in Poland in 2000–2001 (Jędrzejewski *et al*. 2002). The census was conducted by the services of the Polish State Forestry and National Parks, under the supervision of the Mammal Research Institute, Polish Academy of Sciences in Białowieża (MRI PAS). All year round, the forest and national park personnel recorded wolf tracks, kills, dens, and other observations. One or two times during the winter, the mapping of fresh wolf tracks and trails was performed by inspecting 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 6.5 (MapInfo Corporation). One of the results was the map of all wolf records in Poland (Fig. 1).

For habitat analysis, we randomly (though with exclusion of big cities) selected 149 circular sample plots each with a 14-km diameter (area 154 km^2). The plots did not overlap and their diameter was based on empirical values of the nearest neighbour distance among the 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

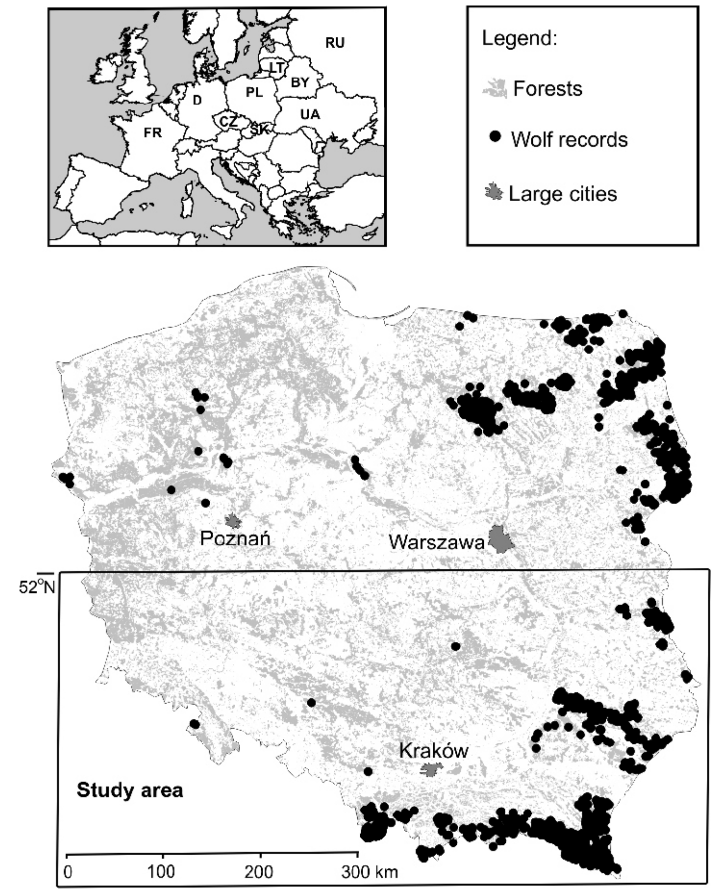

Fig. 1. Distribution of wolves *Canis lupus* in Poland according to the National Wolf Census in 2000 – 2001 (after Jędrzejewski *et al.* 2002) and the area for wolf habitat analysis (southern Poland).

wolves' territory studied by radio tracking in eastern Poland (Jędrzejewska and Jędrzejewski 1998). In total, the sample plots covered 22 946 km^2 (nearly 15% of southern Poland area) and included 52 plots where wolf occurrence has been recorded and 97 plots with no signs of wolf presence. The number of sample plots without wolves had to be larger because in southern Poland the area free of wolves is much bigger than the area where they occur. As indices of wolf abundance, we used: (1) a total number of wolf records (all observations from years 2000–2001 combined) in a sample plot, and (2) the maximum number of wolves recorded in one pack inside a plot (a proxy of pack size).

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 included only large and medium-size rivers, and not streams and very small waterways), (4) length of main roads (national roads and international motorways), (5) length of secondary (regional) roads (two lower categories, district and communal roads, were not included), (6) length of railways, (7) number of villages (usually <1000 inhabitants), (8) number of towns (usually >1000 inhabitants), (9) the shortest straight-line distance to the eastern or southern border of Poland, as a proxy of the distance to continuous range of wolves in Ukraine or Slovakia, and (10) the average altitude of the plot (meters a.s.l.). The variables 1 and 2 were obtained from a database granted to us by the General Directorate of the Polish State Forests (Ministry of the Environment, Warsaw). The variables 3–9 were measured or counted on the numerical maps prepared by the IMAGIS Company. The maps were prepared as vector layers and each of these 3–9 variables was created as a separate layer. We used the number of villages and towns as an index of human population because detailed data about human density in each sample plot were not available. Variable 10 was obtained from the topographic maps (the scale 1:100 000), by calculating the mean between the lowest and the highest points within each sample plot. Data on wolf habitat selection in southern Poland were then compared with those for the northern part of the country, collected and analysed by the same methods (see Jędrzejewski *et al.* 2004).

Results

Each sample plot with wolves contained from 1 to 103 observations of these predators (mean 30.4). The pack sizes varied from 1 to 10 wolves, on average 5.0 (Table 1). There was a significant correlation between the number of wolf records and pack size within sample plots ($r = 0.53$, $n = 52$, $p < 0.005$), which suggests that both variables were adequate indices of wolf abundance.

Percent forest cover was significantly higher in the sample plots with wolves (mean 63.8%) than in those with no wolves recorded (mean 32%; Table 1). The presence of wolves was not detected on plots having less than 30% area covered by woodland. There was also a positive relationship between the number of wolf records in a plot and its forest cover (Fig. 2). Sample plots with wolves were characterized by lower number of villages and towns (Table 1). Although we did not find a significant negative correlation between the number of villages and the number of wolf records in a plot, this tendency can be noticed (Fig. 2). However, it must be mentioned that forest cover and density of villages were mutually negatively correlated (see Fig. 2), so the wolves' selection of dense forest cover coincided with their avoidance of human settlements.

Furthermore, the plots with wolves differed significantly from wolf-free plots in respect to the lengths of railways, main motorways, and secondary roads (Table 1). In each of these human-related habitat variables, wolves selected plots with 1.4–2.4-fold lower density of transportation infrastructures than that recorded on

Table 1. Habitat characteristics of sample plots with wolves (n = 52) and those with no wolves recorded (n = 97) in southern Poland. Sample plots were circles of diameter 14 km. Comparison of wolf and wolf-free plots was done with Mann-Whitney U-test; ns – not significant.

Parameter (n, km, or km^2 per plot)	Plots with wolf records		Wolf-free plots		Statistical significance of difference (p)
	Mean ± SE	(min–max)	Mean ± SE	(min–max)	
Sum of wolf observations	30.4 ± 3.6	(1–103)	0	–	–
Maximum pack size	5.0 ± 0.3	(1–10)	0	–	–
Forest cover (%)	63.8 ± 2.1	(31–92)	32.0 ± 2.1	(0–84)	< 0.0001
Number of villages	4.9 ± 0.3	(1–12)	8.3 ± 0.3	(2–18)	< 0.0001
Straight-line distance to the nearest border of Poland (km)	35.1 ± 7.8	(3–370)	140.5 ± 10.7	(10–405)	< 0.0001
Length of railway (km)	4.6 ± 0.9	(0–20)	10.8 ± 1.0	(0–36)	0.0003
Number of towns	0.3 ± 0.1	(0–2)	0.7 ± 0.8	(0–3)	0.004
Altitude (m a.s.l.)	469 ± 44	(100–1350)	306 ± 20	(100–875)	0.004
Length of main motorways (km)	2.6 ± 0.7	(0–18)	6.3 ± 0.9	(0–33)	0.007
Length of secondary roads (km)	11.6 ± 1.3	(0–34)	16.1 ± 1.0	(0–37)	0.010
Forest fragmentation (n forest patches)	16.8 ± 1.3	(4–43)	19.1 ± 0.9	(2–46)	ns
Length of rivers (km)	14.6 ± 1.2	(0–40)	13.5 ± 0.8	(0–37)	ns

wolf-free plots. Forest fragmentation and length of rivers were not important for wolf distribution (Table 1). Sample plots with wolves were placed higher in the mountains and closer to the southern and eastern border of Poland (as an indicator of a distance to the continuous range of wolves) (Table 1).

Since wolves in southern Poland occurred mainly in the upland and mountains, we checked if the mountain habitats *per se* could have been a driving factor in habitat choice by wolves. We selected all sample plots with average altitude > 500 m a.s.l. and compared habitat variables on those with wolves (n = 24) and without wolves (n = 19). Again, wolves preferred areas with a significantly larger forest cover and fewer villages and towns (Table 2). They also avoided railway lines and main roads. The density of secondary roads had weaker influence on wolf distribution in the mountains.

Based on the results of habitat analysis and following the statistical approach by Mladenoff *et al.* (1995), we conducted a logistic regression analysis to find a set of variables essential for wolf distribution in southern Poland. The model, that contained four habitat characteristics: forest cover, length of railway lines, number of villages, and length of roads correctly classified 77% of plots with wolves and 91% of plots without wolves (Table 3). Still, however, the strongest component of the model was the forest cover. The model containing only this factor correctly classified 73% wolf plots and 88% plots with no wolves (Table 3). Comparison of the two models with Akaike's Information Criterion method (Anderson *et al.* 2000) has shown that the model involving one independent variable, the forest cover, was the most parsimonious one (Akaike's weight ω_i = 0.9998).

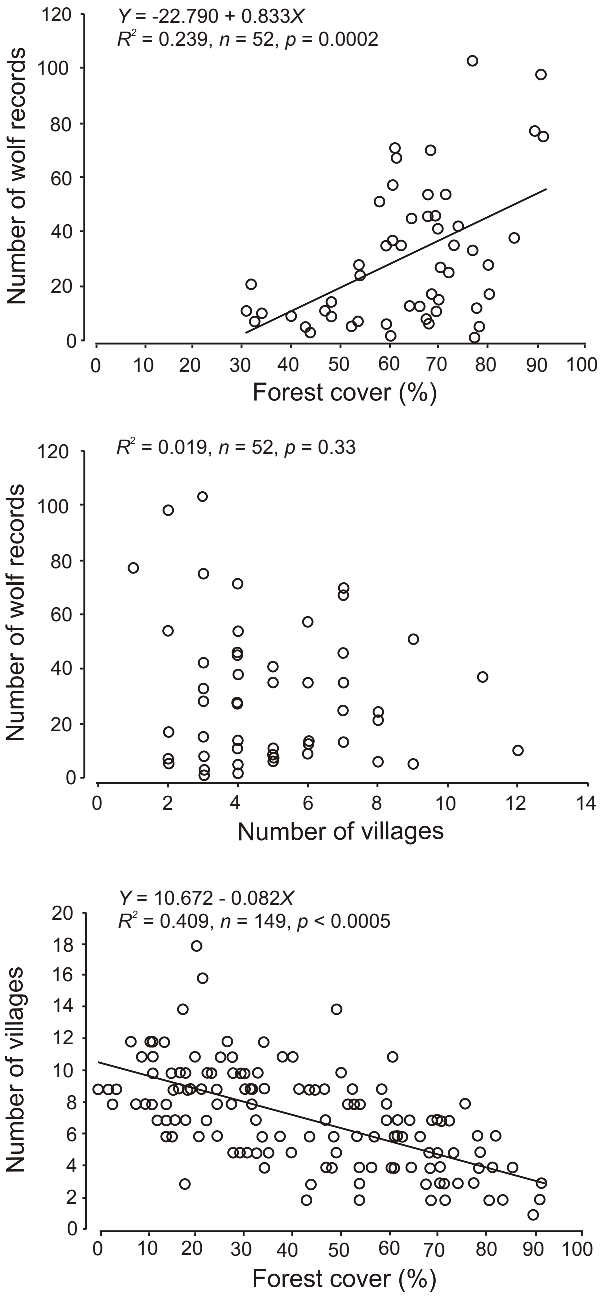

Fig. 2. Relationship between index of wolf abundance (sum of wolf observations per occupied plot, 154 km^2 each) and percent forest cover (upper graph). Relationship between number of wolf records and number of villages in wolf-occupied plots (middle graph). Forest cover and number of villages in all sample plots (52 plots with wolves and 97 without wolves) in southern Poland (lower graph).

Table 2. The mean (± SE) values of habitat variables in sample plots with and without wolves in the Polish mountains. Number of sample plots in parentheses. Comparison of wolf and wolf-free plots was done by Mann-Whitney U-test.

Parameter	Sample plots in the mountains (> 500 m a.s.l.)				Statistical significance of difference (p)
	With wolves (24)		No wolves (19)		
	Mean ± SE	(min–max)	Mean ± SE	(min–max)	
Forest cover (%)	67.2 ± 3.1	(32–92)	46.2 ± 2.9	(28–72)	< 0.0001
Length of railway (km)	2.5 ± 1.1	(0–17)	14.6 ± 1.5	(0–24)	< 0.0001
Number of towns	0.3 ± 0.1	(0–2)	1.3 ± 0.2	(0–3)	0.001
Number of villages	5.5 ± 0.6	(1–12)	7.7 ± 0.7	(3–14)	0.016
Length of main roads	1.9 ± 1.0	(0–18)	7.5 ± 2.2	(0–33)	0.028
Length of secondary roads	12.0 ± 2.0	(0–28)	18.1 ± 2.1	(0–35)	0.057

Table 3. Logistic regression analysis of habitat variables explaining wolf distribution in southern Poland, based on 52 sample plots with wolves recorded and 97 plots without wolves. Both models are statistically significant at $p <$ 0.0005. Main and secondary roads summed.

Variable	Statistical significance (p)	
	Model with four variables	Model with one variable
Forest cover (%)	< 0.0005	< 0.0005
Length of railways (km)	0.013	–
Number of villages (km)	0.017	–
Length of roads (km)	0.045	–
	Percent of correct classification	
Samples with wolves	77	73
Samples without wolves	91	88

Comparison of wolf habitat selection in northern and southern Poland

In both northern and southern Poland, the occurrence of wolves was connected with forest cover but the distribution of sample plots with wolves in relation to forest cover differed between the regions (G-test for homogeneity of percentages, $G = 37.21$, df = 4, $p < 0.001$, Fig. 3). In northern Poland, 41% of plots with wolves were characterized by forest cover < 40% (Jędrzejewski *et al.* 2004) (Fig. 3). In southern Poland, only 10% of wolf plots had such a low share of woodland. In both northern and southern Poland wolves were most abundant near the state border, and the indices of their numbers declined with increasing distance from the

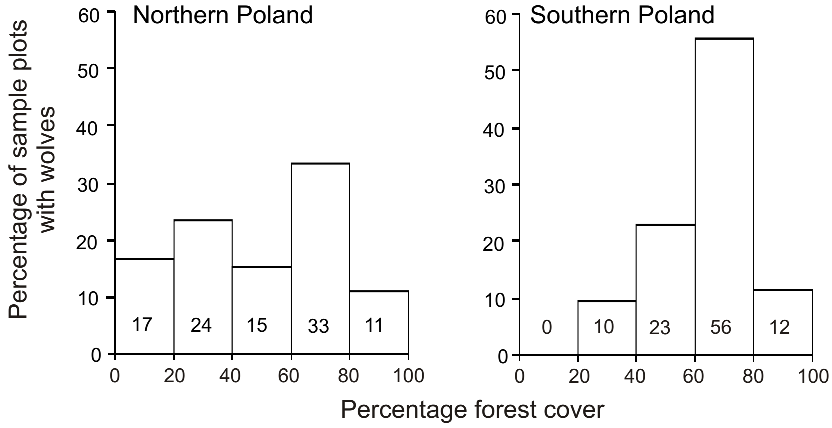

Fig. 3. Frequency distributions of plots with wolves in classes of percentage forest cover in northern and southern Poland. All plots with wolves in each region taken as 100%.

border (Jędrzejewski *et al.* 2004, and this paper). That decline, however, was faster in southern Poland, where wolves occurred mainly in a 100-km belt along the border, and only 4–7% of sample plots located >100 km from the border had signs of wolf presence (Table 4). In northern Poland, the decline of wolf abundance towards the interior of the country was slower: 55% of sample plots in the belt 101–200 km from the border had wolves, and 30% plots located further than 200 km form the border were wolf plots (Table 4). These differences between southern and northern Poland were highly significant (G = 21.45, df = 2, $p < 0.001$).

To find the explanation for those differences, we compared the main environmental variables in all sample plots grouped according to the distance from the Poland's eastern and southern border (Table 4). While percentage forest cover did not show any consistent changes between regions or distance classes (Kruskal--Wallis test: H = 4.43, n = 281 plots, p = 0.49), the three human-related variables exhibited statistically significant variation in this respect (H from 30.40 to 43.01, $p < 0.00005$). Furthermore, pairwise comparisons evidenced that the densities of human-made infrastructure in the same distance classes were always bigger in southern Poland (differences statistically significant in 6 out of 9 pairwise comparisons). In northern Poland, significant difference in all anthropogenic barriers occurred between distance classes 0–100 and > 200 km (p from < 0.0005 to 0.001), whereas in southern Poland a big habitat change in that respect was already recorded between the belts 0–100 and 101–200 km from the border (p < 0.0005 for settlements, roads, and railways). In conclusion, despite a similar forest cover, southern Poland offered markedly worse habitats for wolves than the northern part of the country. The main reason for lower habitat suitability in the South was a significantly denser network of settlements and transportation routes.

Table 4. Comparison of wolf occurrence and habitat variables (mean ± SE) in northern and southern Poland in all sample plots grouped in classes of distance from the eastern or southern state border. Main and secondary roads summed.

Parameter	Distance to the state border (km)		
	0–100	101–200	> 201
Northern Poland			
Number of all sample plots	40	38	54
Forest cover (%)	43.4 ± 3.9	38.9 ± 3.6	44.9 ± 3.3
Number of settlements	5.0 ± 0.4	6.0 ± 0.4	6.3 ± 0.4
Length of roads (km)	12.8 ± 1.2	17.7 ± 1.7	19.1 ± 1.5
Length of railways (km)	4.9 ± 1.1	7.5 ± 1.2	11.0 ± 1.3
Percent plots with wolves	87	55	30
Southern Poland			
Number of all sample plots	93	28	28
Forest cover (%)	45.6 ± 2.6	35.7 ± 4.2	42.2 ± 4.2
Number of settlements	7.5 ± 0.4	8.6 ± 0.6	7.4 ± 0.5
Length of roads (km)	16.9 ± 1.1	20.6 ± 1.5	27.2 ± 2.1
Length of railways (km)	5.5 ± 0.8	11.7 ± 1.7	15.9 ± 1.7
Percent plots with wolves	53	7	4

Discussion

According to the analysis made by Salvatori *et al.* (2002a), most of the mountain range in the Carpathians contained highly suitable habitats for wolves. Almost all of them have already been inhabited by the present wolf population. As wolves are now protected by law in Poland, the main problem of their dispersal into new areas is the lack of corridors for migration and largely hostile habitats in the northern foothills of the Polish Carpathians. Furthermore, the increasing numbers of tourists, which reach 3 million annually in the Tatra Mountains, are a big problem to large predator conservation (Zięba *et al.* 1996, Nowak and Mysłajek 2003).

In southern Poland, wolves occurred more often in areas of higher altitude and denser forest cover than random plots with no wolves. In the temperate zone of Europe, woodland that provides food resources and safe den sites (Theuerkauf *et al.* 2003, Jędrzejewski *et al.* 2004), was the most important factor determining wolf occurrence. In the Polish Carpathians, montane forests grow up to 1250–1350 m a.s.l, and in Tatra Mountains (the highest ridge) up to 1650 m a.s.l (Starkel 1999), thus wolves inhabited areas to the upper timber line. In Slovak Carpathians, the upper timber line is between 1400 and 1550 m a.s.l. and wolves were recorded between 518 to 1680 m a.s.l. (Find'o and Chovancová 2004). In the Apennines, Italy, those carnivores occurred more often at intermediate elevations

(800–1600 m a.s.l.; Boitani 1982, Ciucci *et al.* 2003). Glenz *et al.* (2001) claimed that, in the Alps, areas below 800–900 m a.s.l., due to high human disturbance and places above 1800–2000 m a.s.l., due to lack of prey would not be suitable for wolves.

In southern Poland, wolves were much less tolerant of low forest cover than in northern Poland. The main reason for that was high density of human population, settlements, and transportation infrastructure in that region compared to the lowlands of northern Poland (Jędrzejewski *et al.* 2004; this paper). Human--related infrastructure was reported to influence wolf distribution in other parts of the world as well (Conway 1996, Ciucci *et al.* 2003, Oakleaf *et al.* 2003) and it is a good feature used to predict habitats suitable for large carnivores (Conway 1996, Harrison and Chapin 1998, Masolo and Meriggi 1998, Wydeven *et al.* 2001). Negative effects of roads and railways on wildlife are well documented (Stein 2000, Clevenger *et al*. 2001, Wydeven *et al.* 2001, Kerley *et al.* 2002, Saunders *et al.* 2002, Singleton *et al.* 2002). These linear features significantly influence the movements of large carnivores (Wydeven *et al.* 1998, Stein 2000, Singleton *et al.* 2002). However, if anthropogenic impact is not too high, wolves can get used to human presence by a spatiotemporal segregation from man. They avoid open areas, settlements, and public roads much more during the day than during the night (Boitani 1982, Theuerkauf *et al*. 2003).

In some regions, wolves were able to live in the mosaic, forest-agriculture areas but in those areas they frequently caused damage to livestock (Ciucci and Boitani 1998, Sidorovich *et al*. 2003). Such a situation took place in some parts of Podlasie and Masurian Lakeland, northern Poland, where pastures for cattle were located outside forests (Jędrzejewski *et al.* 2004). In southern part of Poland the situation was different. Wolves killed sheep within the forested area, because most of the pastures (small subalpine meadows) were usually located in the montane forest zone (Jędrzejewski *et al.* 2002).

In conclusion, except for the Carpathian Mountains and some upland regions, southern Poland offers markedly less suitable habitats for wolves than the northern part of the country. Despite relatively high forest cover, southern Poland is characterized by dense human population and high density of anthropogenic barriers such as settlements, roads, and railways. In the mountains, additional threats for large predators are the development of tourist infrastructure and rapid increase in tourist numbers.

Acknowledgements: We thank the General Directorate and all the Regional Directorates of the State Forests, and the Department of Nature Conservation of the Ministry of the Environment for their cooperation during the National Wolf Census. We direct our special thanks to the personnel of all State Forest districts and National Parks, who participated in the field work. The study was financed by the General Directorate of State Forests (Poland), Euronatur (Germany), Norwegian Research Council (Norway), BIOTER Centre of Excellence (EVK2-CT-2002-80011), and the budget of the Mammal Research Institute PAS in Białowieża.

References

Adamic M. 1992. Status of the wolf (*Canis lupus L.*) in Slovenia. [In: Proceedings of the workshop: Wolves in Europe – current status and prospects. C. Promberger and W. Schröder, eds]. Oberammergau, Germany: 71–73.

Anderson D. R., Burnham K. P. and Thompson W. L. 2000. Null hypotheses testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64: 912–923.

Boitani L. 1982. Wolf management in intensively used areas of Italy. [In: Wolves of the World. Perspectives of behavior, ecology, and conservation. F. H. Harrington and D. C. Paquet, eds]. Noyes Publications, Park Ridge, New York, USA: 158–172.

Boitani L. 2003. Wolves conservation and recovery. [In: Wolves. Behavior, ecology, and conservation. D. Mech and L. Boitani, eds]. The University of Chicago Press, Chicago and London: 317–340.

Central Statistical Office. 2000. Forestry statistical yearbook 2000. Warszawa. [In Polish]

Central Statistical Office. 2002. Statistical yearbook of the Republic of Poland 2002. Warszawa: 1–761. [In Polish]

Ciucci P. and Boitani L. 1998. Wolf and dog depredation on livestock in central Italy. Wildlife Society Bulletin 26: 504–514.

Ciucci P., Masi M. and Boitani L. 2003. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. Ecography 26: 223–225.

Clevenger A. P., McIvor M., McIvor D., Chruszcz B. and Gunson K. 2001. Tiger salamander, *Ambystoma tigrium*, movements and mortality on the trans-Canada highway in Southwestern Alberta. Canadian Field-Naturalist 115: 199–204.

Conway K. 1996. Wolf recovery – GIS facilitates habitat mapping in the Great Lake States. GIS World 11: 54–57.

Corsi F., Duprè E. and Boitani L. 1999. A large-scale model of wolf distribution in Italy for conservation planning. Conservation Biology 13: 150–159.

Farago S. 1992. Current status of the wolf (*Canis lupus*) in Hungary. [In: Proceedings of the workshop: Wolves in Europe – current status and prospects. C. Promberger and W. Schröder, eds]. Oberammergau, Germany: 45–49.

Find'o S. and Chovancová B. 2004. Home ranges of two wolf packs in the Slovak Carpathians. Folia Zoologica 53: 17–26.

Frkovic A. and Huber D. 1992. Wolves in Croatia: Baseline data. [In: Proceedings of the workshop: Wolves in Europe – current status and prospects. C. Promberger and W. Schröder, eds]. Oberammergau, Germany: 67–69.

Glenz C., Massolo A., Kuonen D. S. and Schlaepfer R. 2001. A wolf habitat suitability prediction study in Valais (Switzerland). Landscape and Urban Planning 55: 55–65.

Harrison D. J. and Chapin T. G. 1998. Extent and connectivity of habitat for wolves in eastern North America. Wildlife Society Bulletin 26: 767–775.

Jędrzejewska B. and Jędrzejewski W. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer, Berlin: 1–450.

Jędrzejewski W., Nowak S., Schmidt K. and Jędrzejewska B. 2002. The wolf and lynx in Poland – results of the census conducted in 2001. Kosmos 51: 491–499. [In Polish with English summary]

Jędrzejewski W., Niedziałkowska M., Nowak S. and Jędrzejewska B. 2004. Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. Diversity and Distributions 10: 225–233.

Kerley L. I., Goodrich J. M., Miquelle D. G., Smirnov E. N., Quigley H. B. and Hornocker M. G. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16: 97–108.

Massolo A. and Meriggi A. 1998. Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. Ecography 21: 97–107.

Mladenoff D. J., Sickley T. A., Haight R. G. and Wydeven A. P. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9: 279–294.

Nowak S. and Mysłajek R. 2003. [Conservation problems of wolves *Canis lupus* in Western Bieszczady landscape parks]. [In: Selected species of endangered animals in the Western Bieszczady Mts and ways of their protection. M. Broda and J. Mastaj, eds]. Zespół Parków Krajobrazowych Województwa Śląskiego, Będzin: 14–19. [In Polish]

Oakleaf J. K., Murray D. L., Bangs E. E., Mack C. M., Smith D. W., Fontaine J. A., Oakleaf J. R., Jimenez M. D., Meier T. J. and Niemeyer C. C. 2003. Habitat selection by recolonizing wolves in the Northwestern United States. [In: World Wolf Congress 2003. Bridging science and community]. September 25–28, 2003. The Banff Centre, Banff, Alberta, Canada: 23–24.

Promberger C. 1992. Population trends of wolves in Portugal. [In: Proceedings of the workshop: Wolves in Europe – current status and prospects. C. Promberger and W. Schröder, eds]. Oberammergau, Germany: 111–112.

Promberger Ch., Mertens A., Promberger-Fürpass B. and Blumer A. 2000. Economic evaluation. [In: Carpathian Large Carnivore project. Annual report]. S and G Print, HACO International Publishing: 1–72.

Salvatori V., Corsi F., Milton E. J. and Boitani L. 2002a. Use of satellite images for regional modelling of conservation areas for wolves in the Carpathian Mountains, Central Europe. [In: Information for sustainability and development. Proceedings of the 29th International Symposium on Remote Sensing of Environment]. Buenos Aires, Argentina.

Salvatori V., Okarma H., Ionescu O., Dovhanych Y., Find'o S. and Boitani L. 2002b. Hunting legislation in the Carpathian Mountains: implications for the conservation and management of large carnivores. Wildlife Biology 8: 3–10.

Saunders S. C., Mislivets M. R., Chen J. and Cleland D. T. 2002. Effects of roads on landscape structure within nested ecological units of the Northern Great Lakes Region, USA. Biological Conservation 103: 209–225.

Sidorovich V. E., Tikhomirova L. L. and Jędrzejewska B. 2003. Wolf *Canis lupus* numbers, diet and damage on livestock in relation to hunting and ungulate abundance in northeastern Belarus. Wildlife Biology 9: 103–111.

Singleton P. H., Gaines W. L. and Lehmkuhl J. F. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, Research Paper PNW-RP-549: 1–89.

Starkel L. 1999. [Geography of Poland]. Wydawnictwo Naukowe PWN. Warszawa: 1–593. [In Polish]

Stein J. T. 2000. From extermination to reintroduction: A snapshot of North America large carnivore conservation at the millenium. Unpublished MSc thesis, Yale School of Forestry and Environmental Studies, New Haven.

Theuerkauf J., Jędrzejewski W., Schmidt K. and Gula R. 2003. Spatiotemporal segregation of wolves from humans in the Białowieża Forest (Poland). The Journal of Wildlife Management 67: 706–716.

Vila C., Castroviejo J. and Urios V. 1992. The Iberian wolf in Spain. [In: Proceedings of the workshop: Wolves in Europe – current status and prospects. C. Promberger and W. Schröder, eds]. Oberammergau, Germany: 105–109.

Wydeven A. P., Fuller T. K., Weber W. and MacDonald K. 1998. The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. Wildlife Society Bulletin 26: 776–784.

Wydeven A. P., Mladenoff D. J., Sickley T. A., Kohn B. E., Thiel R. P. and Hansen J. L. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes Region. Endangered Species 18: 110–114.

Zięba F., Bodziarczyk J. and Szwagrzyk J. 1996. The limits to renaturalization: large carnivores in the Tatry Biosphere Reserve. Przegląd Przyrodniczy 7: 245–256. [In Polish with English abstract]

Received 3 January 2005, accepted 6 June 2005.

Associate Editor was Karol Zub.