Mammalian Biology 76 (2011) 217–221

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.de/mambio

Original Investigation

Presence of Iberian wolf (*Canis lupus signatus*) in relation to land cover, livestock and human influence in Portugal

Julia Eggermann[a,*], Gonçalo Ferrão da Costa[b], Ana M. Guerra[b], Wolfgang H. Kirchner[a], Francisco Petrucci-Fonseca[b,c]

[a] Faculty of Biology and Biotechnology, Ruhr University Bochum, Universitätsstraße 150, 44801 Bochum, Germany
[b] Grupo Lobo, Faculdade de Ciências da Universidade de Lisboa, Bloco C2, 3° Piso, Departamento de Biologia Animal, Campo Grande, 1749-016 Lisboa, Portugal
[c] Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

ARTICLE INFO

Article history:
Received 19 August 2009
Accepted 30 October 2010

Keywords:
Canis lupus signatus
Habitat utilization analysis
Human influence
Logistic regression model
Portugal

ABSTRACT

From June 2005 to March 2007, we investigated wolf presence in an area of 1000 km^2 in central northern Portugal by scat surveys along line transects. We aimed at predicting wolf presence by developing a habitat model using land cover classes, livestock density and human influence (e.g. population and road density). We confirmed the presence of three wolf packs by kernel density distribution analysis of scat location data and detected their rendezvous sites by howling simulations. Wolf habitats were characterized by lower human presence and higher densities of livestock. The model, developed by binary logistic regression, included the variables livestock and road density and correctly predicted 90.7% of areas with wolf presence. Wolves avoided the closer surroundings of villages and roads, as well as the general proximity to major roads. Our results show that the availability of prey (here: livestock) is the most important factor for wolf presence and that wolves can coexist with humans even in areas of poor land cover, unless these areas are excessively fragmented by anthropogenic infrastructures.

Introduction

Wolves in Europe had been eradicated from most of their original range by the middle of the 20th century (Boitani 2000). However, since these animals became protected in many countries, their numbers increased and their range expanded (Boitani 2000). Most of the former wolf habitat has become urbanized and industrialized, so the species' current expansion frequently leads to conflicts with humans, especially in livestock farming areas (Cayuela 2004; Treves et al. 2004; Kusak et al. 2005; Bisi et al. 2007). In Portugal, wolf numbers and distribution decreased dramatically during the 20th century (Bessa-Gomes and Petrucci-Fonseca 2003), until they were legally fully protected in 1988 (Grilo et al. 2002). Since then, wolf numbers have somewhat stabilized, even though in some areas local extinctions may still occur (Bessa-Gomes and Petrucci-Fonseca 2003; Álvares 2004).

Livestock farming is an important field of Portuguese economy. Livestock, often unguarded or with just one shepherd, generally roams freely in the mountains rather than in fenced pastures. Therefore, wolf depredation on goats (*Capra hircus*), sheep (*Ovis aries*), cows (*Bos taurus*) and horses (*Equus caballus*) is commonplace (Álvares et al. 2000; Carreira and Petrucci-Fonseca 2000; Roque et al. 2001). As a result, wolves are often killed illegally by shooting, poison or snares (Álvares et al. 2000; Carreira and Petrucci-Fonseca 2000). Other threats to Portuguese wolves include habitat fragmentation by new roads, decrease of forest cover caused by fires during dry summers, new settlements in formerly uncultivated areas and lack of wild prey (Santos et al., 2007). The human-wolf conflict, therefore, needs to be reduced in order to prevent a further decline of wolf numbers and enable the resettlement of the species over their former range. For this purpose, knowledge about minimal requirements for the survival of wolves, comprising land cover, food availability and human influences, are essential. Wolf habitat models can help to gain this information and improve the carnivore's conservation by determining priority areas, developing conservation corridors between important wolf habitats and highlighting potential conflict zones between wolves and humans (Kramer-Schadt et al., 2005; Rhodes et al., 2006; Rodriguez-Freire and Crecente-Maseda, 2008). The aim of our study was, therefore, to develop a habitat model based on data about wolf presence in central northern Portugal and gain insight into potentially important environmental factors (biotic and abiotic) for wolf distribution, with a particular emphasis on the impact of anthropogenic variables on the predator's presence.

* Corresponding author. Tel.: +49 234 32 29014.
E-mail address: julia.eggermann@web.de (J. Eggermann).

1616-5047/$ – see front matter © 2010 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.
doi:10.1016/j.mambio.2010.10.010

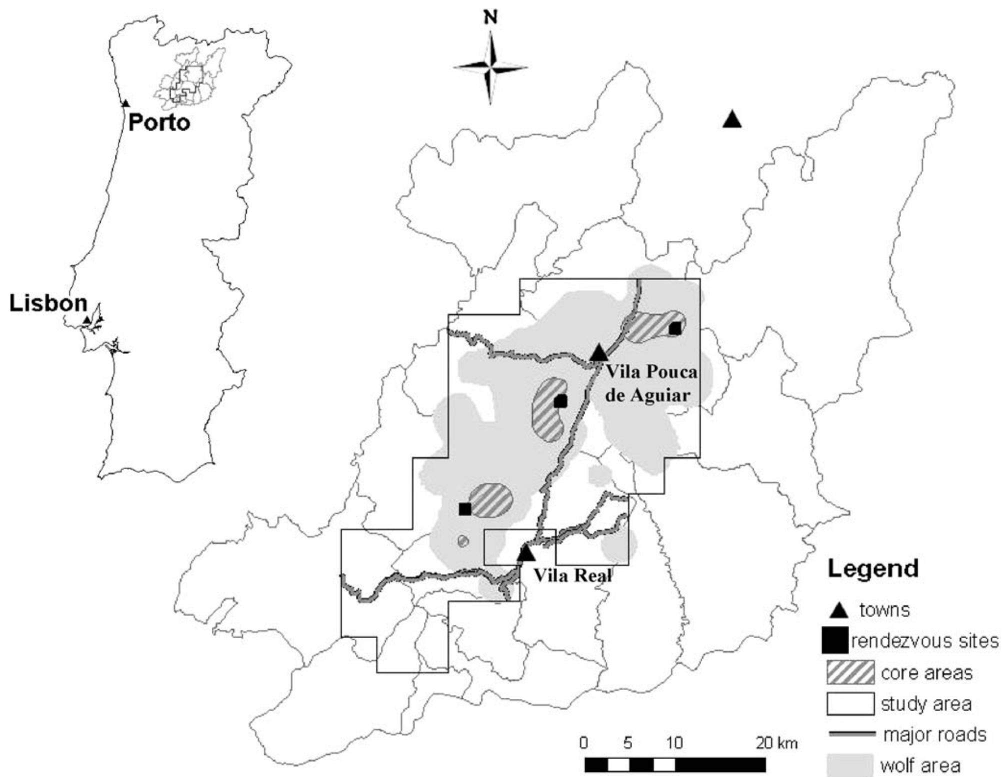

Fig. 1. Location of the study area within Portugal and wolf distribution within the study area. Shown are major roads, areas of wolf presence (light grey area), core areas of three wolf packs (shaded areas), and location of rendezvous sites of three packs (dots), detected by howling simulations.

Material and methods

The study was conducted in the Vila Real district, in central northern Portugal, and included the Natura 2000 site, Alvão/Marão (Fig. 1). The study area covered 1000 km^2 with mountains up to 1400 m a.s.l. (41°10′–41°51′N, 07°13′–07°59′E). The area included numerous small villages as well as two bigger towns. Average population density was 48 km^{-2} and road density around 0.83 km km^{-2}. The area was cut by three major roads and two newly constructed fenced highways. The region's land cover was mainly shrub land (38%), agricultural land (24%) and forests (21%). The forest was composed in 62% of coniferous, pine (*Pinus pinaster*) forests and secondary of broad-leaved forests (*Quercus sp.* and *Castanea sativa*). Important economic resources included forestry and livestock grazing.

We conducted the study from June 2005 to March 2007. We estimated wolf presence by scat surveys on 220 transects (550 km). Wolf scats were differentiated from dog and fox scats by their shape, contents and smell. If doubt persisted about identification, the respective scats were not included into the analysis. We placed a grid above the study area with 4 km^2 mesh size and chose transects pseudo randomly within each grid cell. Transects were situated on unpaved roads and distributed over the whole study area. We inspected 60 transects (200 km) every three months to detect changes in wolf distribution and the other 160 transects (350 km) once during the study for a more detailed knowledge about habitat preferences. The location of each wolf scat was assessed by GPS. We used fixed kernel-analysis with a band-width of 1500 m to calculate probabilities of wolf presence from the resulting wolf location data. Recognition of individual packs was based on a 50% probability-analysis, showing the most intensively used areas, and confirmed by howling simulations (human imitation). In summer, when pups still remain at rendezvous sites, wolves were stimulated to howl and, in case of answers by adults and pups, the location was considered a rendezvous site of the pack. We related the distance of each wolf scat from settlements and roads to the same measures obtained for a set of random points, generated within the pack's ranges, by Ivlev's electivity index (Jacobs 1974):

$$\text{Selection index} = (p_s - p_r)(p_s + p_r - 2p_s p_r)^{-1} \quad (1)$$

with p_s being the proportion of wolf scats in a given distance to the next settlement/road and p_r the proportion of random points in the same given distance to the next settlement/road. Selection indices vary from +1 (total selection) to −1 (total avoidance).

For the analysis of habitat preferences of wolves we used the above mentioned 4 km^2 grid cells, labeled with wolf presence and wolf absence. Recognition of cells with wolf presence was based on a 95% kernel density distribution; the cells outside the 95% kernel probability range were defined as cells with wolf absence. We chose variables of possible importance to wolves and assessed them for each of the 248 grid cells. These variables described the land cover (urban areas, open areas, forest cover, agricultural land and shrub land), extracted from CORINE 2000 maps, and livestock density (animals km^{-2}), based on a national census of agriculture in 2003 providing total numbers of goats, sheep and cows per municipality. Road density and number of settlements were calculated from topographic military maps of Portugal (1996–1998), with a 1:25,000 scale. Human density (humans km^{-2}) was estimated based on a national census of the population in 2002 providing absolute numbers per municipality. We focused on livestock as main prey, as data on wild ungulate densities were not available. Moreover, several studies throughout northern Portugal found that the wolves' diet consists to more than 80% of domestic ungulates, while wild prey, such as roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), contribute to only 18.9% (Álvares et al. 2000; Carreira and Petrucci-Fonseca 2000; Roque et al. 2001). In these studies, the diet of 22 wolf packs was analyzed in three separate areas of around 4500 km^2 in total, including the present study area. To com-

Table 1
Mean values and 95% confidence intervals (CIs) for the variables "human influence", "land cover" and "livestock density" in cells with and without wolf presence (based on scat surveys along line transects from June 2005 to March 2007 and 95% Kernel-analysis of resulting wolf location data). The *P*-values show the results of a Mann–Whitney U-test to compare means of cells with and without wolf presence.

	Wolf presence ($n = 162$ cells) mean ± CI (95%)	Wolf absence ($n = 86$ cells) mean ± CI (95%)	*P*-value
Road density (km km^{-2})	0.71 ± 0.10	1.04 ± 0.17	0.002
Human density (no km^{-2})	42.3 ± 6.1	59.7 ± 10.7	0.001
Settlements (no km^{-2})	1.37 ± 0.20	2.09 ± 0.43	0.017
Urban areas (km^2 km^{-2})	0.16 ± 0.04	0.22 ± 0.05	0.016
Agricultural land (%)	24.7 ± 3.1	23.9 ± 4.3	0.778
Shrub land (%)	35.8 ± 3.6	42.4 ± 6.0	0.124
Open areas (%)	19.5 ± 4.1	4.8 ± 3.1	0.001
Forest cover (%)	17.8 ± 3.0	27.6 ± 4.8	0.001
Livestock density (no km^{-2})	47.0 ± 3.2	24.6 ± 3.2	0.001
Goats	19.5 ± 3.70	9.08 ± 2.03	0.001
Sheep	11.3 ± 1.53	9.09 ± 1.33	0.008
Cows	18.6 ± 1.94	11.8 ± 1.75	0.001

pare wolf habitat with non-wolf habitat, we calculated the mean of each variable for the 4 km^2 grid cells with wolf presence and for the 4 km^2 grid cells with wolf absence, together with 95% confidence intervals. Afterwards, we tested for significant differences between means of variables in wolf areas and non-wolf areas with the Mann–Whitney U-test.

For the development of the habitat model we chose logistic regression (SPSS 13.0 for Windows), as it identifies critical habitat factors for wolf presence. We first divided the data set, consisting of 248 grid cells, into two randomly chosen sub samples of 70% (174 cells) and 30% (74 cells). We developed the model based on 174 cells and tested it with the remaining 74 cells. We used the forward stepwise method to select variables contributing most to the model and counterchecked it by the backward stepwise method. We used the Hosmer–Lemeshow goodness-of-fit test to estimate the fit of the model.

Results

We found a total of 1723 wolf scats between June 2005 and March 2007. We distinguished three wolf packs and confirmed their core areas and rendezvous sites by howling simulations (Fig. 1). 95% kernel density distribution revealed that wolves frequently used 65% (162 cells) of the study area, whereas no signs of wolf presence could be found in the remaining 35% (86 cells). Road density was lower in areas frequently used by wolves (U-test, $P = 0.002$; Table 1). Wolves avoided a zone of 2 km each side of major roads and usually avoided a corridor of 0.5 km each side of small roads (Fig. 2). Wolves, however, selected a zone within 1–2 km from small roads. Human population density was lower in the wolf range (U-test, $P < 0.001$), which included less villages and smaller urbanized areas (U-test, $P = 0.017$ and $P = 0.016$ respectively; Table 1). Wolves avoided both, the close proximity of settlements and areas farther than 2 km from villages (Fig. 2). They selected areas that were within 1–1.5 km from settlements. Livestock density was higher in areas that wolves visited regularly (U-test; $P < 0.001$), with a stronger tendency for goats and cows (U-test, $P < 0.001$) than for sheep (U-test, $P = 0.008$; Table 1). Areas occupied by wolves were less forested than areas where wolves were virtually absent (U-test, $P < 0.001$).

The variable 'livestock density' classified 77.1% of cells correctly during model development and 84.1% during model testing (Table 2). Wolf areas were correctly classified to 89.1% and 93.0% (during model development and model testing, respectively) and non-wolf areas were correctly classified to 53.3% and 69.2%. We then added 'road density' as a second variable to the model, since the difference (calculated by the Hosmer–Lemeshow goodness-of-fit test) between observed and predicted wolf presence was nearly

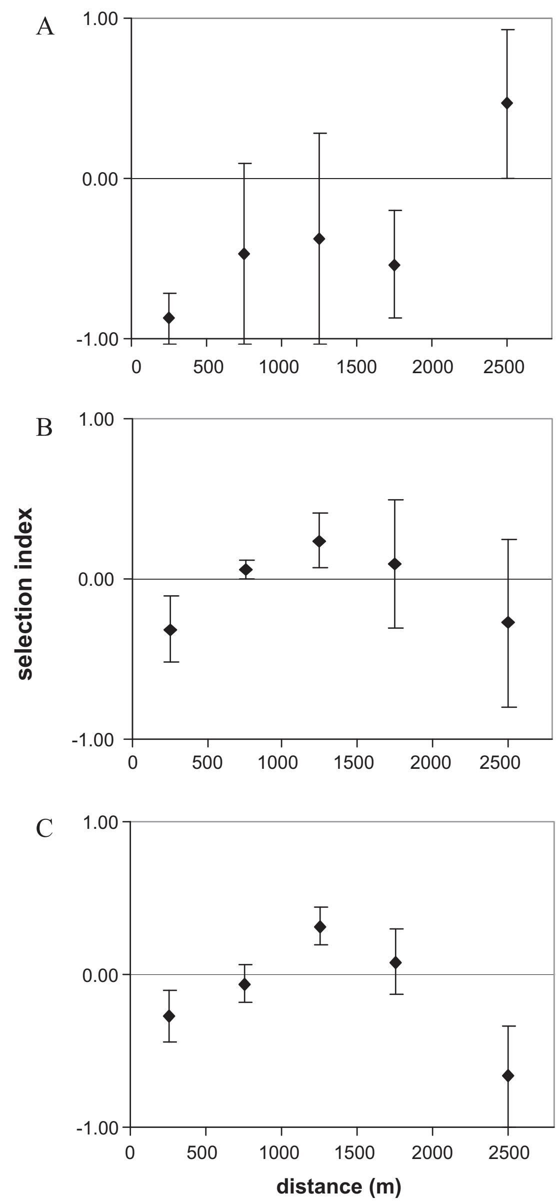

Fig. 2. Selection and avoidance of major roads (A), small roads (B) and settlements (C) by wolves, calculated by Ivlev's electivity analysis. Selection indices can vary from +1 (total selection) to −1 (total avoidance). The analysis is based on scat surveys along line transects from June 2005 to March 2007.

Table 2
Results of the logistic regression analysis and percentages of correct classifications obtained during model development and during model testing. Sensitivity and specificity refer to the correctly classified cells with and without wolf presence, respectively.

	Variable	β ± S.E.	Wald statistic	d.f.	*P*-value	Sensitivity (model/test)	Specificity (model/test)	Correct predictions (model/test)
Step1	Livestock	0.08 ± 0.01	29.93	1	0.0001	89.1%/93.0%	53.3%/69.2%	77.1%/84.1%
	Constant	−1.93 ± 0.48	16.36	1	0.0001			
Step2	Livestock	0.08 ± 0.02	31.19	1	0.0001	88.2%/90.7%	60.0%/69.2%	78.8%/82.6%
	Roads	−0.96 ± 0.27	12.54	1	0.0001			
	Constant	−1.32 ± 0.50	6.87	1	0.0001			

significant ($\chi^2 = 14.0$, $P = 0.112$) and, thus, the model showed a poor fit. The second model, with 'livestock density' and 'road density' as explaining variables, classified 78.8% of squares correctly during model development and 82.6% during model testing, with a sensitivity of 88.2% and 90.7% and a specificity of 60.0% and 69.2%. The Hosmer–Lemeshow goodness-of-fit test detected no significant difference between observed and predicted wolf presence ($\chi^2 = 2.963$, $P = 0.937$) and, therefore, this model provided a considerably better fit.

Discussion

Our results imply that wolves are not habitat specific concerning land cover. Land cover variables, such as shrubs and agriculture, did not vary between wolf habitat and non-wolf habitat. The lower amount of forest in the wolves' ranges was probably due to the selection of areas where livestock is grazing (open areas and shrub land). Studies from Poland (Jędrzejewski et al. 2004, 2005), as well as from Slovakia (Findo and Chovancová 2004), showed a considerably higher amount of forest in areas inhabited by wolves. This might as well just reflect the wolves' selection of areas used predominantly by their main prey species, which in Poland and Slovakia is red deer (*Cervus elaphus*; Jędrzejewski et al. 2000, 2002; Gula 2004; Findo and Chovancová 2004; Nowak et al. 2005; Gula 2008). Our findings agree with conclusions drawn by Fuller (1995) and Mech (1995), who state that wolves are generalists regarding their habitat requirements. They stand at the top of the food chain and can survive wherever they have enough to eat and are not killed by humans (Peterson 1988; Mech 1995). In our study, livestock density was the factor that best explained wolf presence. As wolves preferentially use small dirt roads for traveling from rendezvous sites to preying sites (Thurber et al. 1994), the question arises whether the selection of areas with higher livestock densities by wolves might be biased by a denser network of dirt roads around herds of domestic animals. Our data, however, do not support this idea, as there is rather a slight, but not significant negative correlation between length of dirt roads and livestock density (Spearman rank correlation, $P = 0.102$). Findings of Fuller (1989) and Fuller et al. (1992) agree with our findings, as in their studies prey density explained 72% of wolf occurrences. However, they restricted their statement to unexploited wolf populations. Boitani (1992) and Carroll et al. (1999) emphasize that studies carried out in regions with different exploitation histories, e.g. in North America and Europe, have to be regarded in their own context.

The human dimension seems to be the next important factor for explaining wolf presence. Boitani and Ciucci (1993) state, that the human attitude towards wolves is the determining factor of wolf presence. However, the relationship between wolves and humans is very complex (Linnell et al. 2001), as for instance wolves are nocturnal in southern Europe (Italy and Spain) with human densities of 20–30 km^{-2}, but are rather diurnal in southeastern Poland with a human density of 44 km^{-2} (Vilá et al. 1995; Ciucci et al. 1997; Theuerkauf et al. 2007). In our study, areas with higher human presence (measured by human population density, road density, and urban areas) were avoided by wolves; though roads had the highest impact on them. However, the negative impact of roads might just reflect the negative impact of humans (Thiel 1985; Mech et al. 1988; Musiani and Paquet 2004). As mentioned above, it seems that wolves select roads seldom used by humans for ease of travel, but avoid bigger ones (Thurber et al. 1994; Theuerkauf et al. 2003, 2007; Kaartinen et al. 2005; this study). Other studies on habitat use also pointed to the negative impact of roads on wolf presence (Mladenoff et al. 1995; Cayuela 2004; Jędrzejewski et al. 2005; Kaartinen et al. 2005). In north-central Spain, however, Blanco et al. (2005) and Blanco and Cortes (2007) did not find a major impact of roads on wolves, which live in areas with road densities of 1.53 km km^{-2} and cross highways frequently on bridges. In other studies, wolf avoidance of people was indirect through selection of high altitudes, where people seldom appear (Glenz et al. 2001; Grilo et al. 2002). In the herein studied part of Portugal, higher altitudes have been a major refuge for wolves until recently (Carreira and Petrucci-Fonseca 2000). With the increasing construction of wind farms and road networks to enable their access, human disturbance in highland regions is becoming an issue for wolf conservation.

In spite of the present human pressure, we conclude that the most important factor for wolf presence in this region is the availability of prey. Human presence has some negative impact on wolves and might even prevent the settlement of wolves in a given area. But this is likely to occur only in regions with uncontrolled killing, particularly high human activities, insufficient hiding conditions (forest and shrub cover) and low food availability. The behavioral plasticity of wolves is the main reason for their survival, despite persecution throughout the centuries in Europe, as well as for their recent range expansion.

Acknowledgements

The study was funded by Norscut, S.A. and Aenor, S.A. and financially supported by a scholarship of the "Allgemeines Promotionskolleg" of the Ruhr University Bochum (JE). We thank the Alvão Natural Park services for their cooperation and Sílvia Silva for her help during field work. We also would like to thank Dr. Roman Gula and Dr. Jörn Theuerkauf for their helpful suggestions on earlier drafts of the manuscript.

References

Álvares, F., 2004. Status and conservation of the Iberian wolf in Portugal. WolfPrint 20, 4–6.
Álvares, F., Pereira, E., Petrucci-Fonseca, F., 2000. O lobo no parque internacional Geres-Xures. Situacão populational, aspectos ecologicos e perspectivas de conservacão. Galemys 12, 223–239.
Bessa-Gomes, C., Petrucci-Fonseca, F., 2003. Using artificial neural networks to assess wolf distribution patterns in Portugal. Anim. Conserv. 6, 221–229.
Bisi, J., Kurki, S., Svensberg, M., Liukkonen, T., 2007. Human dimensions of wolf (*Canis lupus*) conflicts in Finland. Eur. J. Wildlife Res. 53, 304–314.
Blanco, J.C., Cortes, Y., 2007. Dispersal patterns, social structure, and mortality of wolves living in agricultural habitats in Spain. J. Zool. 273, 114–124.
Blanco, J.C., Cortes, Y., Virgós, E., 2005. Wolf response to two kinds of barriers in an agricultural habitat in Spain. Can. J. Zool. 83, 312–323.
Boitani, L., 1992. Wolf research and conservation in Italy. Biol. Conserv. 61, 125–132.
Boitani, L., 2000. Action plan for the conservation of the wolves (*Canis lupus*) in Europe. Nature and Environment, Council of Europe Publishing 113.

Boitani, L., Ciucci, P., 1993. Wolves in Italy: critical issues for their conservation. In: Promberger, C., Schröder, W. (Eds.), Wolves in Europe: Status and Perspectives. Munich Wildlife Society, Ettal, Germany, pp. 74–90.

Carreira, R.S., Petrucci-Fonseca, F., 2000. Lobo na região oeste de Trás-os-Montes (Portugal). Galemys 12, 123–134.

Carroll, C., Paquet, P.C., Noss, R.F., 1999. Modeling carnivore habitat in the Rocky Mountain Region: a literature review and suggested strategy. WWF, Toronto, Canada.

Cayuela, L., 2004. Habitat evaluation of the Iberian wolf *Canis lupus* in Picos de Europa National Park. Spain. Appl. Geogr. 24, 199–215.

Ciucci, P., Boitani, L., Francisci, F., Andreoli, G., 1997. Home range, activity, and movements of a wolf pack in central Italy. J. Zool. 243, 803–819.

Findo, S., Chovancová, B., 2004. Home ranges of two wolf packs in the Slovak Carpathians. Folia Zool. 53, 17–26.

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monogr. 105, 41pp.

Fuller, T.K., 1995. Guidelines for gray wolf management in the Northern Great Lakes Region. International Wolf Center Technical Publication 271, Ely, Minnesota.

Fuller, T.K., Berg, W.E., Radde, G.L., Lenarz, M.S., Joeslyn, G.B., 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Soc. Bull. 20, 42–55.

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

Grilo, C., Moco, G., Candido, A.T., Alexandre, A.S., Petrucci-Fonseca, F., 2002. Challenges for the recovery of the Iberian wolf in the Duoro river south region. Revista de Biologia 20, 121–133.

Gula, R., 2004. Influence of snow cover on wolf *Canis lupus* predation patterns in Bieszczady Mountains. Poland. Wildlife Biol. 10, 17–23.

Gula, R., 2008. Wolf depredation on domestic animals in the Polish Carpathian Mountains. J. Wildlife Manage. 72, 283–289.

Jacobs, J., 1974. Quantitative measurements of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14, 413–417.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K., Musiani, M., 2000. Prey selection and predation by wolves in Białowieża Primeval Forest. Poland. J. Mammal. 81 (1), 197–212.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K., Szymura, L., 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). Ecology 83 (5), 1341–1356.

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

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

Kaartinen, S., Kojola, I., Colpaert, A., 2005. Finnish wolves avoid roads and settlements. Ann. Zool. Fenn. 42, 523–532.

Kramer-Schadt, S., Revilla, E., Wiegand, T., 2005. Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biol. Conserv. 125, 169–182.

Kusak, J., Skrbinsek, A.M., Huber, D., 2005. Home ranges, movement, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. Eur. J. Wildlife Res. 51, 254–262.

Linnell, J.D.C., Swenson, J.E., Andersen, R., 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Anim. Conserv. 4, 345–349.

Mech, L.D., Fritts, S.H., Radde, G.L., Paul, W.J., 1988. Wolf distribution and road density in Minnesota. Wildlife Soc. Bull. 16, 85–87.

Mech, L.D., 1995. The challenge and opportunity of recovering wolf populations. Conserv. Biol. 9, 270–278.

Mladenoff, D.J., Sickley, T.A., Haight, R.G., Wydeven, A.P., 1995. A regional landscape analysis and prediction of favorable Gray wolf habitat in the northern great lakes region. Conserv. Biol. 9 (2), 279–294.

Musiani, M., Paquet, P.C., 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. BioScience 54, 50–60.

Nowak, S., Myslajek, R.W., Jędrzejewska, B., 2005. Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland). Acta Theriol. 50, 263–276.

Peterson, R.O., 1988. The pit or the pendulum: issues in large carnivore management in natural ecosystems. In: Agee, J.K., Johnson, D.R. (Eds.), Ecosystem Management for Parks and Wilderness. University of Washington Press, Seattle, WA, USA, pp. 105–117.

Rhodes, J.R., Wiegand, T., McAlpine, C.A., Callaghan, J., Lunney, D., Bowen, M., Possingham, H.P., 2006. Modeling species' distributions to improve conservation in semiurban landscapes: Koala case study. Conserv. Biol. 20, 449–459.

Rodriguez-Freire, M., Crecente-Maseda, R., 2008. Directional Connectivity of wolf (Canis lupus) populations in northwest Spain and anthropogenic effects on dispersal patterns. Environ. Model. Assess. 13, 35–51.

Roque, S., Álvares, F., Petrucci-Fonseca, F., 2001. Utilizacion espacio-temporal y habitos alimentarios de un grupo reproductor de lobos en el noroeste de Portugal. Galemys 13, 179–198.

Santos, M., Vaz, C., Travassos, P., Cabral, J.A., 2007. Simulating the impact of socio-economic trends on threatened Iberian wolf populations Canis lupus signatus in north-eastern Portugal. Ecol. Indic. 7, 649–664.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Gula, R., 2003. Spatiotemporal segregation of wolves from humans in the Białowieża Forest. J. Wildlife Manage. 67 (4), 706–716.

Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S., Radler, S., 2007. Human impact on wolf activity in the Bieszczady Mountains, SE Poland. Ann. Zool. Fenn. 44, 225–231.

Thiel, R.P., 1985. The relationship between road densities and wolf habitat suitability in Wisconsin. Am. Midl. Nat. 113, 404–407.

Thurber, J.M., Peterson, R.O., Drummer, T.D., Thomasma, S.A., 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Soc. Bull. 22, 61–68.

Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A., Wydeven, A.P., 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. Conserv. Biol. 18, 114–125.

Vilá, C., Urios, V., Castroviejo, J., 1995. Observations on the daily activity patterns in the Iberian wolf. In: Carby, L.N., Fritts, S.H., Seip, D.R. (Eds.), Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, Alberta, pp. 335–340 (Occasional Publication No. 35).