Available online at www.sciencedirect.com
SCIENCE @ DIRECT®
Applied Geography 24 (2004) 199–215
APPLIED GEOGRAPHY
www.elsevier.com/locate/apgeog

Habitat evaluation for the Iberian wolf *Canis lupus* in Picos de Europa National Park, Spain

Luis Cayuela *

Department of Geography, University College London, 26 Bedford Way, London WC1H OAP, UK

Abstract

A GIS multivariate model based on the Mahalanobis distance statistic is proposed to evaluate habitat suitability for the wolf *Canis lupus* in northern Spain. Results derived from the model show that wolves can potentially thrive in some habitats on the southern and western side of the study area where conflicts with the human population are minimum. However, some other areas that have been recently occupied by wolves were determined as largely unsuitable. If appropriate management strategies are not implemented, negative human attitudes towards wolves could increase. The consequences of this might be a rise in unregulated killing of wolves in both suitable and unsuitable areas.

Keywords: Habitat evaluation; Mahalanobis distance; Modelling; Iberian wolf; Picos de Europa

Introduction

The wolf *Canis lupus* in the Iberian Peninsula is currently increasing and expanding its range north of the River Duero where it is occupying new territories in which it had been extinct for decades (Blanco & Cortés, 2002; Blanco, Reig, & Cuesta, 1992). This process is taking place mainly because of: (1) changes in human perceptions (Blanco & Cortés, 2002), which has led to increasing legal protection since the early 1980s; (2) rural depopulation in the last few decades, which has decreased human-carnivore conflicts and allowed regeneration of natural vegetation (Bunce, Bell, & Farino, 1998; Mladenoff, Sickley, Haight, & Wydeven, 1997), resulting in substantial increases in potential wild preys such as wild boar

* Present address: Departamento Interuniversitario de Ecología, Edificio de Ciencias, Universidad de Alcalá, Alcalá de Henares, 28871 Madrid, Spain; tel.: +34-91-8856407; fax: +34-91-8852949.
E-mail address: luis.cayuela@uah.es (L. Cayuela).

0143-6228/$ - see front matter
doi:10.1016/j.apgeog.2004.04.003

Sus scrofa, roe deer *Capreolus capreolus* and red deer *Cervus elaphus*, particularly in northern Spain (Palacios, 1997; Tellería & Sáez-Royuela, 1984). In Picos de Europa National Park, this expansion is taking place from the southern and less populated areas towards the northern more populated ones, where extensive livestock rearing has been traditionally practised. Sheep and cattle guarding in some of these areas is no longer carried out by traditional anti-wolf methods and shepherds are not likely to resume traditional methods due to the reduction in labour associated to free-ranging sheep and cattle. Thus the damage caused by wolves is notably higher than previously (De Sebastián, 1997). This inevitably leads to anti-wolf responses by shepherds and livestock breeders, which often involve wolf killings.

As the wolf is a rather generalist species in terms of habitat requirements, corridors and/or barriers that might be important for other animals have little apparent effect on wolf dispersal (Carroll, Paquet, & Noss, 1999). Thus, the best predictor of newly occupied areas may simply be adjacency with habitat already occupied by wolves (Blanco & Cortés, 2002). When wolves enter a new area the factors that reflect the degree of intensity of human use of the territory and the so-called 'cultural carrying capacity' of the habitat (i.e. human tolerance to wolf presence; see Fuller, 1995) determine the probability of the population persisting and continuing to expand (Blanco & Cortés, 2002; Blanco et al., 1992).

Because of the difficulties wildlife managers must face when dealing with the conflicts associated with human–wolf coexistence, a first step in planning would be to characterise wolf habitat selection as a function of various interrelating driving variables. These can be grouped as socio-economic (indicating human-associated disturbance) and environmental variables (indicating natural features favouring wolf presence). In the present study, habitat selection is estimated by with respect to land-cover (as an index of inherent habitat characteristics such as density of wild ungulates), livestock and human density, and road density between a region considered suitable (in terms of stability of wolf occupancy during the last 10 years) and an adjacent region where wolf presence has been recently recorded but characterised by absence of wolves in the past decades. The Mahalanobis distance statistic is used for this purpose as an index of the distance from individual 1×1 km cells to the wolf optimal habitat vector in the study area. This study uses geographic information systems (GISs) in order to generate habitat suitability indices, which identify areas where wolf expansion is less likely to generate new conflicts. The main goals are: (1) to apply an inductive model to evaluate wolf habitat suitability in Picos de Europa based on available information of variables influencing wolf distribution in this area; and (2) to explore the ecological and social implications of this model for wildlife management. The outcome of the study is intended to help in establishing general guidelines that can be used by non-governmental organisations and national and regional governments in preparing management plans and strategies for wolf conservation.

Study area

Field work was conducted in Picos de Europa and the nearby Cuera mountain range, in north-west Spain, covering an area of ca. 1670 km^2. The area comprises the whole of the National Park and the surrounding land, encompassing three different regions (Autonomous Communities): Asturias, Cantabria and Castile-Leon (Fig. 1).

There are three massifs in Picos de Europa arranged from east to west. To the North, the Cuera mountain range runs parallel to the coast (Fig. 1). The whole area is a region of jagged carboniferous limestone mountains running from north-west to south-east, reaching up to 2600 m.a.s.l. The regional climate is a complex mixture of Atlantic, Alpine and Mediterranean influences. Altitude, aspect and exposure to the west are key factors in determining local climate (Bunce et al., 1998). The combination of high rainfall and limestone rock has led to the creation of many karstic landforms (Gómez-Sal, 1994).

Vegetation in the region comprises five broad communities: (1) subalpine and alpine vegetation on rocky slopes on the most exposed and highest parts of the mountains; (2) pastures on intermediate mountain slopes and valley bottoms; (3) scrublands (*Genista* spp., *Cytisus* spp., *Erica* spp., *Calluna* spp.), which represent a high percentage of the territory; (4) fragmented stands of mixed-deciduous forest of durmast oak *Quercus petraea*, Pyrenean oak *Q. pyrenaica*, and beech *Fagus sylvatica*, on valley bottoms and mid-slopes; and (5) stands of deciduous and conifer plantations. The flora has been well described in the Spanish literature by Rivas-Martínez, Díaz, Prieto, Loidi and Peñas (1984), but only limited descriptions

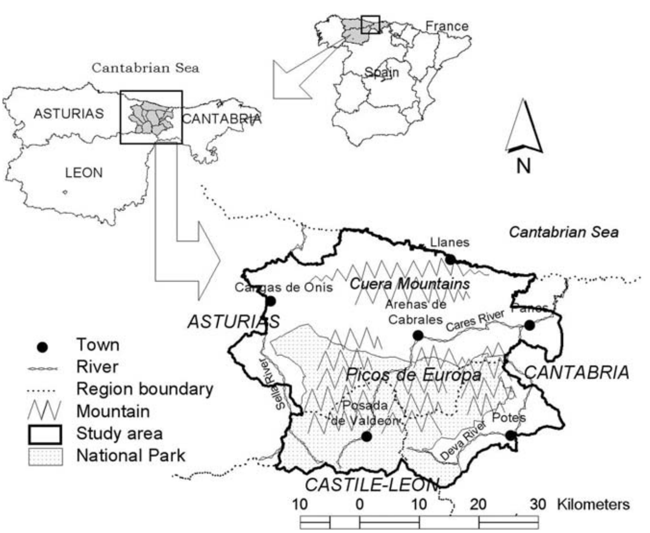

Fig. 1. Location of the study area within Spain, region boundaries and main geographical features.

of the ecology are available in English, notably by Farino (1987) and by Goldsmith and García (1983).

The four main wild ungulate species present in the study region are the roe deer *C. capreolus*, the red deer *C. elaphus*, the Pyrenean chamois *Rupicapra pyrenaica*, and the wild boar *S. scrofa*. Although there are no formal data available upon which to base estimates of population size for these species, there is evidence of a higher abundance of roe deer and red deer in the southern face of the mountain chains in comparison to the northern slopes (J.C. Blanco, pers. comm.). The Pyrenean chamois seems to be locally abundant at high elevations, with ca. 3000 estimated individuals in the western massif (the former Covadonga National Park) in 1997 (Menéndez de la Hoz, 1997).

Human density ranges from ca. 3 to 200 people/km^2. Economic activity in the region mainly consists of livestock rearing and tourism which has been promoted in the last decade by local governments (Bunce et al., 1998). The region has a long history of human settlement. Agriculture probably started in Roman times, as in much of the Mediterranean region. The present appearance of this culturally determined landscape is therefore the product of many centuries of interaction between humankind and the environment (Gómez-Sal, 1994). Livestock rearing is traditionally based on small family based units with an average of 10–12 cows and ca. 50 sheep and/or goats (De Sebastián, 1997). A common practice is the transhumance, which involves the seasonal displacement of the animals from the valley bottoms, where they spend the coldest months of winter in pens and private lawns, to common mountain pastures in summer, where most of the livestock ranges unguarded.

Material and methods

Wolf distribution and location data

Following the criterion adopted by Corsi, Duprè, and Boitani (1999), the wolf area (i.e. the area considered suitable as wolf habitat) includes all those territories where wolves have either always been present or maintained stable populations for at least the last 10 years. This seems an appropriate threshold for the present study as wolves started recolonising the southern face of Picos de Europa during the period 1986–1992 (Palacios, 1997). The entire study area is within the dispersion range of permanent wolf populations in the Cantabrian mountain range and southern face of Picos de Europa (i.e. <100 km, Corsi et al., 1999). Two key assumptions are thus made which are central to the development of the model: (1) it is assumed that wolves have maintained stable populations in certain territories and not others due to optimal conditions, especially with regard to human influence; and (2) the diversity of environmental and socio-economic conditions within these territories represents the best average conditions for steady presence of the wolf.

Stable wolf presence was identified using all available records. Studies based on radio-tracking are usually used to provide information about habitat selection within a geographical area (e.g. Clark, Dunn, & Smith, 1993; Corsi et al., 1999; Mladenoff, Sickley, Haight, & Wydeven, 1995). At the time of the study, no radio-tracking of wolves had been undertaken in the appropriate area. It was thus not possible to precisely determine wolf packs' home ranges. However, various studies on wolves in the National Park and the three regions within the study area provided useful information (Blanco & Cortés, 1997; Llaneza, 2002; Llaneza & Ordiz, 1999; Llaneza et al., 2002; Ordiz, 2002; Palacios, 1997). These studies used direct and indirect evidence (Table 1) to identify wolf packs and their distribution area. Wolf evidences include sightings, presence of tracks, locations of killed wolves, and interviews with local people. Information concerning livestock depredation, although available, was not included in the model as wolves are known to be frequently blamed for animal deaths that are actually attributable to wild dogs. Additionally, two independent consultants and a resource manager of the National Park were interviewed in this study about changes on wolf distribution in the last 15 years.

Wolf area was depicted using all available records of wolf presence within the study area prior to 1992, which provided evidence of continuous presence of wolves up to the present. Population stability was a key criteria used in determining optimum habitat. Nevertheless it must be emphasised that the distribution of the wolf has always shown notable fluctuations, particularly around the borders. Table 1 shows the different studies and reports reviewing wolf presence within the study area. These have been used in combination with direct observations of wolf researchers to define the core wolf area and the present distribution area (i.e. areas where wolves are occasionally present but not steadily settled for the last 10 years or more), as shown in Fig. 2.

Model attributes

All habitat variables (Table 2) were selected (i) to take into account information relevant to wolf requirements in highly humanised territories, but also (ii) with respect to their availability and degree of coverage for the entire study area. Wolf distribution in the study area appears to be influenced primarily by factors

Table 1
Characteristics of the various studies reporting wolf presence within the study area

Study reference	Area covered	Period of time	Evidence of wolf presence
Palacios (1997)	National Park	1986–1997	Sightings, tracks and faeces
Blanco and Cortés (1997)	Cantabria	1988–1997	Livestock depredation, locations of killed wolves, sightings and interviews with local people
Llaneza and Ordiz (1999)	Asturias	1999	Sightings, howling points and faeces
Llaneza et al. (2002)	Asturias	2001–2002	Sightings, howling points and faeces
Llaneza (2002)	Asturias	1999	Sightings, howling points and faeces
Ordiz (2002)	Castile-Leon	2000–2001	Sightings, howling points, interviews with local people, tracks and faeces

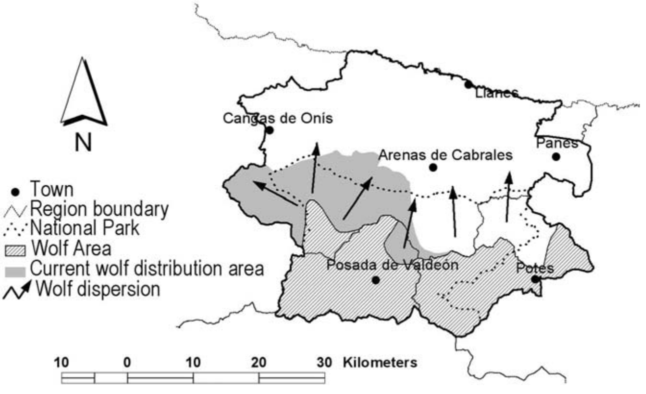

Fig. 2. Wolf area or area of maintained wolf presence during the last 10 years (striped area) and current wolf distribution area (shaded area). Arrows refer to possible attempts of dispersion towards areas where there has recently been some, albeit unconfirmed, evidence of wolf presence.

associated with human disturbance (Blanco & Cortés, 1997). In addition, vegetation cover also exerts some of influence on wolf presence (Massolo & Meriggi, 1998). The selected set of variables includes five concerned with anthropogenic pressure and seven linked to land uses and vegetation types (Table 2). Although the influence of each of the 12 variables, and the interactions between them could not be determined, it is assumed that taken together these variables provide a good description of the diversity of conditions to which the wolf is known to occur. A larger set of variables would inevitably lead to a degree of statistical redundancy. For example, the number of wild ungulates was not included in the model as data

Table 2
The 12 variables used in the analysis

Variable	Origin and resolution of data
Sheep/goat density (animals/km^2)	Agrarian Census 2002 (source: Municipal City Councils and
Cattle density (animals/km^2)	Regional Ministries in Rural Affairs), aggregated by mountain
Horse density (animals/km^2)	pastures
Human density (people/km^2)	Instituto Nacional de Estadística (INE) 2001
Distance to nearest roadway (km)	National Road Atlas (2000), scale 1:200,000
Urban settlement[a]	National Road Atlas (2000), scale 1:200,000
Eucalyptus and pine plantations[a]	Forestry maps (2000), scale 1:50,000
Pasture[a]	Forestry maps (2000), scale 1:50,000
Scrubland[a]	Forestry maps (2000), scale 1:50,000
Mixed forest[a]	Forestry maps (2000), scale 1:50,000
Bare and rocky soil[a]	Forestry maps (2000), scale 1:50,000
Miscellaneous land[a,b]	Forestry maps (2000), scale 1:50,000

[a] Variable rated on a presence/absence matrix.
[b] Including several categories with very low frequency in the study area, e.g. vegetation associated to mobile sand dunes.

were unavailable. However, this variable is known to be related to vegetation cover, with higher density of wild ungulates being associated to mixed forest, scrubland, and bare and rocky soil (in the case of the Pyrenean chamois). Thus, the model, although data driven rather than process based, did seek to use key variables linked to the main factors presumed to determine wolf habitat occupancy. Uncertainty associated with the lack of potentially informative variables is inevitable in most modelling exercises (Conroy, Coeh, James, Matsinos, & Maurer, 1995). In the applied context of this study it is to be hoped that an adaptive approach to management would be adopted in order to make use of the best available data under the assumption that future developments will lead to greater model accuracy (Holling, 1978; Walters, 1986).

Variables associated with livestock density were extracted from yearly Agrarian Censuses (aggregated by mountain pastures except for Cantabria, where data have been collected at the municipality level) and digitised in ArcView3.2. (ESRI, 1992). Data refers to livestock subsidised by agri-environmental and extensification schemes and represents an estimation of herbivores grazing in open fields, which are potential targets for wolves. Although these figures are likely to comprise most of the livestock grazing extensively in the study area, it must be borne in mind that there is still a small fraction of livestock not subject to such subsidies.

Human population density and *distance to nearest road* were used as indices of human presence (Thurber, Peterson, Drummer, & Thomasma, 1994). *Human population density* was derived from total population numbers aggregated by municipalities. The use of lumped statistics for *human population density* is known to lead to aggregation problems (Unwin, 1996). However, it is necessary to consider the influence of data aggregation at the relevant spatial scale for the organism under study. For some organisms, such as many bird, reptile or plant species, small scale spatial variations may influence viability of these populations in a fine-grained landscape. On the other hand, wolves range over large areas and thus small scale spatial variations (e.g. at the municipality level) are not likely to influence their spatial distribution. A proposed alternative to lumped data is dasymetric mapping (Langford & Unwin, 1994). Yet this approach assumes null or low human influence outside human settlements, which is not the case in a prominently agricultural landscape as the one we are studying. Lumped statistics result in an underestimation of human population in population nuclei while dasymetric mapping leads to underestimation of human population influence in their hinterland. Errors are inevitable under either approach, but those arising from lumped statistics have a weaker influence on this particular analysis.

Distance to nearest road was computed directly from the original digital road network (ArcView, ESRI, 1992). Roadways are defined here as being all paved routes including highways and rural roads.

Vegetation types and land use variables were reclassified into seven groups from a set of 22 initial categories obtained directly from governmental forestry maps and stored in ArcView3.2. (ESRI, 1992). These new categories, consisting of *urban settlements*, *eucalyptus and pine plantations*, *pasturelands*, *scrublands*, *mixed forest*, *bare and rocky soil* with alpine and subalpine vegetation, and a *miscellaneous* group were then converted into separate map layers accounting for presence or absence of the particular category.

After transposing all the variables onto thematic maps, they were converted from raster to grid with a square cell size of 1 km (ArcView3.2., ESRI, 1992). Data were then exported to SPSS 11.0 for statistical processing (SPSS, 2001). Variables were tested for normal distribution. Varying transformations were performed in all continuous variables and selected those that best approached a normal distribution as determined by the Kolmogorov–Smirnov test. *Sheep/goat* and *cattle density* were transformed by $(x+1)^{0.5}$, *horse density* and *population density* by $x^{0.01}$, and *road distance* by $x^{0.8}$. Land use/vegetation type variables were not transformed at all. The probability of deviation from normal distribution remained significant ($p < 0.01$) for all transformed variables, as a result of high statistical power due to large sample sizes and/or spatial dependencies within the data. However, kurtosis and skewness were largely reduced through transformations (between -1 and 1, except in the case of horse density whose kurtosis was of -1.34). Homocedasticity was explored using Box's *M*-test. The analysis, at level $p < 0.05$, showed homocedasticity of the variances. Likewise, the Mann–Whitney statistic was used to test differences on *sheep/goat*, *cattle* and *horse density*, *population density* and *road distance* between wolf and non-wolf areas, whereas Chi-squared goodness of fit tests were used for similar purposes for the land use/vegetation-related variables. These analyses showed some significant differences between wolf and non-wolf areas. All human disturbance-associated variables, except for *sheep density* ($p = 0.88$), showed significant differences between wolf and non-wolf areas, with the wolf area being characterised by a lower *density of cattle*, higher *density of horses*, lower *human population density* and greater *road distance* (all at $p < 0.01$) than the non-wolf area. Similarly, differences were found for almost all land use and vegetation type variables between the two zones (all at $p < 0.01$), except for *bare rocky soil* ($p = 0.29$). The wolf area was characterised by a higher proportion of *urban settlements* and *mixed forest* cells, whereas the non-wolf area was occupied by a significantly higher percentage of *plantations*, *pastureland*, *scrubland* and *miscellaneous land*.

Basic statistics for the wolf area were calculated for the 12 variables (mean values and standard deviation or percentage of coverage). Principal Components Analysis (PCA) was used as an exploratory tool (Tabachnick & Fidell, 1996) to assess the contribution of each of the variables determining wolf presence in the study area. Component solutions were not rotated to extract factors in order of their importance (Hair, Anderson, Tatham, & Black, 1998). PCA showed multicollinearity to be low. No values within the correlation matrix exceeded $r = 0.3$. The highest correlations were between human disturbance-associated variables.

Data analysis

The habitat model is based on the Mahalanobis distance statistic. The Mahalanobis distance statistic measures the dissimilarity, based on the standard squared distances, between an ideal habitat ($\hat{u}$), assumed to be determined by wolf occupancy in the long run, and the available habitat in each map cell represented by x. This allows one to build an index of spatial conditions for the wolf based on the Mahalanobis distance of any given location from the wolf area centroid, as defined by the following equation:

$$\text{distance} = (x - \hat{u}) \sum (x - \hat{u})$$

where x is a vector of habitat characteristics associated with each cell; $\hat{u}$ is a mean vector of habitat characteristics estimated from the set of cells that constitute the wolf area; and $\sum$ is the estimated covariance matrix, also from the wolf area. Calculation of the Mahalanobis distance to the wolf area centroid was performed with the SPSS 11.0 package (SPSS, 2001). Because the Mahalanobis distance is dimensionless it does not imply an actual probability of the cells to be suitable for wolf occupancy (Knick & Dyer, 1997), rather the method is more suited to identify spatial patterns (Corsi et al., 1999). However, as equal values do imply an equal probability of similarity to the mean, fractional ranks as percentages (i.e. rescaling the Mahalanobis distances into quantiles) were used to produce a map of probability values associated to the Mahalanobis distance (Knick & Dyer, 1997). The advantage of recoding was that it placed all values between 0 and 1, whereas Mahalanobis distance has no upper boundary (Clark et al., 1993). Once recoding was performed, data were exported to ArcView3.2. (ESRI, 1992) resulting in a grid map of probabilities that would reflect wolf habitat selection.

The advantages of this statistic over other techniques, such as the discriminant function or logistical regression, include the following: (i) only the set of used habitats needs to be correctly defined, which eliminates problems in binary classification techniques caused by misclassification of used versus unused habitats (Clark et al., 1993; Corsi, De Leeuw, & Skidmore, 2000); (ii) the Mahalanobis distance takes into account not only the mean values of the variables measured at observation sites, but also their variance and covariance; it therefore reflects the fact that variables with identical means may have a different range of acceptability and eliminates the problems that can arise when correlated variables are used in multiple regression techniques (Corsi et al., 2000; Knick & Rotenberry, 1998); (iii) it can be calculated for variables of any distribution and thus it is not necessary to fulfil the assumption of multinormality, although the properties of the model are best known when this is achieved (Knick & Dyer, 1997).

Results

Analyses of habitat maps

PCA was performed in order to simplify the system of variables and to combine them into more meaningful ones (Robinson, 1998). Seven components were identified, which explained 81.75% of total variance (Table 3). Component I explained most of the variance (20.67%) and grouped all human disturbance-associated

Table 3
Results of principal component analysis: correlation coefficients between components and wolf habitat-related variables (unrotated solution). The model retained only those components whose eigenvalues equalled or exceed one

Variables	Components						
	I	II	III	IV	V	VI	VII
Sheep/goat density[a]	*0.62**	0.13	0.29	0.47	0.08	0.08	0.15
Cattle density[a]	*0.60**	0.23	0.41	0.39	0.17	0.08	0.15
Horse density[a]	*0.70**	−0.31	0.08	−0.03	−0.16	0.11	−0.10
Population density[a]	*−0.63**	0.43	0.29	0.27	0.23	0.00	0.09
Road distance[a]	*0.63**	0.29	0.06	−0.26	0.13	−0.16	−0.03
Mixed forest	0.00	*−0.84**	−0.12	0.34	0.27	−0.14	0.05
Scrubland	0.27	*0.75**	*−0.58*	0.06	−0.07	−0.04	−0.05
Pastureland	−0.27	0.05	*0.55*	0.10	*−0.72**	−0.22	−0.13
Bare and rocky soil	0.26	−0.02	0.48	*−0.73**	0.23	0.07	0.04
Pine and eucalyptus plantations	−0.43	0.13	0.16	0.02	*0.54**	0.19	−0.32
Human settlement	−0.11	−0.06	−0.03	−0.02	−0.23	*0.91**	0.22
Miscellaneous land	−0.21	0.03	−0.06	−0.14	0.04	−0.21	*0.88**
Eigenvalue	2.48	1.71	1.26	1.19	1.12	1.04	1.00
Explained variance (%)	20.67	14.22	10.54	9.96	9.33	8.67	8.37
Cum. % of variance	20.67	34.89	45.42	55.38	64.71	73.38	81.75

[a] Transformed variables were used.
* Largest correlation coefficients.

variables together, with all livestock density-related variables and *road distance* being positively correlated, and *population density* negatively correlated (Table 3); component II indicated a negative relationship between *mixed forest* and *scrubland*;

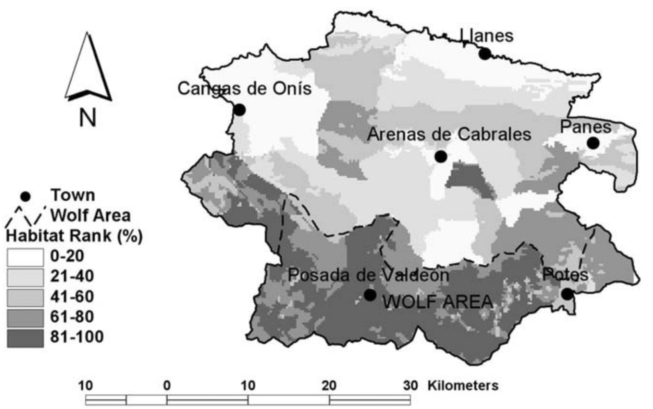

Fig. 3. Map depicting probability values of suitable habitat for wolves based on the Mahalanobis distance. Ranks are expressed as 20% quantiles of the distribution for the entire map. Darker colours indicate areas where Mahalanobis distance approach the ideal (i.e. closely approach the suite of habitat characteristics that best determine wolf presence within the study area).

Table 4
Area of habitat probability classes for wolf (WA) and non-wolf areas (NWA)

Probability class (p)	Wolf area (km^2)	WA (%)	Cumulative frequency of WA (%)	Non-wolf area (km^2)	NWA (%)	Cumulative frequency of NWA (%)
>80	269.62	58.45	58.45	51.50	4.50	4.50
61–80	155.44	33.69	92.14	166.00	14.51	19.01
41–60	33.50	7.26	99.40	286.62	25.06	44.07
21–40	2.75	0.60	100.00	318.12	27.81	71.88
≤20	0.00	0.00	100.00	321.56	28.05	100.00

component III was positively correlated with *pastureland* and negatively correlated with *scrubland*; component V was positively correlated with *pine and eucalyptus plantations* and negatively correlated with *pastureland*; and finally components IV, VI and VII referred to single uncorrelated variables (*bare rocky soil*, *human settlements* and *miscellaneous land* respectively).

The values of the Mahalanobis distances range from 2 to 982 (mean = 133; standard deviation = 178). These absolute values have no specific meaning per se and so they are better interpreted when transformed to probabilities using simple ranking frequency (Fig. 3). Table 4 shows the area included within each probability class for wolf and non-wolf areas.

Discussion

Wolf habitat evaluation

Most authors agree that the wolf is a generalist in its habitat requirements (Blanco & Cortés, 2002; Fuller, 1995; Mech, 1995). Because of the species' exceptional mobility, high reproduction rate and low habitat specificity, the wolf shows a high level of ecological resilience compared with other large carnivores (Carroll et al., 1999). Consequently, wolf habitat selection cannot be ascribed to biological parameters alone, but also to human-associated disturbance factors. It is, however, unlikely that all wolves react equally to human-induced changes as the species shows an inherent variable behaviour, largely conditioned by the disturbance history (Boitani, 1992; Carroll et al., 1999). This must therefore be considered when evaluating the factors affecting patterns of wolf occupancy, and comparisons with other studies, particularly those carried out in North America (as general reference see Mech, 1995), must be regarded in their own context, avoiding extrapolations that can be misleading.

Multivariate techniques take into account the simultaneous interaction of the driving variables. All human disturbance-associated variables are to some extent interconnected, as confirmed by their grouping in the first and most important component resulting from PCA (Table 3). Land use and vegetation-related variables, on the contrary, are poorly interrelated and most often this relationship can be explained by substitution of one successional stage of the vegetation by another. *Scrubland*, therefore, seems to be negatively correlated with both *mixed forest* and *pastureland*, and *pastureland* with *pine and eucalyptus plantations* (Table 3).

The most clearly observed patterns in the Mahalanobis map (Fig. 3) are a high proportion of land with high probability of wolf presence within the wolf area and a high proportion of land with low probability of wolf presence within the non-wolf areas (Table 4). The former is tautological, wolf area having been used to define the mean vector of optimum wolf habitat on which the Mahalanobis distance statistic was based. The latter observation was more interesting. The Mahalanobis distance does not rely upon binary classification (i.e. used versus unused habitats), thus the analysis helped to clearly point out the differences in characteristics of the occupied from non-occupied areas.

Most of the cells within the wolf area were correctly classified (i.e. with a high probability of wolf occupancy). Only a few cells on the south-eastern range of the wolf area were classified as having a low probability of wolf occupancy, which largely corresponds to higher human population density (Table 4).

As for the non-wolf area, only one zone has been identified as potentially suitable for wolf occupancy. This habitat extends on the western side of the study area, in Amieva (Fig. 3), overlapping with part of the current wolf distribution area (L. Llaneza, pers. comm.) (Fig. 2). On the other hand, two main zones were identified with low suitable habitat for wolves: a coastal one, with high human population density, characterised by increasing tourism and development along a major east-west highway; and a mountainous one, covering the northern face of the three massifs, which also exhibits increasing tourism and development, but is particularly unsuitable because of free-range livestock activities (Fig. 3). Despite an estimated low probability of wolf occupancy in this zone, signs of wolf presence have been recently recorded for the northern side of the western and central massifs of Picos de Europa (Fig. 2). This suggests an expansion of the wolf populations from contiguous suitable areas, which is increasing conflicts as livestock killings now occur with greater frequency (La Nueva España, 21/06/2002). As a result, the National Park authorities and the regional administration have agreed on the need of control of the wolf populations, possibly through culling. Shepherds continue to press for permission to implement such measures in order to make them effective (La Nueva España, 21/06/2002). This confirms the patterns of habitat suitability proposed by the model (Fig. 3). The fact that the probability of wolf occupancy is low does not necessarily refer to wolf avoidance of these areas but to the adverse conditions for its survival in the long term due to negative attitudes from the local people.

Extending the model

Although the advantages of using a broad-scale approach to conservation of the wolf populations have been broadly recognised (Corsi et al., 1999; Mladenoff et al., 1995), it is suggested that a fine-scale approach may be more suitable in a highly heterogeneous landscape mosaic such as that of northern Spain. A fine grain resolution depends not only on the aims of the study but also on the appropriateness of the original digital layers and species' occurrence data. If the most appropriate information is not contained in the data set, it is clearly very challenging to derive a fine-scale analysis. In addition, it is logistically difficult to engage in a fine-scale study at spatially large areas (Turner et al., 1995). Thus, a compromise between spatial scale and grain must be found.

Predictions from fine-scale models, however, may not be fully justified given range size and spatial needs of wolves. Wolves have a complex social structure and behaviour and their populations interact at large spatial scales (Carroll et al., 1999; Mladenoff et al., 1995). Consequently, additional caution should be taken in the face of insufficient recognition of the role of these interactions and the broad scales at which they take place.

Whereas it is suggested to use the current model at a small spatial scale as a first indication of wolf habitat suitability, at a larger scale, different sub-models could be designed in order to take into account wolf dynamics and link them together within a model of landscape connectivity where dispersal fluxes were considered (Carroll et al., 1999). Regional and local conservation interests could then be weighted against human interests in order to better define management policies.

In order to improve the accuracy of the model, a validation of the model is highly recommended to test the predictive power of the model (Conroy et al., 1995). This could be achieved, for example, by calculating the distance of locations where wolves were killed or poached in the last few years to the centroid of the wolf optimum habitat vector (see Corsi et al., 1999). This was not however done due to lack of relevant and sufficient information.

The model is therefore best regarded as a first indication of wolf habitat suitability. Caution must always be used when applying the predictions of computer models to make real-life decisions without a critical analysis of their inherent limitations. Further knowledge of wolf home ranges and distribution area is needed. It would be particularly useful to increase the number of wolf radio-tracking studies, not only in the study area, but at other relevant scales. The high mobility of wolves emphasises the need to carry out similar studies in the neighbouring territories and link them together within a larger-scale model of landscape connectivity.

Implications for management

One of the main applications of geographically based multivariate models for large carnivores management is regional planning. Map-based conservation planning can help to facilitate human-wolf coexistence by identifying areas where potential for conflicts is high (Carroll et al., 1999). Once these areas are identified adaptive management can be implemented using the results from monitored wolf populations as an input to evaluate and feedback the model in subsequent steps (Conroy et al., 1995). The question arising then is how to manage wolf populations where conflicts are likely to arise. Treves and Karanth (2003) have identified three possible management strategies: (1) eradication; (2) regulated control; and (3) preservation. Pros and cons of each strategy should be evaluated within a given socio-political scenario. Opponents of carnivore recovery or population persistence are active both politically and on the ground. Thus preventing and mitigating human-carnivore conflict should be based on an improved understanding of carnivore behavioural ecology and public acceptance of wildlife management. Because the wolf is increasing its population in northern Spain, regulated culling seems a plausible alternative in those areas where wolf is likely to cause human conflicts. The cost of regulated culling tends to be low. Placing control in local hands, under the supervision of trained wildlife managers, could satisfy the proponents of private property rights and self-determination. At the same time, it might help to raise public tolerance for this species (Linnell, Swenson, & Andersen, 2001). Further, licensed hunting could provide funding for protection or rural development (see e.g. Stowell & Willging, 1992). The combination of regulated control and conservation tactics, could allow managers to optimise political, economical, and ecological priorities (Treves & Karanth, 2003). However, carnivore hunting is a controversial option. Critics usually cite animal welfare concerns, although conservation and scientific issues also arise (Treves, 2002). As pointed out by Treves and Karanth (2003), carnivore management now stands at a crossroads in many regions of the world. Lethal control is an expedient approach that might satisfy some stakeholders for a brief period. Deeper rooted solutions to human-carnivore conflict could perhaps go further than lethal control and be oriented towards: (1) modifying behaviour of humans, livestock, and carnivores; (2) preventing the activities of humans and carnivores from intersecting in space. The former include changes in husbandry and guarding practices. A few studies have already investigated how far incentive schemes and outreach campaigns can promote the needed behavioural changes (e.g. Fox, 2001). The latter approach implies the use of barriers to protect livestock or the protection of areas to impede certain human activities in order to avoid the intersection of human and carnivore activities. This policy is being effectively implemented, for instance, for brown bear (*Ursus arctos*) in northern Spain, through instalment of electric fences around bee hives in order to avoid aggression by brown bears (R. Hartasánchez, pers. comm.). Unfortunately protection of free ranging livestock from wolves cannot be so easily addressed unless shifting the husbandry system towards intensification.

Conclusions

Although wolves have developed ways of coping with the ecology of the human environment in their range, wolf habitat suitability still seems to be a function of human-associated disturbance. Consequently, as human pressure increases northwards, the study area, the probabilities for stable wolf recolonisation of a certain habitat decreases. Because of this continuous process of expansion of the wolf population northwards and the subsequent disappearance due to human-induced mortality, these areas can be considered sinks for dispersing or colonising wolves.

The current model seems to explain fine-grained patterns of wolf occupancy. However, it would be recommendable to consider different complementary models at a larger spatial scale in order to take into account wolf dynamics and link them together within a model of landscape connectivity where dispersal fluxes were considered (Carroll et al., 1999). Although real-world data are rarely available for complex and robust simulations (Dunning et al., 1995), this approach can provide a first indication of wolf habitat suitability at a fine-grained scale and can be used as part of a sequential process of adaptive management. Areas where wolves are likely to cause conflicts can be thus identified and wildlife management goals established in order to minimise such conflicts and optimise political, economical, and ecological priorities (Treves & Karanth, 2003). Yet solutions to human-carnivore conflicts should take into account both long term and short term goals and aim to go beyond lethal control. These can be oriented towards: (1) modifying behaviour; and (2) preventing the activities of humans and wolves from intersecting in space.

Acknowledgements

I am especially grateful to A. Mackay for his willingness to supervise this project and continuous advice during the work. G. Thackrah, A. Justel and J. Traba provided valuable logistic support with data handling, statistics and usage of GIS software. I am particularly thankful to R. Hartasánchez for helping initiate this study and supporting it throughout its different stages. J.C. Blanco provided worthy comments on the different stages of this work. L. Llaneza and B. Palacios provided useful information on wolf distribution in the study area and contributed with many valuable ideas to this work. My friend and colleague B. Singer provided comments about earlier versions of this manuscript. The valuable commentaries of J.D. Golicher undoubtedly improved this article. E.M. Makow and L. Martín encouraged me to write this paper. Finally, thanks to V. Salvatori, M. Posillico and two anonymous reviewers. This research was funded through a studentship provided by the British Council and Caja de Ahorros del Mediterráneo (British Council-CAM) and logistic support was given by Fondo Asturiano para la Protección de Animales Salvajes (FAPAS).

References

Blanco, J. C., & Cortés, Y. (1997). *Estudio aplicado para la gestión del lobo en Cantabria*. Universidad de Cantabria (Unpublished report).

Blanco, J. C., & Cortés, Y. (2002). *Ecología, censos, percepción y evolución del lobo en España: Análisis de un conflicto*. Málaga: Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM).

Blanco, J. C., Reig, S., & Cuesta, L. (1992). Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation*, *60*, 73–80.

Boitani, L. (1992). Wolf research and conservation in Italy. *Biological Conservation*, *61*, 125–132.

Bunce, R. G. H., Bell, M., & Farino, T. (1998). The environmentally sensitive area legislation in the United Kingdom and its potential application to the Picos de Europa mountains in north-west Spain. *Environmental Conservation*, *25*(3), 219–227.

Carroll, C., Paquet, P. C., & Noss, R. F. (1999). *Modelling carnivore habitat in the rocky mountain region: A literature review and suggested strategy*. Toronto: WWF Canada.

Clark, J. D., Dunn, J. E., & Smith, K. G. (1993). A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management*, *57*(3), 519–526.

Conroy, M. J., Coeh, Y., James, F. C., Matsinos, Y. G., & Maurer, B. A. (1995). Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications*, *5*(1), 17–19.

Corsi, F., De Leeuw, J., & Skidmore, A. (2000). Modeling species distribution with GIS. In L. Boitani, & T. K. Fuller (Eds.), *Research techniques in animal ecology. Controversies and consequences* (pp. 389–434). New York: Columbia University Press.

Corsi, F., Duprè, E., & Boitani, L. (1999). A large-scale model of wolf distribution in Italy for conservation planning. *Conservation Biology*, *13*(1), 150–159.

De Sebastián, J. (1997). Los aprovechamientos ganaderos en los Picos de Europa. In B. Palacios, & L. Llaneza (Eds.), *Primer Simposio sobre el Lobo en los Picos de Europa* (pp. 63–76). Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM)—Grupo Lobo.

Dunning, J. B., Stewart Jr., D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H., & Stevens, E. E. (1995). Spatially explicit population models: current forms and future uses. *Ecological Applications*, *5*, 3–11.

ESRI. (1992). *ArcInfo user's manual. Version 6.1*. California: Redlands.

Farino, T. (1987). The Picos de Europa. In F. V. Grunfeld (Ed.), *Wild Spain* (pp. 45–47). London: Ebury.

Fox, C. H. (2001). Taxpayers say "no" to killing predators. *Animal Issues*, *32*, 1–2.

Fuller, T. K. (1995). *Guidelines for gray wolf management in the Northern Great Lakes region*. Ely, MN: International Wolf Center Technical Publication 271.

Goldsmith, B., & García, C. (1983). *The meadows of the Picos de Europa. Discussion paper in conservation 43*. London: University College London.

Gómez-Sal, A. (1994). The rural landscapes of northern Spain. *Landscape Issues*, *11*(1), 5–12.

Hair, J. F., Anderson, R. E., Tatham, R. L., & Black, C. (1998). *Multivariate data analysis*. (5th ed.). New Jersey: Prentice Hall.

Holling, C. S. (1978). *Adaptive environmental assessment and management*. New York, USA: John Wiley.

Knick, S. T., & Dyer, D. L. (1997). Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management*, *61*(1), 75–85.

Knick, S. T., & Rotenberry, J. T. (1998). Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. *Journal of Agricultural, Biological and Environmental Statistics*, *3*(3), 311–322.

Langford, M., & Unwin, D. J. (1994). Generating and mapping population density surfaces within a geographical information system. *Cartographic Journal*, *31*(1), 21–26.

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. *Animal Conservation*, *4*, 345–349.

Llaneza, L. (2002). Actualización del estatus del lobo en Asturias. In A. Lucio, & M. Sáenz de Buruaga (Eds.), *Aportaciones a la gestión sostenible de la caza* (pp. 263–293). Madrid: Federación para el Estudio y Defensa de la Naturaleza y la Caza (FEDENCA)—Escuela Española de Caza (EEC).

Llaneza, L., & Ordiz, A. (1999). *Situación del lobo en Asturias, 1999*. Principado de Asturias: Consejería de Medio Ambiente (Unpublished report).

Llaneza, L., Ordiz, A., Uzal, A., Palacios, V., Fernández, A., & Naves, J. (2002). *Situación del lobo en Asturias, 2001*. Principado de Asturias: Consejería de Medio Ambiente (Unpublished report).

Massolo, A., & Meriggi, A. (1998). Factors affecting habitat occupancy by wolves in northern Apennines (Northern Italy): a model of habitat suitability. *Ecography*, *21*(2), 97–107.

Mech, L. D. (1995). The challenge and opportunity of recovering wolf populations. *Conservation Biology*, *9*(2), 270–278.

Menéndez de la Hoz, M. (1997). Incidencia del lobo en la cabaña ganadera. In B. Palacios, & L. Llaneza (Eds.), *Primer Simposio sobre el Lobo en los Picos de Europa* (pp. 79–93). Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM)—Grupo Lobo.

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. *Conservation Biology*, *9*(2), 279–294.

Mladenoff, D. J., Sickley, T. A., Haight, R. G., & Wydeven, A. P. (1997). Causes and implications of species restoration in altered ecosystems. *Bioscience*, *47*, 21–31.

Ordiz, A. (2002). El lobo en León. In: L. Llaneza, & J. C. Blanco, *Diagnóstico de las poblaciones de lobo ibérico en Castilla y León* (pp. 34–61). Valladolid: Junta de Castilla y León, Consejería de Medio Ambiente (Unpublished report).

Palacios, B. (1997). El lobo en el Parque Nacional de los Picos de Europa. In B. Palacios, & L. Llaneza (Eds.), *Primer Simposio sobre el Lobo en los Picos de Europa* (pp. 43–60). Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM)—Grupo Lobo.

Rivas-Martínez, S., Díaz, T. E., Prieto, J. A., Loidi, J., & Peñas, A. (1984). *La vegetación de la Alta Montaña Cantábrica. Los Picos de Europa*. León: Ediciones Leonesas.

Robinson, G. M. (1998). *Methods and techniques in human geography*. Chichester: John Wiley and Sons.

SPSS (2001). *SPSS base 11.0 User's guide package*. Chicago, IL.

Stowell, L. R., & Willging, R. C. (1992). Bear damage to agriculture in Wisconsin. *Proceedings of the Eastern Wildlife Damage Control Conference*, *5*, 96–104.

Tabachnick, B. G., & Fidell, L. S. (1996). *Using multivariate statistics*. (3rd ed.). New York: Harper and Row.

Tellería, J. L., & Sáez-Royuela, C. (1984). The large mammals of Central Spain. An introductory view. *Mammal Review*, *14*(2), 51–56.

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

Treves, A. (2002). Wolf justice: managing human-carnivore conflict in the 21st century. *Wolf Print*, *13*, 6–9.

Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, *17*(6), 1491–1499.

Turner, M. G., Arthaud, G. J., Engstrom, R. T., Hejl, S. J., Liu, J., Loeb, S., & McKelvey, K. (1995). Usefulness of spatially explicit population models in land management. *Ecological Applications*, *5*(1), 12–16.

Unwin, D. J. (1996). GIS, spatial analysis and spatial statistics. *Progress in Human Geography*, *20*(4), 540–551.

Walters, C. J. (1986). *Adaptive management of natural resources*. New York, USA: MacMillan.