

# Endangered Species Constrained by Natural and Human Factors: the Case of Brown Bears in Northern Spain

JAVIER NAVES,\* THORSTEN WIEGAND,† ELOY REVILLA,\*†‡ AND MIGUEL DELIBES\*

\*Department of Applied Biology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, CSIC, Avda. María Luisa s/n, Pabellón del Peru, E-41013 Seville, Spain

†Department of Ecological Modelling, UFZ-Centre for Environmental Research, Permoserstrasse 15, D-04318 Leipzig, Germany

**Abstract:** We developed a conceptual framework for classifying habitat quality that requires the construction of separate habitat models for each key demographic feature; the framework can be applied when the factors that determine different demographic processes differ substantially. For example, survival of large carnivores is mainly determined by human-induced mortality, whereas nutritional condition determines reproductive rate. Hence, a two-dimensional habitat model built for reproduction and survival yields five hypothetical habitat categories: matrix, with no reproduction and/or very high mortality; sink, with low reproduction and high mortality; refuge, with low reproduction and low mortality; attractive sink, with high reproduction and high mortality; and source, with high reproduction and low mortality. We applied this framework to two endangered brown bear (*Ursus arctos*) populations in the Cantabrian Mountains, Spain. Our aim was to generate working hypotheses about the quality and spatial arrangement of bear habitat to analyze the present conditions of the different population nuclei and to facilitate identification of core areas of high conservation value, conflictive areas, or areas with unoccupied potential habitat. We used a geographic information system and two spatial long-term data sets on presence and reproduction and performed logistic regressions for building a two-dimensional model. The analysis reveals that both populations exist under different suboptimal conditions: the eastern population mainly occupies areas of suboptimal natural habitat and relatively low human impact, whereas the western population is located mainly in areas with high human impact but otherwise good natural quality. To test hypotheses about demographic features of the obtained habitat categories, we classified data on historic extinction in northern Spain (fourteenth to nineteenth centuries) with the two-dimensional model. Extinction probabilities within each habitat category confirmed the hypotheses: most extinctions occurred in matrix habitat, and the fewest occurred in source habitat.

Especies Amenazadas Limitadas por Factores Naturales y Humanos: el Caso del Oso Pardo en el Norte de España

**Resumen:** Desarrollamos un marco conceptual para clasificar la calidad del hábitat que requiere la construcción de modelos de hábitat separados para cada característica demográfica clave. El marco se puede aplicar cuando difieren sustancialmente los factores que determinan diferentes procesos demográficos. Por ejemplo, la supervivencia de grandes carnívoros está determinada principalmente por mortalidad inducida por humanos, mientras que la condición nutricional determina la tasa reproductiva. Consecuentemente, un modelo bidimensional del hábitat construido para reproducción y supervivencia produce cinco categorías hipotéticas de hábitat: matriz (sin reproducción y/o mortalidad muy alta), sumidero (reproducción baja, mortalidad alta), refugio (reproducción baja, mortalidad baja), sumidero atractivo (reproducción alta, mortalidad alta) y fuente (reproducción alta, mortalidad baja). Aplicamos este marco a dos poblaciones en peligro de oso pardo (*Ursus arctos*) en la Cordillera Cantábrica, España. Nuestra meta fue generar hipótesis de trabajo sobre la calidad y la distribución espacial del hábitat de los osos para analizar las condiciones actu-

‡Address correspondence to E. Revilla, email revilla@ebd.csic.es

Paper submitted April 4, 2002; revised manuscript accepted January 21, 2003.

ales de los diferentes núcleos de población, para facilitar la identificación de áreas núcleo de alto valor de conservación, áreas conflictivas o áreas con hábitat potencial desocupado. Utilizamos un sistema de información geográfica y dos conjuntos de datos históricos de presencia y reproducción y aplicamos regresiones logísticas para construir un modelo bidimensional. El análisis revela que ambas poblaciones existen bajo diferentes condiciones sub-óptimas: la población oriental ocupa principalmente áreas de hábitat natural sub-óptimo y relativamente bajo impacto humano, mientras que la población occidental se localiza principalmente en áreas con alto impacto humano, pero por lo demás con buena calidad natural. Para evaluar las hipótesis sobre las características demográficas de cada tipo de hábitat, clasificamos datos de extinciones históricas en el norte de España (siglos XIV a XIX) con el modelo bidimensional. Las probabilidades de extinción en cada categoría de hábitat confirmaron las hipótesis: la mayoría de las extinciones ocurrieron en hábitat matriz y la minoría ocurrió en hábitat fuente.

## Introduction

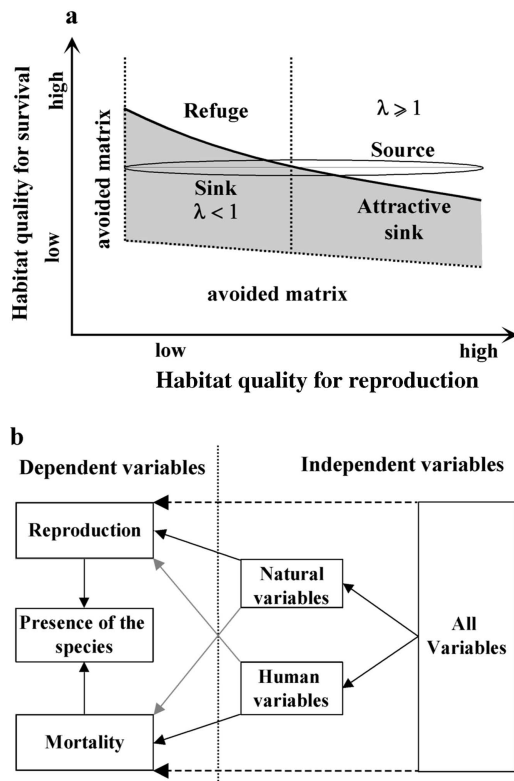
Habitat modeling has become an important field in conservation biology because it improves our understanding of the factors that determine the distribution of habitats and the human factors leading to habitat change. The basic idea of most habitat models is to predict the probability of occupancy from a set of landscape-scale explanatory variables (Manly et al. 1993). The obtained function can then be mapped over the whole area of interest. One usual assumption of this approach is that a single function best describes habitat quality. However, such a one-dimensional approach may be insufficient in some cases because, to be useful, habitat quality should be derived from the biological requirements of the species and explicitly linked with demographic features, such as reproduction and mortality (e.g., Hall et al. 1997; Thomas & Kunin 1999). If we define habitat as an area with enough resources and conditions to permit occupancy—including survival and reproduction—by a given organism (Hall et al. 1997), it might be more appropriate to construct for each of the basic demographic processes a separate model and to classify a given area within the multidimensional phase diagram spanned by these models (Fig. 1a). Such a multidimensional approach that focuses on biological processes and requirements (Caughley & Gunn 1996; Hall et al. 1997; Beutel et al. 1999) would be especially useful when the factors that determine the different demographic processes differ substantially.

For long-lived species with low reproductive rates, such as most large carnivores, it is well known that deaths are mainly caused by humans (reviewed in Woodroffe & Ginsberg 1998), whereas nutritional condition determines reproductive rate (e.g., Bunnell & Tait 1981; Rogers 1987; Stringham 1990). Additionally, a poorly perceived risk of human-caused mortality in otherwise good habitats, where resources are abundant and reproductive potential could be high, may create “deceptive” sources (Fig. 1) that act functionally as attractive sinks

(Delibes et al. 2001a, 2001b). Attractive sinks are commonly associated with human activities in the literature on endangered species or reported as “ecological traps” for breeding birds (Knight et al. 1988; Merrill et al. 1999; Novaro et al. 2000; Revilla et al. 2001). On the other hand, suboptimal refuge areas with scarce nutritional resources but a lower risk of human-induced mortality may allow for population persistence. These phenomena could be common when relicts of endangered species persist in the periphery of their historical geographical range (Channell & Lomolino 2000). In this case the species survives not because the habitat is good for them but because it is poor for its enemies.

In practice, however, it might be difficult to apply this framework because information on the spatial heterogeneity of demographic features is rarely available. In contrast, data on presence and absence, which contain information on both mortality and reproduction, are easier to obtain. For large carnivores, an indirect approach can use the potential separation of habitat factors influencing mortality (anthropogenic factors, hereafter human factors) and reproduction (nutritional factors, hereafter natural factors). Instead of relating a set of independent variables that describe habitat characteristics to the two dependent variables, mortality and reproduction (Fig. 1b), we relate two separate sets of potentially explanatory variables (one comprising the human factors and another comprising the natural ones) to the same dependent variable of presence and absence (Fig. 1b). The two critical assumptions of this indirect approach are that (1) human factors mainly determine mortality, whereas natural factors mainly determine reproduction and (2) presence is a surrogate for reproduction and survival.

We used the case of brown bears (*Ursus arctos*) in northern Spain as an example of the application of the framework. The plight of brown bears in Spain, where they have been protected since 1973 and are listed as endangered (Clevenger & Purroy 1991; Naves & Palomero 1993; Swenson et al. 2000), is typical of many



**Figure 1.** (a) Conceptual framework for classifying habitat within a two-dimensional space spanned by two separate models for reproduction and survival. Classical source-sink theory assumes, on evolutionary time scales, an approximately constant mortality rate, and variation of reproduction according to habitat quality results in sources (growth rate  $\lambda > 1$ ) and sinks ( $\lambda < 1$ ; see ellipse). On an ecological time scale, however, disturbances by humans may cause large variations in habitat quality for survival and the appearance of new habitat types. Refuge areas with low habitat quality for reproduction but good for survival can guarantee population persistence ( $\lambda > 1$ ), while high human-caused mortality in otherwise good habitat (where reproduction could be high) can create “deceptive” sources which act functionally as attractive sinks (i.e.,  $\lambda > 1$ ). (b) Application of the framework to large carnivores (mortality and reproduction, dashed arrows; presence and absence, solid arrows). Where factors determining mortality and reproduction are largely separated (i.e., the relations indicated by the gray arrows are less important), presence of the species in a certain area can be used as surrogate for mortality and reproduction because it indicates both low mortality and sufficient reproduction. In such cases, one can construct the habitat model for reproduction by relating data on presence of the species to the subset of natural habitat variables and the habitat model for survival by relating data on presence to the subset of human habitat variables (pathway of solid arrows).

wildlife populations that have suffered long-lasting persecution and progressive loss and fragmentation of their habitat. The surviving populations are relicts from a distribution that once covered the entire Iberian Peninsula (Nores 1988; Nores & Naves 1993). Extinction appears imminent in the Pyrenees (Swenson et al. 2000), and the two remaining subpopulations in the Cantabrian Mountains are remnants of a distribution that during the eighteenth through nineteenth centuries still extended over the entire mountain range. Wiegand et al. (1998) performed a nonspatial demographic population viability analysis (PVA) to diagnose the state and dynamics (for 1982–1995) of the western population and found that it is not viable if mortality rates remain at the level of the last years of analysis. They identified adult female survival as key to population recovery and argued that mortality can be assessed in terms of human access to bears. This view is supported by several intensive studies of carnivores (Woodroffe & Ginsberg 1998) and data on grizzly bears showing that since the 1970s humans have directly caused 70–90% of known deaths in Yellowstone National Park (Mattson et al. 1996; Mattson 1998; Pease & Mattson 1999) and 77–85% in the Rocky and Columbia mountains (McLellan et al. 1999). Thus, it is apparent that, to manage the species adequately, an analysis is needed of the spatial arrangement of risk areas—areas of high risk of human-bear contact and otherwise good habitat quality—within the habitat network.

We aimed to generate working hypotheses about the quality the spatial arrangement of brown bear habitat in northern Spain to analyze the present conditions and conflicts of the different population nuclei and to identify core areas of high conservation value and areas with unoccupied potential habitat. We used geographic information system (GIS) data to obtain several logistic models that describe habitat quality in the traditional manner with a one-dimensional model (e.g., Tyre et al. 2001) and, following our framework, another that describes habitat quality with a two-dimensional model (Fig. 1a). To test hypotheses about the demographic features of the habitat categories, we classified areas where extinction occurred during the fourteenth through nineteenth centuries within the two-dimensional habitat model. We hypothesize that extinction should be most frequent in areas classified at present as matrix and the least frequent in habitat with low human impact and good natural quality.

## Methods

### Study Area and Spatial Grain

Our study area was the northwestern Iberian peninsula, including the entire range of the Cantabrian Mountains north of Spain (Fig. 2). The two brown bear subpopula-

tions are apparently isolated (Fig. 2), both occupying similar areas of approximately 3700 km<sup>2</sup> in the Cantabrian Mountains (Naves et al. 1999). These mountains run east-west along the Atlantic coast, with a maximum elevation of 2648 m and average elevations and gradients of north- and south-facing slopes of 700 m and 34% and 1300 m and 21% slope, respectively. Proximity to the ocean and the geographic orientation of the chain result in high rainfall on the north-facing slopes and a rain shadow on southern slopes (average annual rainfall of 900–1900 mm and 400–700 mm, respectively). Forest cover is more varied on north-facing slopes, with oak (*Quercus petraea*, *Q. pyrenaica*, and *Q. rotundifolia*), beech (*Fagus sylvatica*), and chestnut (*Castanea sativa*) trees, whereas on the south-facing slopes forest is dominated by deciduous durmast oak (*Q. petraea*, *Q. pyrenaica*) and beech. Above 1700–2300 m, climatic conditions prevent forest growth, and subalpine matorral (*Juniperus communis*, *Vaccinium uliginosum*, *V. myrtillus*, *Arctostaphylos uva-ursi*) dominates. Human densities are 12.1 and 6.1 inhabitants/km<sup>2</sup> for the western and eastern bear populations, respectively (Reques 1993). The main economic activity is livestock farming, mostly cattle. Mining, tourism and mountain sports, hunting, agriculture, and timber harvesting are of local importance. Human activities have resulted in conversion of former forest into pasture and brushwood (*Genista*, *Cytisus*, *Erica*, and *Calluna*).

To balance between a large-scale regional analysis and differentiating landscape information inside individual home ranges, we used a 25-km<sup>2</sup> grid to summarize all data on bear observations, sightings of females with cubs, and landscape-scale variables. This resolution is slightly finer than the reported seasonal home ranges for radio-tagged bears in both subpopulations (Clevenger & Purroy 1991; J.N. and M.D., unpublished analysis). Additionally, we considered multiple spatial scales by introducing variables that describe larger-scale properties of the original potentially explanatory variables.

## Bear Data Sets

The total number of cells with bear observations was 155 in the western and 147 in the eastern population (Fig. 2), based on 1595 bear observations compiled between 1982 and 1991 during systematic investigations of the distribution of brown bears in northern Spain (Campo et al. 1984; Purroy 1991; Naves & Palomero 1993). The observations were made by research teams and by rangers and were completed through interviews of local people.

To provide a range of comparable data for areas not used by bears, we created a buffer in the neighborhood of bear observations (comprising the same number of cells as bear observations), thus assuring that nonobservation areas were those that bears could have visited. We used the variable of bear presence (0, no observation; 1, observation) as the dependent variable in logistic models of the probability of bear presence.

We also used data on observations of females with cubs. Annual censuses of females with cubs were performed between 1982 and 1995 (compiled in Naves et al. 1999), except in 1985. The total number of cells with presences was 131 (based on a total of 417 and 174 observations of families for the western and eastern populations, respectively; Fig. 2). We defined as core areas for reproduction those cells (44 of the 131 cells) in which females with cubs were observed in 3–9 years (i.e., >20% of the years). We analyzed habitat quality for reproduction with a logistic model to investigate which variables characterize core areas for reproduction (value of 1) in comparison with cells used for reproduction in only 1 or 2 years (value of 0; Fig. 2).

Historical data on bear presence were compiled from different historic sources (Alfonso XI 1348; Madoz 1846–1850) and compilations by contemporaneous authors (Nores 1988; Nores & Naves 1993; Torrente 1999). In total, we obtained 573 cells with historic bear presence between the fourteenth and the nineteenth century, of

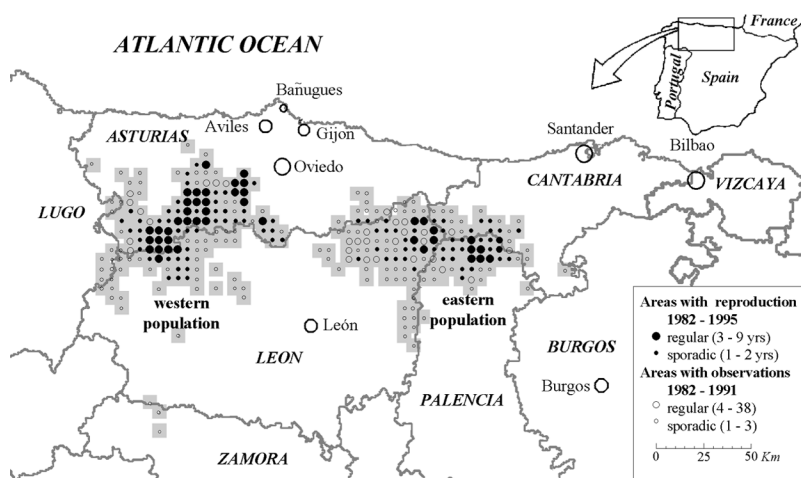


Figure 2. Present distribution of brown bears in the Cantabrian Mountains, northern Spain, after Naves et al. (1999). Filled circles indicate, on a 5 × 5 km grid, areas with reproduction (observations of females with cubs), open circles indicate areas with bear observations, and solid black lines show the borders between provinces.

which 297 differed from the present distribution and were considered as extinctions.

### Potential Predictive Landscape-Scale Variables

#### HUMAN AND NATURAL VARIABLES

We compiled five potential variables describing human activities that in the short-term may facilitate encounters between bears and humans, causing disturbances and increasing the risk of human-induced mortality: human population (pobl), number of villages (pueblos), agriculture surface cover ([ha], SAU), number of agriculture machines (maqui), and stocking rate (number of equivalent large livestock units, UG). Human population and number of villages differ because in some areas villages are typically small and scattered, whereas in others people are concentrated in less numerous but larger villages. The human variables were obtained from the county databases (CERCA + 100 1995). We were unable to access compatible data sets on road density for the study area or to determine the numbers of tourists. Consequently, we did not consider these two variables. However, analyses performed only for the area of Asturias (Fig. 1), where we could access data on the density of paved roads, showed that including this variable did not improve the final models.

The major food categories in the area are herbaceous vegetation in spring; herbs, berries, and other pulpy fruits in summer; and dry fruits such as acorns, beechnuts, and chestnuts in autumn (Braña et al. 1988; Clevenger et al. 1992). Extensive consumption of dry fruits in autumn could be indispensable for hibernating females that give birth and stay in the den with the cubs until April. Because detailed data on food availability only exist for selected areas, we used forest cover of masting species (bosque) and annual precipitation (prec) as potential surrogates of mast production (Picton 1978; Wiegand et al. 1998). As an indicator of spatial heterogeneity, and hence habitat productivity for spring and summer herbs and berries, we used an index of landscape ruggedness (rug), calculated as  $x + SD$ , where  $x$  is the mean value of the slope and SD the standard deviation calculated on the 25 1-km<sup>2</sup> squares forming each 25-km<sup>2</sup> cell. Potential surrogates for shelter are cover of forest, cover of shrub and reforestations (mainly pine and eucalyptus trees, mr), and the ruggedness index of the landscape (rug). We obtained data on the natural variables from the National Atlas of Spain (Anonymous 1995), the topographical cartography 1:200,000 (BCN200, Geographical National Institute 1990–1995), and from the Second National Inventory of Forest (General Administration of Nature Conservation 1986–1995).

#### CONSIDERING LARGER SCALES

The variables described above represent only local properties (25 km<sup>2</sup>) of the landscape and do not contain information at larger spatial scales, which may be important for bears. For example, bears may perceive the connectivity of landscape features (e.g., forest) at scales above one cell, and human activity may diffuse from focal points (e.g., villages) into neighboring cells. To consider these multiple scales, we calculated, from the original 25-km<sup>2</sup> raster data, scale-dependent indices that describe connectivity and diffusion of a given variable at spatial scale  $r$  (for details see Wiegand et al. 1999; Schadt et al. 2002). Briefly, we calculated the diffusion following a circular moving-window algorithm (assigning to the focal cell the mean value of the variable within the circle of radius  $r$ ) and the connectivity following a ring-shaped moving-window algorithm (assigning the mean value of the variable within the ring of radius  $r$  to the focal cell). By moving the circle or ring over the entire grid, we obtain the values of the indices for each cell of the grid. Because we did not know a priori at which scale diffusion and connectivity occur, we calculated the indices for  $r = 1, \dots, 4$ . We applied the connectivity indices to natural variables and the diffusion indices to human variables, obtaining 20 additional variables.

#### Analysis

Spatial autocorrelation in the dependent variable can lead to pseudoreplication problems because data are not independent, and hence the increased power produces overfitted models with little biological interpretation (Clifford et al. 1989; Lennon 1999). To test for spatial independence, we calculated, inside the area that comprises cells with observations and no observations, a coefficient  $c(r)$ , which describes the autocorrelation of a variable  $x$  with lag  $r$  analogously to the Pearson correlation. To reduce problems with severe spatial correlation between cells, we determined the spatial lag at which locations were not strongly correlated (i.e.,  $c[r] < 0.7$ ) and used only those cells sufficiently separated (Schadt et al. 2002).

Correlation between explanatory variables is not a principal problem in logistic regressions, but it can make the comparison of alternative models difficult (Lennon 1999), impeding a direct interpretation of the coefficients. To test for correlation between the potentially explanatory variables, we calculated a correlation matrix with all landscape variables. Among strongly correlated variables ( $r > 0.7$ ), we retained those with the greatest explanatory effects in univariate analysis on the dependent variable (bear presence or reproduction; Schadt et al. 2002). After this procedure, 10 independent variables remained (Table 1). We screened the

**Table 1.** Comparison of the means ( $\pm$  SD) of the 10 independent variables between cells with bear observations (obs) and cells with no observations (nob.), separately for the areas of the western population (W), the eastern population (E), and the total population (T).

	Western population (n) <sup>a</sup>		Eastern population (n) <sup>a</sup>		Total population (n) <sup>a</sup>		Comparisons (p) <sup>b</sup>			
	nob	obs	nob	obs	nob	obs	$\frac{obs-nob}{W \quad E \quad T}$			obsE-obsW
	47	37	34	33	81	70				
<b>Natural variables</b>										
landscape ruggedness index (rug)	8.0 $\pm$ 3.1	11.4 $\pm$ 2.6	7.9 $\pm$ 5.5	9.5 $\pm$ 4.0	8.0 $\pm$ 4.2	10.5 $\pm$ 3.4	**		**	*
forest cover (%) (bosque)	6.3 $\pm$ 3.5	16.1 $\pm$ 14.1	11.6 $\pm$ 14.6	15.3 $\pm$ 14.5	9.6 $\pm$ 11.8	15.7 $\pm$ 14.2	*		*	
forest connectivity at $r = 2$ (bosq2)	6.3 $\pm$ 3.5	7.9 $\pm$ 3.2	8.2 $\pm$ 5.2	8.5 $\pm$ 3.0	7.1 $\pm$ 4.4	8.2 $\pm$ 3.1	*			
shrub and replantation cover (%) (mr)	15.7 $\pm$ 16.3	9.8 $\pm$ 10.4	12.0 $\pm$ 15.6	11.8 $\pm$ 18.2	14.2 $\pm$ 16.0	10.7 $\pm$ 14.5				
connectivity of mr at $r = 1$ (mr1)	10.1 $\pm$ 9.5	7.8 $\pm$ 5.7	8.6 $\pm$ 6.1	7.2 $\pm$ 5.6	9.5 $\pm$ 6.0	7.7 $\pm$ 5.6				
annual precipitation (mm) (prec)	1251 $\pm$ 272	1397 $\pm$ 241	1041 $\pm$ 301	1051 $\pm$ 200	1163 $\pm$ 300	1235 $\pm$ 281	*			**
<b>Human variables</b>										
no. of villages (pueblos)	7.3 $\pm$ 7.9	5.2 $\pm$ 4.1	3.3 $\pm$ 2.8	2.1 $\pm$ 1.2	5.6 $\pm$ 6.5	3.7 $\pm$ 3.4		*	*	**
human population (pobl)	742 $\pm$ 1786	273 $\pm$ 236	259 $\pm$ 355	250 $\pm$ 275	540 $\pm$ 888	262 $\pm$ 253	*		*	
diffusion of pobl at $r = 3$ (pobl3)	544 $\pm$ 349	455 $\pm$ 197	289 $\pm$ 139	173 $\pm$ 119	437 $\pm$ 307	322 $\pm$ 217		**	*	**
agricultural surface (ha) (SAU)	729 $\pm$ 591	826 $\pm$ 640	956 $\pm$ 462	586 $\pm$ 453	824 $\pm$ 549	713 $\pm$ 569	*			

<sup>a</sup>The n is sample size (grid cells).<sup>b</sup>\* $p < 0.05$ , \*\* $p < 0.01$ . Based on t test.

univariate relationship between independent and dependent variables with a  $t$  test.

We obtained several logistic models that predict the probability of bear presence and that of belonging to a reproductive core area. We built a “general” model ( $f_G$ ) with all 10 potentially explanatory variables, and, in accordance with our framework, we built a “natural” ( $f_N$ ) and a “human” ( $f_H$ ) habitat model, with data on bear presence as the dependent variable and the six natural and four human variables (Table 1), respectively, as potentially predictive variables. We performed a second set of logistic regressions with data on reproduction ( $f_R$ ).

We tested the goodness-of-fit of the resulting models by using log-likelihood chi-square analysis because this method is better than the intercept-only model and because of the classification accuracy of the response variable from the original data. In all cases we performed back and forward stepwise analyses, and analyses in which we manually added or deleted the variables. We used the Akaike information criterion (AIC) to evaluate the stepwise procedure. The final decision between alternative nested models was based on parsimony (lowest AIC) and simplicity (the simplest model among plausible models with  $\Delta AIC < 3$ ; Burnham & Anderson 1998).

For the final grading of habitat suitability, we used an index that combines bear presence and reproduction into one axis. Because bear reproduction can only occur

where bears are present, we can apply this model only if the model of bear presence yields a high probability (i.e.,  $f_P > 0.5$ , where  $f_P$  is  $f_H$  or  $f_N$ ). To combine both indices, we use  $f_P$  if  $f_P < 0.5$  and  $f_R$  otherwise. To obtain a continuous final index  $Q$  of habitat quality, we linked both at  $f_P = 0.5$ :

$$Q = \begin{cases} f_P & \text{for } f_P < 0.5 \\ (1 + f_R)/2 & \text{for } f_P \geq 0.5 \end{cases}$$

## Results

The spatial autocorrelation of landscape-scale variables was only high at  $r = 1$  (neighboring cells) and dropped rapidly with increasing scales. For  $r = 2$  the spatial correlation coefficient yielded  $< 0.7$  for all variables. Human population was the variable for which spatial autocorrelation dropped most rapidly with increasing spatial scale, whereas the number of villages was still weakly correlated at large spatial scales. The spatial autocorrelation structure of bear presence showed behavior similar to that of the independent variables, with high correlation only for neighboring cells. To reduce the effect of spatial autocorrelation, we retained for further analyses cells separated by more than 5 km.

Cells in which bears were observed had higher ruggedness and forest cover, fewer villages, and lower pop-

ulation density and human population diffusion than cells in which bears were not observed (Table 1). Within the area of observations, the number of villages, human population diffusion, landscape ruggedness, and precipitation differed between the two populations (Table 1). Different factors seemed to control the presence of bears in the western and the eastern population: areas in which bears were observed in the western population differed from areas where no bears were observed with respect to four natural variables, whereas in the eastern population there were differences in several of the human variables (Table 1).

### Model Outcomes

The most parsimonious unidimensional model contained three variables: ruggedness of the landscape (*rug*), forest cover (*bosque*), and number of villages (*pueblos*; Table 2). The natural variables (*rug* and *bosque*) were positively associated with bear presence, whereas human impact (*pueblos*) was negatively associated with bear presence (Table 2). At the cut level of  $f_G > 0.5$ , the model correctly classified 44 of 70 cells with observations and 61 of 81 cells with no observations. The general model misclassified large areas with observations in the western population, where it adequately predicted cells with no observations, and performed poorly in the eastern population, where it misclassified cells with no observations in the north and cells with observations in the south.

The model with natural variables contained the same natural variables as the general model, yielding a similar classification accuracy (Table 2; Fig. 3a). For the eastern and western populations, the natural model yielded a classification accuracy of 59.7% and 75.0%, respectively, suggesting that natural variables explain bear presence in the western population but fail in the eastern population (Fig. 3a). Additionally, the natural model performed generally well in predicting cells with observations on the north-facing slopes and cells without observations on the south-facing slopes and performed poorly in predicting cells with no observations on north-facing slopes and cells with observations on south-facing slopes (Fig. 3a).

Two variables were included in the human-variable model: human population and human population diffusion at  $r = 3$  (Table 2; Fig. 3b). This model classified 57% of all cells correctly (Fig. 3b). It weakly predicted cells with observations for the western population (only 40.5% were correct) and cells with no observations for the eastern population (only 38.2% were correct). However, the human model classified 75.8% of all observations in the eastern population correctly and 70.2% of all no observations in the western population. Complementary to the model with natural variables, human factors seemed to characterize bear presence for the eastern population and bear absence for the western population.

The model of reproductive core areas included only the variable of connectivity of the forest at  $r = 1$  (Table 2).

**Table 2.** Logistic-regression models built with data on bear observations versus no observations and with reproduction data.<sup>a</sup>

Variable	Symbol	$\beta$	SE	p	Goodness-of-fit		
					$\chi^2$	df	p
General model <sup>b</sup>	$f_G$				28.87	3	< 0.0001
landscape ruggedness	rug	0.1593	0.0501	0.0015			
forest cover (%)	bosque	0.0384	0.0151	0.0113			
number of villages	pueblos	-0.1194	0.0454	0.0085			
constant	c	-1.5493	0.5055	0.0022			
Human model <sup>c</sup>	$f_H$				10.931	2	0.0042
human population	pobl	-0.0009	0.0006	0.1238			
population diffusion	pobl3	-0.8723	0.6494	0.1792			
constant	c	0.5374	0.3010	0.0742			
Natural mode <sup>d</sup>	$f_N$				19.438	2	0.0001
landscape ruggedness	rug	0.1522	0.0484	0.0017			
forest cover [%]	bosque	0.0278	0.0138	0.0436			
constant	c	-1.8975	0.4885	0.0001			
Reproduction model <sup>e</sup>	$f_R$				9.119	1	0.0025
connectivity of forest at scale $r = 1$	bosq1	1.4358	0.5598	0.0103			
constant	c	-2.7766	1.1057	0.0120			

<sup>a</sup>Significance level of the coefficients for the Wald statistic (p).

<sup>b</sup>Next most parsimonious models at  $\Delta AIC = 0.4$  (also including agricultural surface cover [SAU]) and  $\Delta AIC = 1.7$  (also including SAU and human population [pobl3]). All other models at  $\Delta AIC > 3$ .

<sup>c</sup>Next most parsimonious model at  $\Delta AIC = 1.4$  (also including SAU). All other models at  $\Delta AIC > 3$ .

<sup>d</sup>Next most parsimonious models at  $\Delta AIC = 0.6$  (also including forest connectivity [bosq2]) and  $\Delta AIC = 1.1$  (also including bosq2 and annual precipitation [prec]). All other models at  $\Delta AIC > 3$ .

<sup>e</sup>Next most parsimonious models at  $\Delta AIC = 0.3$  (also including prec) and  $\Delta AIC = 1.4$  (including additionally prec and forest cover of masting species [bosque]). All other models at  $\Delta AIC > 3$ .

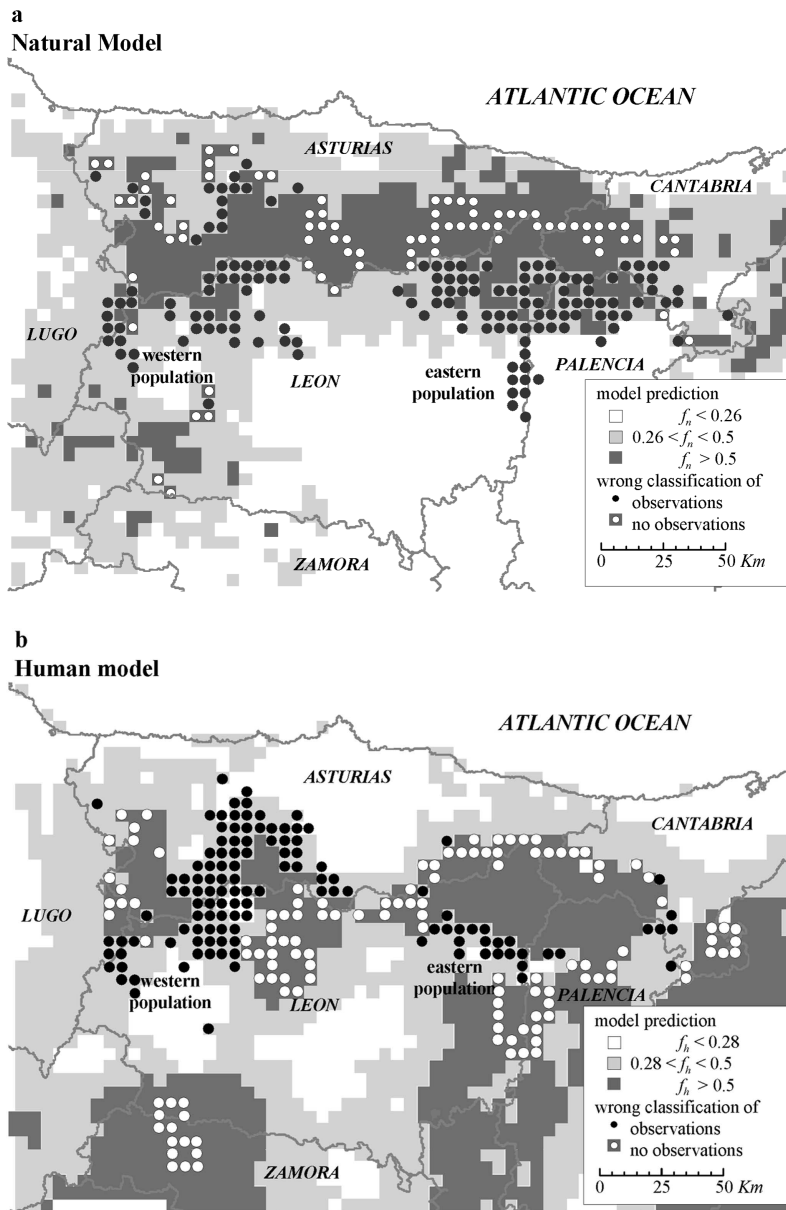


Figure 3. The two models built with (a) natural and (b) human variables and their misclassifications. Shown are all wrongly classified cells, including those cells not included in the logistic regression analysis. We define cells without observations in the immediate neighborhood of cells with observations.

At the cut level of  $f_R > 0.5$ , the model correctly classified 65.7% of all cases. By repeating the analysis with only the four human variables, the fitting algorithm did not converge on any model. The fact that we could not find a human model for predicting habitat quality for breeding is in accordance with our basic assumption that natural factors control reproduction.

#### Spatially Explicit Working Hypotheses about Habitat Quality

The final natural habitat index  $Q_N$  combines bear presence and reproduction (Eq. 1), whereas for human habitat quality we used the human model for presence (i.e.,  $Q_H = f_H$ ) because there was no model for reproduction with human variables. To generate hypotheses for the

habitat categories, we divided the range of each model into matrix, poor, and good habitats. We defined the threshold between poor and good as  $f = 0.5$  and the threshold between matrix and poor in a way that only 5% of all data with observations were located in matrix, thus categorizing the area into matrixlike, sinklike, sourcelike, refugelike, and attractive sinklike. Here we used *sinklike* or *sourcelike* instead of *sink* or *source* to indicate that the categories represent working hypotheses based on static habitat models without explicit consideration of dynamic demographic features.

A priori, we expected that the general model would be (for bear presence) essentially the same as the average of the human and the natural models; thus, functionally different areas with pronounced differences be-



tween human and natural habitat quality would merge (Fig. 4). The general model classified 59% of the refuge-like areas as low quality and 73% of the attractive sink-like areas as high quality. On the other hand, 80% of the cells classified as matrix and sinklike were predicted to be low quality, whereas 94% of all cells classified as source-like were predicted to be of high quality. Therefore, the general model accorded well with the two-dimensional model in predicting the “traditional” habitat types of source-like and sinklike (Fig. 4b), but it failed in areas with large differences between natural and human habitat quality, the refugelike and attractive sinklike habitat types.

### Brown Bear Habitat in the Cantabrian Mountains

The Cantabrian Mountains are a complex patchwork of habitat types (Figs. 5 & 6). Refuge habitat was situated at the south-facing slopes, covering, together with source-like habitat, most of the eastern population. The spatial pattern was more complex for the western population. On the north-facing slopes, large areas of attractive sinklike habitat were interspersed with areas of source- and refugelike areas. The high human impact in central Asturias was especially marked, creating a large block of matrixlike, sinklike and attractive sinklike habitat that separated both populations.

Cells with reproduction were more frequently (66%) situated in areas with good natural habitat ( $Q_N > 0.5$ )

than cells with only presence (37%) (Fig. 5a). Differences were less pronounced for human habitat quality (61% and 54% of cells with reproduction and only observation, respectively, were in areas with  $Q_H > 0.5$ ). Differences between the eastern and the western populations were marked: 96% and 36%, respectively, of the cells with reproduction were situated in areas of good human habitat quality ( $Q_H > 0.5$ ), whereas 44% and 74%, respectively, of the cells with reproduction were situated in areas of good natural habitat ( $Q_N > 0.5$ ) (Fig. 5). Both populations included similar areas classified as source-like habitat (23 and 25 cells in the eastern and western populations, respectively) and the same amount of suboptimal habitat: attractive sinklike for the western population (31 cells) and refugelike for the eastern population (30 cells; Fig. 6).

### Accordance between Working Hypotheses about Habitat Quality and Historic Extinctions

We expected that areas classified as matrixlike, sinklike, and attractive sinklike would have a higher probability of extinction than areas classified as refugelike and source-like. Therefore, most historical extinctions should have occurred in the first group of habitats. In total, there were 297 cells with bear presence during the fourteenth through the nineteenth centuries but with no presence from 1982 to 1995, when we collected the data used to parameterize the models. We used these ex-

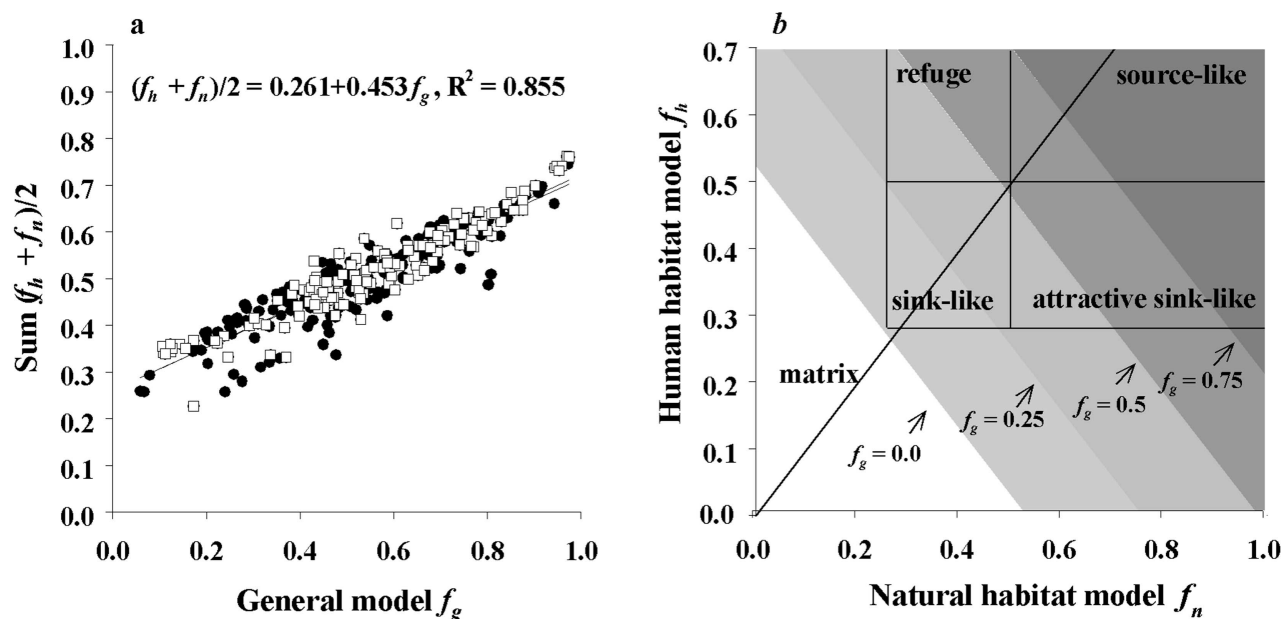


Figure 4. Comparison between one- and two-dimensional habitat models. (a) Linear regression of the average of the human and the natural models  $[(f_N + f_H)/2]$  over the general model  $f_G$  for the 302 cells with observations. Data for the eastern population are shown as squares and data for the western population as filled circles. (b) Resulting categorization of the general model within the two-dimensional model spanned by the human and the natural model. The limits between the lightest to darkest gray levels are  $f_G = 0, 0.25, 0.5$ , and  $0.75$ , respectively.

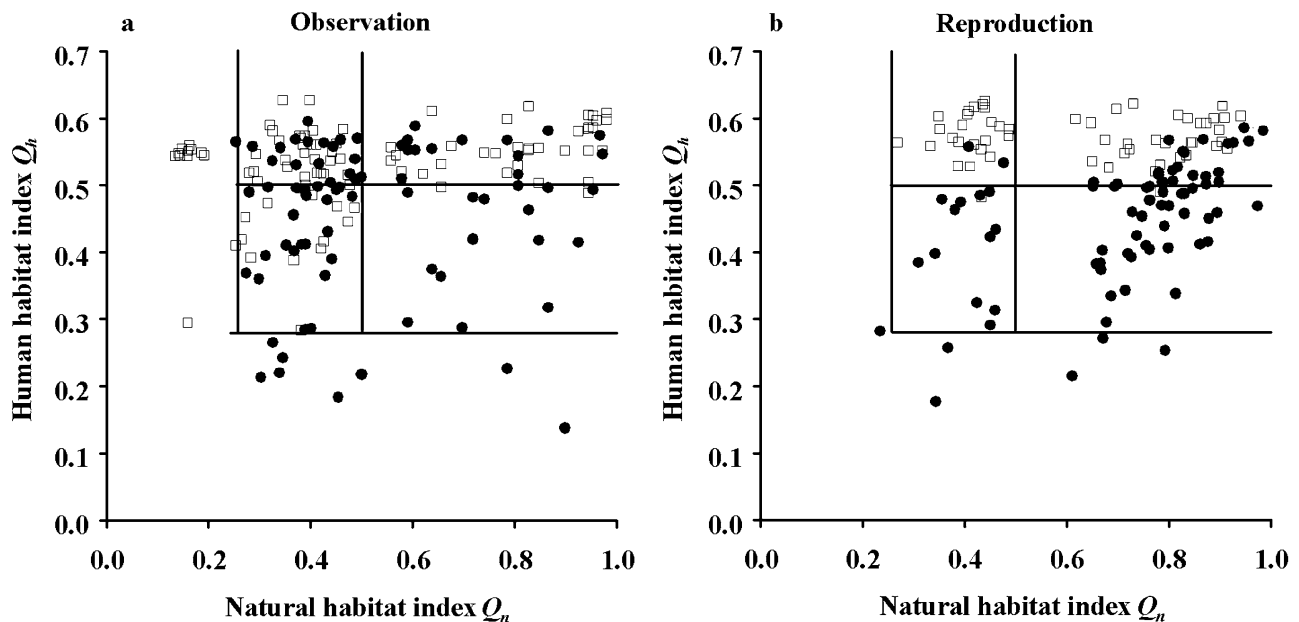


Figure 5. Classification of cells with (a) bear observations and (b) reproduction separately for the eastern (open squares) and western (filled circles) populations. The locations of cells with reproduction and observation are shown as symbols within the two-dimensional phase diagram defined by the final natural model (x-axis) and the human model (y-axis). Solid lines give the thresholds  $Q_N = 0.26, 0.5$  and  $Q_H = 0.28, 0.5$  that define the habitat categories.

tinct areas to test predictions about the dynamic properties of the habitat types (most of them were far from the area used to parameterize the models; Fig. 6a). The five descriptive habitat types were approximately equally distributed among the total area of present and past bear observations (Fig. 6d). The probability of extinction was lowest for sourcelike habitat (0.25), followed by refuge-like (0.32), attractive sinklike (0.52), and sinklike (0.62), and highest for matrix (0.77) (Fig. 6d). An analysis of frequencies showed that extinction probability  $p^{\text{ext}}$  differed significantly among all habitat types ( $\chi^2_1 > 15.3$ ,  $p < 0.0001$  in all cases), except for refuge and source-like habitats ( $\chi^2_1 = 2.4$ ,  $p = 0.1224$ ), following the ranking  $p^{\text{ext}}_{\text{matrix}} > p^{\text{ext}}_{\text{sinklike}} > p^{\text{ext}}_{\text{attractive sinklike}} > p^{\text{ext}}_{\text{refugelike}} \sim p^{\text{ext}}_{\text{sourcelike}}$  (overall  $\chi^2_4 = 86.63$ ,  $p < 0.0001$ ). These results seem to confirm our initial hypothesis about the dynamics and demographic tendencies of our descriptive habitat types.

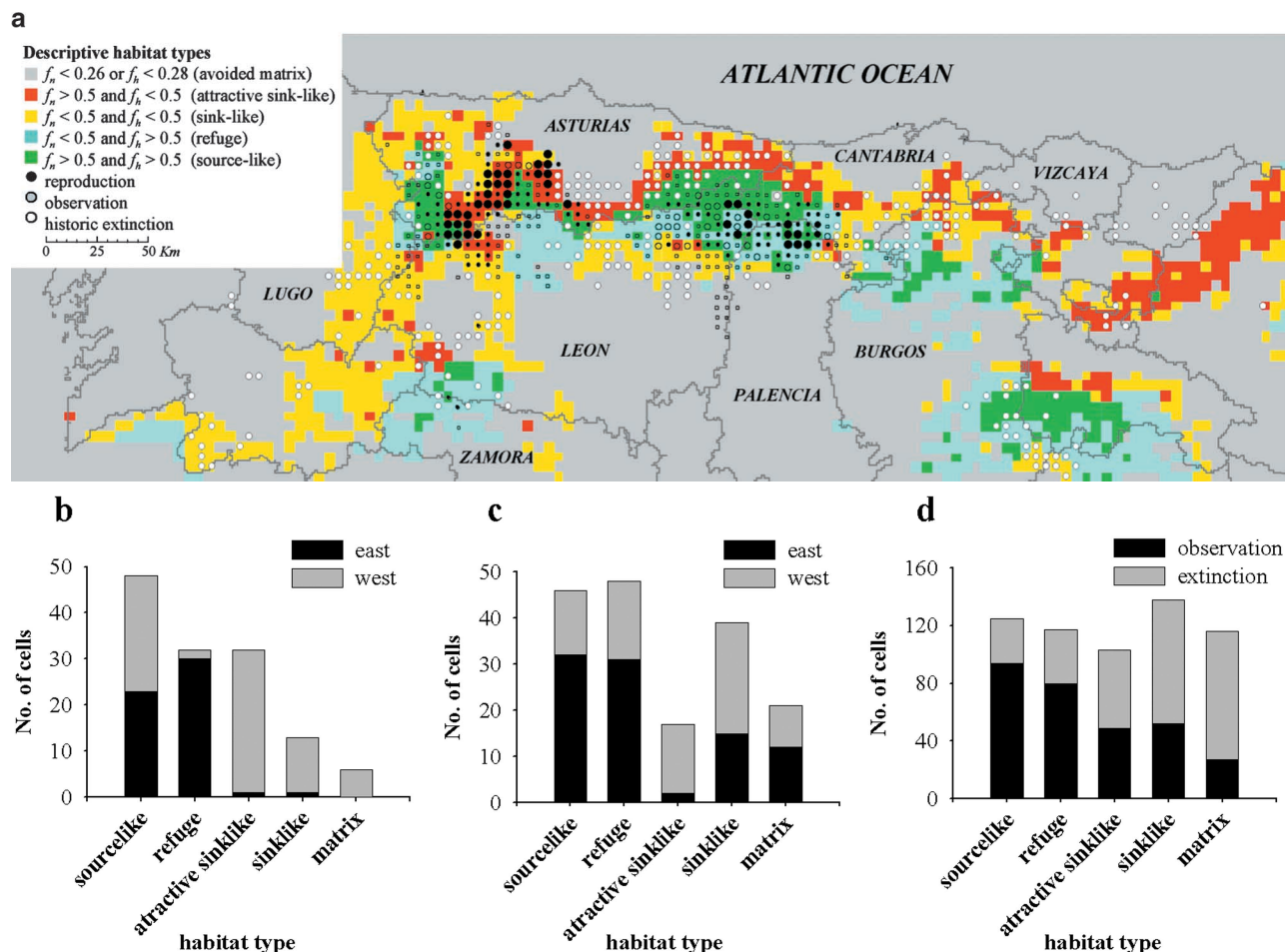
## Discussion

### A Multidimensional Framework for Classifying Habitat Quality

We propose the construction of a separate habitat model for each demographic key feature when these features are differentially affected by distinct regional-

scale habitat factors (Hall et al. 1997). With this framework, habitat quality can be characterized more specifically with commonly used habitat types such as source, sink, matrix, refuge, and attractive sink. In undisturbed ecosystems, the mortality of most large carnivores and other long-lived species with low reproductive capacity would be low and relatively constant, whereas reproduction may vary greatly as a result of differences in resources. Under such conditions, a one-dimensional habitat model would be able to characterize habitat quality, and classical source-sink theory (Pulliam 1988; Pulliam & Danielson 1991) would apply. However, problems with this one-dimensional approach arise when the risk of mortality changes in space, as in areas with low and very high mortality within the range of the population. This may be due to anthropogenic factors, varying predator abundance in predator-prey systems, poisoning from pesticides or pollution, or contagious diseases (Delibes et al. 2001a). Consideration of the two additional habitat types—refuge and attractive sink—is an important extension of the original source-sink concept. Especially attractive sinks have been frequently reported in association with human activities but were not until recently integrated into source-sink theory (Delibes et al. 2001a). Additionally, new insight could be gained by considering other dimensions, such as an axis-describing dispersal habitat.

An inherent problem of validating habitat models that



**Figure 6.** (a) Classification of habitat quality in the Cantabrian Mountain range into matrixlike, sinklike, refuge-like, attractive sinklike, and source-like (solid circles represent cells with reproduction, open circles cells with observations, and white circles historic extinctions). (b) Distribution of cells with reproduction, (c) cells with only observation without reproduction, and (d) historic extinction among habitat types, showing differences between the eastern and western subpopulations (for reproduction and observations) and between all observations (including reproduction) and historic extinction.

aim to describe habitat quality through demographic features is that they are static models built with a set of presence-absence data (Tyre et al. 2001). Therefore, we cannot establish quantitative relationships between the habitat types and expected rates of increase. Also, by modeling habitat with data on contemporaneous occurrence, we may not necessarily identify the good habitat but, rather, the habitat where the species may have survived because it was not extirpated (Caughley & Gunn 1996). Therefore it is desirable to test habitat models not only with independent presence-absence data but also with expected dynamics, such as recolonization of suitable areas (Mladenoff et al. 1999) or extinction of unsuitable areas.

We used data on historic bear presence with no evidence of contemporary bear presence to test the two-dimensional habitat model. The classification of extinct

areas supported our hypotheses. Source-like and refuge-like habitats had the lowest extinction probability, followed by the suboptimal attractive sinklike habitat. This finding is in accordance with general results in demographic models for long-lived species which show that the rate of increase is less sensitive to reproductive parameters than to mortality rates (e.g., Gaona et al 1998; Wiegand et al. 1998) and with recent work on attractive sinks (Delibes et al. 2001a). As expected, sinklike and matrixlike were the poorest habitat types. Because we could not account for features such as area and isolation effects, however, we cannot expect to properly classify all areas of historic extinction.

The one-dimensional habitat model merged functionally different habitat categories (i.e., refuge-like and attractive sinklike) within the same suboptimal category. This poses a problem: the general model classified 59%

of the refugelike areas as areas with lower habitat quality and 73% of the attractive sinklike areas as areas with higher habitat quality, which is the opposite of the expected demographic trends for these habitat categories. Thus, the two-dimensional framework provided a means for developing more appropriate working hypotheses on habitat types.

### Benefits and Shortcomings of the Model

We were constrained in the selection of habitat variables and could select surrogates only for the “real” resources required by brown bears. Nevertheless, on the coarse spatial scale selected, our variables performed well in defining habitat types, and the resulting models described core areas for bear presence and reproduction. The two variables that entered in the natural habitat model, forest cover and landscape ruggedness, make sense biologically: forest of masting species provides food and shelter, and landscape ruggedness is a measure of both shelter (e.g., winter dens) and habitat productivity as a result of higher environmental heterogeneity (e.g., small streams where bears feed in the summer).

Human population diffusion and density were the two variables that defined human habitat quality, whereas number of villages was significant in the general model. We suspect that correlation between these variables may cause changes in the explanatory variables among models. We could not include road density, a classic human explanatory variable (e.g., Mladenoff et al. 1995; Mace et al. 1999), in our analysis. By analyzing bear distribution in the eastern population, Clevenger et al. (1997) found that the mean unpaved road density was more than twice as high in areas with sporadic presence of bears than in their year-round range and even higher in areas outside bear range. Thus, unpaved road density could have great explanatory power in the human axis. Our habitat classification predicted suitable sourcelike habitat east of Asturias (north of Picos de Europa), but bears do not currently occupy this area. There are several possible explanations for this. We cannot expect a population in regression to occupy all suitable habitat and/or there is a missing human variable affecting that area (Picos de Europa is a popular tourist destination, receiving 1.6 million tourists a year).

Logistic habitat models frequently use habitat variables (e.g., forest cover, road density) calculated on the cells defined by map resolution. There are biological arguments, however, that larger-scale properties of the same habitat variables may also influence habitat selection (e.g., Schadt et al. 2002). We used two indices to describe scale-dependent spatial properties and found that they delivered some habitat variables that entered in the final models. The inclusion of such variables is important for capturing the organism's perception of landscape structure above the grain of the landscape map,

which is often arbitrarily defined (Schadt et al. 2002), and for correcting systematic errors introduced when the scale of the analysis does not match the relevant spatial scale of the underlying ecological processes.

The main shortcoming of our modeling approach was that we used a set of a priori assumptions, which should hold true: human factors should be the most important variables affecting mortality, whereas reproduction success should be mostly affected by resource availability. This simplification does not mean that these are the only relationships, given that one would expect some effects of resource abundance on survival and of human disturbances on reproduction (Fig. 1), but we assumed that they are the main factors determining fluctuations in survival and reproductive rates (and so drive population dynamics). In the case of small, fragmented populations of large carnivores, these assumptions are probably commonly met and could form a generalized pattern. We distinguished between short- and long-term human impacts. In the short term, we assumed that human factors mostly affected survival (i.e., our “human” axis), while long-term effects such as habitat loss, fragmentation, and reduction in overall habitat quality were included in our “natural” dimension.

The classification accuracy of the final model was not impressive. However, we cannot expect a small population suffering from a long-term regression both in its range and population size (Wiegand et al. 1998) to occupy all potentially available habitat, and relict populations often exist in the periphery of their historical geographical range in suboptimal habitat (Channell & Lomolino 2000). Also, the large stochasticity that characterizes the dynamics of a small population will always hinder higher classification accuracy (Tyre et al. 2001), especially if one avoids the inclusion of a large number of predictors with scant biological interpretation (in such a case the model would describe the study area, not the biological requirements of the species).

### Habitat of the Two Subpopulations: Implications for Conservation

Our analyses draw a not-too-optimistic picture of the condition of brown bear habitat in northern Spain. There is little unoccupied, good-quality habitat, and the habitat of the two subpopulations comprises a high proportion of suboptimal habitat, a situation typical for many endangered species in highly humanized landscapes (Channell & Lomolino 2000). The area currently occupied by bears is a complex patchwork composed of different habitat types of varying human and natural quality and with only 33% of the current range of the two subpopulations occupying habitat of high natural and human quality. Over the long term, therefore, the entire area could be a demographic sink as a result of a combination of high human impact and low natural quality.

The eastern population occupies mostly sourcelike (38%) and refugelike (41%) habitat, indicating that it persists to a large extent in areas with low human impact but also low natural suitability. In contrast, the western population occupies mostly good-quality natural habitat but with a much higher human impact (41% as attractive sinklike habitat and 16% as sinklike habitat). This result is in accordance with the results of a nonspatial population viability analysis on the western population, showing that the population may have suffered a mean annual decrease of approximately 4–5% during the study period 1982–1995 (Wiegand et al. 1998). Also, it agrees with some demographic data showing that breeding performances, but also known mortality rates, are higher in the western than in the eastern population (mean litter size  $2.26 \pm 0.52$ ,  $n = 23$ , and  $1.79 \pm 0.70$ ,  $n = 14$ ; annual known mortality rates of 0.06–0.078 and 0.051–0.064, respectively; Naves et al. 1999; J.N., T.W., E.R., M.D., unpublished data). In light of these results, the main management goals for the western and eastern subpopulations should be the reduction of human-induced mortality events and the improvement of natural habitat quality by extensive reforestation with masting species, respectively.

We concentrated on spatial aspects to generate working hypotheses about the quality and spatial arrangement of brown bear habitat in the Cantabrian Mountains, hence aiding in large-scale decision-making and landscape management. However, further validation of these habitat types, by estimating reproductive and survival rates over the long term with the aid of standard field-monitoring techniques, is needed. Only with this validation may we reach a new iteration in our understanding of the relationship between habitat quality and demographic processes, and provide the necessary information to adequately manage this endangered population.

## Acknowledgments

We acknowledge the Spanish Ministry of Environment (MIMAM) and the governments of Asturias, Castilla y León, Cantabria, and Galicia for providing data from the official censuses of females with cubs and other data. The MIMAM also provided some digital cartography. Funding provided by the UFZ-Centre for Environmental Research and the Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, CSIC, enabled authors to travel between Germany and Spain for cooperative work. E.R. was supported by a Marie Curie Individual Fellowship (EVK2-CT-1999-50001). We thank M. Boyce, P. Kaczensky, A. Fernandez, F. Knauer, S. Schadt, F. Palomares, B. K. Gilbert, R. A. Powell, J. E. Swenson, and G. E. Belovsky for their ideas and comments on the manuscript.

## Literature Cited

- Alfonso XI. 1348. Re-edited 1976. Libro de la Montería. Ediciones Velázquez, Madrid.
- Anonymous. 1995. Atlas nacional. Climatología. MOPT. Instituto Geográfico Nacional, Madrid.
- Beutel, T. S., R. J. S. Beeton, and G. S. Baxter. 1999. Building better wildlife-habitat models. *Ecography* **22**:219–223.
- Braña, F., J. Naves, and G. Palomero. 1988. Hábitos alimenticios y configuración de la dieta del oso pardo en la Cordillera Cantábrica. *Acta Biologica Montana. Série Documents de Travail* **2**:27–38.
- Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears: implications. Pages 75–98 in C. W. Fowler and T. D. Smith, editors. *Dynamics of large mammal populations*. Wiley, New York.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Campo, J. C., J. Marquinez, J. Naves, and G. Palomero. 1984. Distribución y aspectos poblacionales del oso pardo (*Ursus arctos*) en la Cordillera Cantábrica. *Acta Biologica Montana* **4**:371–381.
- Caughley, G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts.
- CERCA + 100. 1995. Instituto Nacional de Estadística, Madrid.
- Channell, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. *Nature* **403**:84–86.
- Clevenger, A. P., and F. J. Purroy. 1991. Ecología del oso pardo en España. Monografía 4. Museo Nacional de Ciencias Naturales, Madrid.
- Clevenger, A. P., F. J. Purroy, and M. R. Pelton. 1992. Brown bear (*Ursus arctos* L.) habitat use in the Cantabrian Mountains, Spain. *Mammalia* **56**:203–214.
- Clevenger, A. P., F. J. Purroy, and M. A. Campos. 1997. Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. *Biological Conservation* **80**:17–22.
- Clifford, P., S. Richardson, and D. Hemon. 1989. Assessing the significance of the correlation between two spatial processes. *Biometrics* **45**:123–134.
- Delibes, M., P. Gaona, and P. Ferreras. 2001a. Effects of an attractive sink leading into maladaptive habitat selection. *The American Naturalist* **158**:277–285.
- Delibes, M., P. Ferreras, and P. Gaona. 2001b. Attractive sink, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters* **4**:401–403.
- Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian Lynx (*Lynx pardinus*). *Ecological Monographs* **68**:349–370.
- Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* **25**:173–182.
- Knight, R. R., B. M. Blanchard, and L. L. Eberhardt. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. *Wildlife Society Bulletin* **16**:121–125.
- Lennon, J. J. 1999. Resource selection functions: taking space seriously? *Trends in Ecology & Evolution* **14**:399–400.
- Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology* **13**:367–377.
- Madoz, P. 1846–1850. Diccionario geográfico-estadístico-histórico de España y sus posesiones de ultramar. Vol 16. P. Madoz and L. Sagasti, Madrid.
- Manly, B. F. J., L. L. MacDonald, and D. L. Thomas. 1993. Resource selection by animals. Chapman & Hall, London.
- Mattson, D. J. 1998. Changes in mortality by Yellowstone's grizzly bears. *Ursus* **10**:129–138.
- Mattson, D. J., S. Herrero, R. G. Wright, and C. M. Pease. 1996. Science and management of Rocky Mountain grizzly bears. *Conservation Biology* **10**:1013–1025.

- McLellan, B., F. Hovey, R. Mace, J. Woods, D. Carney, D. Gibeau, W. Wakkinen, and W. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management* 63:911-920.
- Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. *Biological Conservation* 87:231-248.
- Mladenoff, J. D., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lake region. *Conservation Biology* 9: 279-294.
- Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. *Ecological Applications* 9:37-44.
- Naves, J., and G. Palomero. 1993. El oso pardo (*Ursus arctos*) en España. Colección técnica. Instituto Nacional para la Conservación de la Naturaleza (ICONA), Madrid.
- Naves, J., T. Wiegand, A. Fernández, and T. Stephan. 1999. Riesgo de extinción del oso pardo cantábrico: la población occidental. Fundación Oso de Asturias, Oviedo, Spain.
- Nores, C. 1988. Reducción areal del oso pardo en la Cordillera Cantábrica. *Acta Biologica Montana. Série Documents de Travail* 2: 7-14.
- Nores, C., and J. Naves. 1993. Distribución histórica del oso pardo en la Península Ibérica. Pages 13-33 in J. Naves and G. Palomero, editors. El oso pardo (*Ursus arctos*) en España. Colección técnica. Instituto Nacional para la Conservación de la Naturaleza (ICONA), Madrid.
- Novaro, A. V., K. H. Redford, and R. E. Bodmer. 2000. Effect of hunting in source-sink systems in the Neotropics. *Conservation Biology* 14: 713-721.
- Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. *Ecology* 80:957-975.
- Picton, H. D. 1978. Climate and reproduction of grizzly bears in Yellowstone National Park. *Nature* 274:888-889.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *The American Naturalist* 132:652-661.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *The American Naturalist* 137:850-866.
- Purroy, F. J. 1991. Distribución y número. Pages 9-16 in A. P. Clevenger and F. J. Purroy, editors. *Ecología del oso pardo en España. Monografía 4*. Museo Nacional de Ciencias Naturales, Madrid.
- Reques, P. 1993. Antropogeografía del área de distribución del oso pardo en la Cordillera Cantábrica. Pages 223-264 in J. Naves and G. Palomero, editors. El oso pardo (*Ursus arctos*) en España. Colección Técnica. Instituto Nacional para la Conservación de la Naturaleza (ICONA), Madrid.
- Revilla, E., F. Palomares, and M. Delibes. 2001. Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. *Conservation Biology* 15:148-158.
- Rogers, L. L. 1987. Effects of food supply and kinship on social behaviour, movements, and population growth of black bears in north-eastern Minnesota. *Wildlife Monographs* 97.
- Schadt, S., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. Cervený, T. Huber, C. Stanisa, and L. Trepl. 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology* 39: 189-203.
- Stringham, S. F. 1990. Grizzly bear reproductive rate relative to body size. *International Conference on Bear Research and Management* 8:433-443.
- Swenson, J. E., N. Gerstl, B. Dahle, and A. Zedrosser. 2000. Action plan for the conservation of the brown bear in Europe (*Ursus arctos*). *Nature and environment* 114. Council of Europe Publishing, Strasbourg.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68:647-657.
- Torrente, J. P. 1999. Osos y otras fieras en el pasado de Asturias (1700-1860). Fundación Oso de Asturias, Oviedo, Spain.
- Tyre, A. J., H. P. Possingham, and D. B. Lindenmayer. 2001. Matching observed pattern with model process: can territory occupancy provide information about life history parameters. *Ecological Applications* 11:1722-1737.
- Wiegand, T., J. Naves, T. Stephan, and A. Fernández. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantábrica, Spain. *Ecological Monographs* 68:539-570.
- Wiegand, T., K. A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *The American Naturalist* 154: 605-627.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126-2128.

