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LANDSCAPE EVALUATION IN CONSERVATION: MOLECULAR SAMPLING AND HABITAT MODELING FOR THE IBERIAN LYNX

NÉSTOR FERNÁNDEZ,[1,2,3] MIGUEL DELIBES,[1] AND FRANCISCO PALOMARES[1]

[1]*Department of Applied Biology, Doñana Biological Station, Spanish Council for Scientific Research–CSIC, Avda. María Luisa s/n 41013 Seville, Spain*
[2]*Department of Ecological Modeling, UFZ–Centre for Environmental Research Leipzig-Halle, Permoser Str. 15, DE-04301, Leipzig, Germany*

Abstract. Conservation of endangered species requires comprehensive understanding of their distribution and habitat requirements, in order to implement better management strategies. Unfortunately, this understanding is often difficult to gather at the short term required by rapidly declining populations of many rare vertebrates. We present a spatial habitat modeling approach that integrates a molecular technique for species detection with landscape information to assess habitat requirements of a critically endangered mammalian carnivore, the Iberian lynx (*Lynx pardinus*), in a poorly known population in Spain. We formulated a set of model hypotheses for habitat selection at the spatial scale of home ranges, based on previous information on lynx requirements of space, vegetation, and prey. To obtain the required data for model selection, we designed a sampling protocol based on surveys of feces and their molecular analysis for species identification. After comparing candidate models, we selected a parsimonious one that allowed (1) reliable assessment of lynx habitat requirements at the scale of home ranges, (2) prediction of lynx distribution and potential population size, and (3) identification of landscape management priorities for habitat conservation. This model predicted that the species was more likely to occur in landscapes with a higher percentage of rocky areas and higher cover of bushes typical of mature mediterranean shrubland mosaics. Its accuracy for discriminating lynx presence was ~85%, indicating high predictive performance. Mapping model predictions showed that only 16% of the studied areas constitute potential habitat for lynx, even though the region is dominated by large extents of well-preserved native vegetation with low human interference. Habitat was mostly clumped in two nearby patches connected by vegetation adequate for lynx dispersal and had a capacity for 28–62 potential breeding territories. The lynx population in Sierra Morena is probably the largest persisting today, but it is still critically small for optimism about its long-term persistence. Model results suggest habitat conservation and restoration actions needed for preserving the species, including reconciliation of hunting management with preservation of mature shrubland over large areas (particularly in rocky landscapes). The approach presented here can be applied to many other species for which the ecological information needed to develop sound habitat conservation strategies is lacking.

Key words: conservation; endangered species; fecal DNA; habitat modeling; information-theoretic approach; Lynx pardinus; *mammalian carnivores; model selection; molecular survey; population assessment; remote sensing; resource selection functions.*

INTRODUCTION

Endangered species frequently persist in small, unconnected populations confined to remnants of natural ecosystems in regions extensively modified by humans (Saunders et al. 1987, Meffe and Carroll 1997). To guarantee the conservation of these populations, it is often critical to develop species-specific habitat management strategies that demand comprehensive understanding on their requirements of space and resources. Assessing these requirements at the home range level is imperative for the conservation of animal populations (Litvaitis et al. 1996, Chapin et al. 1998), since the number, size, and distribution of home ranges determine the reproductive pool and the spatial structure of populations, influencing their viability (Hanski 1999). In general, individuals select home ranges in response to landscape patterns related to resource access (such as food or refuges), or to constraints such as human-related disturbance and risk of mortality (e.g., Carey et al. 1992, Mladenoff et al. 1999, Naves et al. 2003). Therefore, a promising strategy for improving the status of endangered species populations is to manage landscapes to optimize the availability of required resources in areas of low human interference (Fernández et al. 2003).

Unfortunately, specific habitat requirements and the availability or spatial distributions of suitable habitats are poorly understood for many species. Collecting the

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[3] E-mail: nestor@ebd.csic.es

ecological information needed for addressing these questions may require considerable monitoring effort (e.g., Palomares and Delibes 1993, Revilla et al. 2000, Fernández et al. 2003), and it is particularly problematic for rare species with few individuals or relict populations, such as many mammalian carnivores of high conservation concern (Gese 2001). In addition, many endangered species will require specific and detailed habitat studies and conservation planning for different environments where their populations may be found, in order to preserve the full range of the species' ecological roles and adaptations (Meffe and Carroll 1997, Wikramanayake et al. 1998). Therefore, applied ecological research is often challenged by the urgency of providing on-hand criteria for managing relict habitats of declining species with little knowledge of their population ecology.

The Iberian lynx (*Lynx pardinus*) is one of the mammalian carnivores that suffered the most dramatic declines during the last century. Once widely distributed in the Iberian Peninsula, only nine isolated populations persisted during the 1980s (Rodríguez and Delibes 1992, 2002, Delibes et al. 2000). The establishment of a system of Protected Areas encompassing most lynx populations was not enough to prevent the species collapse; currently only two of these populations are known to persist, both facing a serious risk of extinction (Rodríguez and Delibes 1992, 2002, Delibes et al. 2000). As a result, the species has been recently catalogued in the highest category of extinction risk by the International Union for Conservation of Nature (Nowell 2002). Long-term monitoring of one population persisting in Doñana National Park, Spain, has provided detailed knowledge of relevant ecological aspects for conservation (e.g., Delibes 1980, Gaona et al. 1998, Palomares et al. 2000, 2001, Fernández et al. 2003). However, logistic difficulties and limited resources have hindered research on key issues for the conservation of other populations, and it remains unknown whether findings on habitat selection patterns in a single monitored population are applicable to other areas.

Predictive distribution models based on species–landscape associations may be useful tools in compensating for lack of knowledge of population status and habitat constraints in endangered species such as the Iberian lynx (e.g., Boyce and McDonald 1999). However, their utility for designing reliable conservation planning depends on our capacity to obtain the best quality data possible for developing habitat models under the limitations previously noted. There are two main difficulties: to identify areas where the species is present, and to recognize relevant environmental variables that influence individual habitat selection at adequate scales. In the present work, we illustrate an application of habitat models to assess species conservation needs using a poorly known population of the endangered Iberian lynx inhabiting a protected area. Our approach takes advantage of molecular-based methods for species detection, combined with landscape analysis based on remote sensing to evaluate patterns of lynx habitat selection at the home range level. This approach can be extended to various situations in which ecological information is scarce, but needed for habitat conservation, or where the study species is particularly rare or elusive. Our specific goals were: (1) to evaluate relationships between presence of lynx and species-specific landscape patterns in the Sierra Morena Mountains (Spain), where probably the largest Iberian lynx population persists; (2) to predict the amount of habitat available to the species in this area and its potential carrying capacity for lynx; and (3) to assess landscape management needs for the conservation of lynx habitat.

METHODS

Study area

The study area included two contiguous protected Natural Parks in eastern Sierra Morena, a largely unpopulated region of southern Spain (38°13′ N, 4°10′ W; Fig. 1). These Parks, Sierras de Andújar and Sierra de Cardeña y Montoro, comprise an area of 1125 km^2 with elevations between 500 and 1300 m and with soils mainly of granite or slate. The climate is mediterranean subhumid with marked seasons, and average annual precipitation fluctuates spatially from 500 to 900 mm. Vegetation is a product of a large history of traditional human management. Mediterranean shrubland is dominant, although with different degrees of conservation. Best preserved areas include tall, old-growth bush species that reach >2 m height (e.g., *Quercus coccifera*, *Pistacia lentiscus*, *Arbutus unedo*), a diversity of shorter scrub species, and eventually trees (mostly *Quercus* spp.). Bushes are not present in more demoted shrubland, which has a poor vegetation diversity dominated by *Cistus ladanifer* and *Genista hirsuta* scrubs. In most areas transformed for cattle raising, shrub vegetation has been almost completely eliminated and grasslands with scattered trees are dominant (locally called Dehesas). The largest Iberian lynx population occurred in the mountains of eastern Sierra Morena during the early 1980s (Rodríguez and Delibes 1992). This population is believed to be the best preserved today, although there is a lack of specific data on its status.

Sampling and molecular procedures

We modeled the presence of the Iberian lynx in hexagonal sampling units of 4.1 km^2, equivalent in size to the average home range for females as obtained from radiotracking data (Fernández et al. 2003). We used hexagons because they are the packing shapes that best approximate circles. For this, we selected a sample of 50 hexagons covering an area around the Yeguas River where a lynx population was believed to persist (Fig. 1). We surveyed hexagons during late winter and spring of 2001, and determined presence of lynx by molecular-genetic-based species identification of collected fecal samples. Feces surveys are effective means of detecting the presence of resident lynx, which distribute abundant

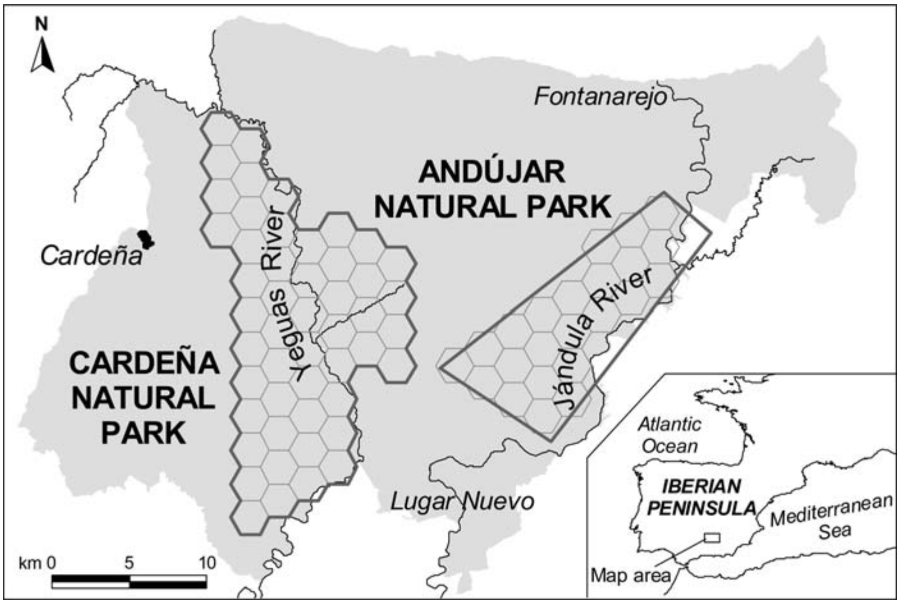

FIG. 1. Map of the study area in Sierra Morena Mountains, Spain, showing hexagons used for systematic sampling of the Iberian lynx (gray outlined area around the Yeguas River) and the sampling area for the evaluation data set (outlined area around the Jándula River). The study area encompasses two Natural Parks (in gray) separated by the Yeguas River. It is largely unpopulated, with only a small village (Cardeña) at the western border.

feces in conspicuous places within their home ranges for purposes of social communication (Robinson and Delibes 1988, Gorman and Trowbridge 1989). The main problem with these surveys is that identification from feces may cause important sampling errors derived from confusion with other sympatric carnivores, such as the wild cat (*Felis silvestris*), the red fox (*Vulpes vulpes*), or the European genet (*Genetta genetta*). Therefore, we used a molecular protocol specifically designed for fecal identification of the Iberian lynx that helps to detect reliably the presence of the species (Palomares et al. 2002).

Two observers surveyed each hexagon together during a fixed interval of six hours. This duration was adequate to determine lynx presence, because positive hexagons were always detected from feces within two hours of sampling. The surveys aimed to cover the maximum hexagon area during the six hours. For this, we followed previously established trails from maps, with the aid of a GPS with the UTM coordinates of the hexagons and reference sites in the trail. This design was consistent among all sampling areas. All carnivore-like feces found during these surveys were collected for molecular analysis except those containing abundant fruit or insect remains that could not have been produced by lynx (Delibes 1980, Calzada 2000). Collection followed a meticulous protocol to prevent genetic contamination among samples. Every sample was taken using disposable latex gloves and was immediately stored in a paper envelope inside a hermetic, sterilized polypropylene sample container. To avoid DNA degradation after collection, fecal fragments were dried and preserved inside the container with silica gel with moisture indicator, which was replaced as needed (Palomares et al. 2002).

Laboratory analyses followed the general protocol described in Palomares et al. (2002). We performed two DNA extractions from each fecal sample using Chelex-100 and two separate polymerase chain reaction (PCR) DNA amplifications per extraction (i.e., four PCRs per sample). Palomares et al. (2002), with a sample size of >200 lynx feces, showed that two PCRs from only one extraction never produced false negatives. Thus our protocol guarantees the detection of lynx positives. We used the primer pair DL7F/CR2bR for the PCR amplification. This primer, specific for the Iberian lynx, amplifies a fragment of 130 pairs of bases from mitochondrial DNA (mtDNA), small enough to be found among the generally low-quality fecal DNA. To control for the performance of the extraction and the amplification, we included two positive controls with lynx DNA in each PCR set, and two negative controls without DNA to reject contamination. The positive controls were one for the PCR amplification (containing diluted blood DNA) and one for the extraction and the amplification, in which we used Iberian lynx scats of known origin. The product of these two controls ensured that amplification occurred in every set. Similarly, the negative controls included one with only the extraction products, and one with all of the PCR products used for testing the samples, but with water instead of DNA. The absence of amplification in these negatives allowed us to reject contamination by exogenous lynx DNA during the process. To test if the fecal sample was indeed from a lynx, PCR products were

TABLE 1. Landscape variables (mean ± SE) measured at lynx sampling hexagons in Sierra Morena, Spain, and test of differences between hexagons with ($N = 13$) and without lynx ($N = 25$; all df = 1).

Variable	Positive	Negative	Kruskal-Wallis χ^2	Kruskal-Wallis P
Percentage of patches				
Dense shrub patches (%S)	46.15 ± 5.29	39.48 ± 4.30	1.23	0.26
Rocky patches (%RO)	4.79 ± 0.95	0.69 ± 0.32	19.05	<0.01**
Mean cover (1–4 code)				
Bushes (MB)	0.62 ± 0.11	0.42 ± 0.05	1.52	0.20
Pastures (MP)	1.37 ± 0.15	1.57 ± 0.20	1.71	0.19
Density (m/km^2)				
Ecotones between dense shrub and pastureland patches (EDG)	2.67 ± 0.29	2.53 ± 0.29	0.06	0.80
Streams (STR)	0.43 ± 0.10	0.58 ± 0.08	0.98	0.32
Slope (degrees) (SLO)	15.2 ± 0.90	12.2 ± 0.63	5.11	0.02*

Notes: Measurements are: %S, portion of the hexagon covered by vegetation polygons with >50% shrub cover; %RO, portion occupied by outcrops; MB, abundance of tall (>1.5 m) shrubs based on patch-area-weighted mean bush cover in the hexagon, coded 1–4 to represent cover intervals of 25%; MP, calculated similarly; EDG, length of edges between patches densely (>50%) covered by pastures and patches densely covered by shrubs (for patches >0.5 ha); STR density, estimated using a vector cartographic layer scaled 1:100 000 of permanent and seasonal rivers and streams; and SLO, estimated for each hexagon from a raster digital elevation model (DEM) obtained by interpolating 20-m contours from 1:50 000 National Topographic Maps.

* $P < 0.05$; ** $P < 0.01$.

separated by agarose gel electrophoresis, and then visualized and photographed under ultraviolet light. The high specificity of this technique assured the accuracy of the Iberian lynx identification from feces, as DNA from other species present in our study area did not yield any amplification product (Palomares et al. 2002). In addition, field trials have demonstrated that the technique is accurate for samples exposed to external conditions for periods up to three months, and that the season of collection does not have any effect on the species identification (Palomares et al. 2002).

Typically, several lynx feces were detected within each positive hexagon, including latrines with feces of different age, which guaranteed the accuracy of positive detections. In addition, negatives were assigned after six hours of sampling without any lynx detection. Although there is no means of unequivocally verifying an absence, the relative ease of finding lynx scats in positive hexagons within two hours indicated that lynx presence was not likely in hexagons with no positive detection after the sampling period of six hours. This assumption was also supported by previous experience and field trials in areas with well-known distribution of lynx territories from radiotracking (e.g., Palomares et al. 1991, 2001, Calzada 2000).

Predictive landscape variables

We measured a set of seven landscape variables within sampling hexagons (Table 1). These variables were selected based on findings on relationships between breeding territory distribution and landscape patterns obtained for a different lynx population (Fernández et al. 2003), and specific predictions for the population of Sierra Morena. We estimated variables using a geographic information system (GIS) by intersecting a digital layer representing the boundaries of sampling hexagons with layers of vegetation, water availability, and topography. Vegetation attributes were derived from two vector layers containing high-resolution information for the studied Natural Parks, which proceeded from the classification of 1:15 000 color-infrared aerial photographs and 5.8-m resolution panchromatic images from the Indian Remote Sensing (IRS) satellite (Quijada-Muñoz et al. 1999, Sánchez-Almendro et al. 2003). The vegetation layer contained 20 128 polygons representing patches of mode size 2.3 ha and minimum size 0.02 ha.

Five variables were derived from this layer (Table 1). (1) *Percentage of dense shrub patches* was the portion of the hexagon covered by vegetation polygons with >50% shrub cover. (2) *Percentage of rocky patches* represented the area occupied by granite outcrops. (3) *Mean bush coverage* measured the abundance of tall (>1.5 m) shrubs (mainly species typical of mature stages of mediterranean shrubland), calculated as the patch-area-weighted mean bush cover among patches in the hexagon. (4) *Mean pasture coverage* was calculated for the grassy vegetation in the same manner. (5) *Density of ecotones* was estimated as the length of edges between patches densely (>50%) covered by pastures and patches densely covered by shrubs, including all patches >0.5 ha. (6) *Density of streams* was estimated using a vector cartographic layer scaled 1:100 000 of rivers and streams, both permanent and seasonal, of southern Spain (Instituto de Cartografía de Andalucía 1999). (7) *Mean slope* was estimated for each hexagon from a raster digital elevation model (DEM) of 50 m of horizontal resolution, obtained by the interpolation of 20-m contours from 1:50 000 National Topographic

TABLE 2. Summary of models postulated to predict Iberian lynx habitat in Sierra Morena, Spain; the best model is in bold type.

Model no.	Model	D^2	AIC$_c$	Δ_i	Akaike w_i	Ranking
Null model						
1	Intercept only		53.17	22.95	<0.01	11
Landscape complexity						
2	%RO SLO STR	0.50	36.08	5.83	0.02	6
3	%RO EDG SLO	0.49	36.60	6.35	0.02	7
Prey habitat						
4	%RO EDG	0.39	39.08	8.83	<0.01	10
5	MB EDG	0.06	55.21	24.96	<0.01	13
6	EDG	0.01	55.52	25.27	<0.01	14
Refuge availability						
7	%S %RO	0.56	30.85	0.60	0.28	2
8	%S	0.02	54.61	24.36	<0.01	12
9	%RO	0.38	36.77	6.52	0.01	8
Prey and refuge						
10	%S MP %RO	0.60	32.18	1.93	0.15	3
11	%S MP	0.03	56.66	26.41	<0.01	16
12	**%RO MB**	**0.57**	**30.25**	**0**	**0.38**	**1**
Global models						
13	%S %RO EDG SLO STR	0.66	34.17	3.92	0.05	5
14	%RO EDG SLO STR	0.50	38.88	8.63	0.01	9
15	%S STR EDG	0.09	56.36	26.10	<0.01	15
16	MB EDG SLO %RO	0.61	33.61	3.36	0.07	4

Notes: Models are classified in five subsets, corresponding to different hypotheses on habitat factors potentially limiting lynx distribution. Variable abrreviations are from Table 1; D^2 is explained deviance; AIC$_c$ is bias-corrected Akaike's Information Criterion for fitted models; Δ_i is $(\text{AIC}_c)_i - (\text{AIC}_c)_{\min}$; Akaike w_i is the Akaike weight.

Maps. The projection for all GIS layers and data was UTM 30S, datum European 1950 (ED50).

We processed vector digital layers and variable derivation using ArcInfo Version 8.02 (ESRI 2000). The DEM was analyzed using Idrisi32 Version 2 (released in 2001 by Clark Labs, Worcester, Massachusetts, USA; *available online*).[4] For a first assessment of landscape patterns in lynx habitats, we analyzed differences between hexagons with and without lynx using the Kruskal-Wallis test, and tested for correlations between variables using Spearman's rank coefficient (r_S).

Design and selection of habitat models

We based our analyses on information-theoretic methods guided by the view that ecological inference can best be approached by weighting evidence for multiple working hypotheses simultaneously (Hilborn and Mangel 1997, Burnham and Anderson 1998, Johnson and Omland 2004). In essence, these methods consist of first identifying a priori the alternative hypotheses for habitat selection and their mathematical formulation, and then testing their support by fitting the relevant equations to species distribution data and examining penalized maximum-likelihood estimates (e.g., Fernández et al. 2003, Johnson et al. 2004). We formulated a set of 15 hypothetical models that could potentially predict lynx distribution in Sierra Morena, therefore restricting the model selection process to a few meaningful combinations of predictors of the species (Table 2). Some models were specified for their confirmed ability to predict lynx territory distribution in a different study region, and their interpretability in terms of species' resource requirements (see Fernández et al. 2003). Other models were postulated specifically for the population of Sierra Morena, and included attributes of topography, water availability, and soil. Highly correlated predictors ($r_S > 0.6$) were never included in the same model. In addition, we fitted an intercept-only equation in order to test improvement over the null model of no effect. Candidate model equations were fitted using Generalized Linear Models (GLM) with logit-link and binomial error structure (McCullagh and Nelder 1989). Because there were fewer positive lynx hexagons than negative, we selected all positives together with two-thirds of randomly chosen negatives for model fitting, which constituted the training data set. The remaining observations were reserved for later evaluation (see *Model evaluation and habitat assessment*). We selected the best approximating fitted model from the complete set using a bias-adjusted Akaike Information Criterion (AIC$_c$). This statistic rewards parsimony by penalizing the maximum likelihood for the number of model parameters. Last, we assessed uncertainty on this selection by weighting all AIC$_c$ scores by the score of the best model (w_i). This approach allowed us: (1) to limit modeling to meaningful combinations of predictors to the species; (2) to obtain the best model possible with the fewest number of habitat variables; and (3) to avoid overfitting and other effects of "data dredging" that may arise when many

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[4] ⟨http://www.clarklabs.org⟩

potential equations are evaluated (Burnham and Anderson 1998).

We additionally designed a simulation procedure to evaluate the effect of violating the assumption of perfect detection of lynx absence on model selection results. Although our sampling appeared to be highly reliable, it is always problematic to guarantee perfect detection of absences in this and many other field surveys (especially for elusive species). In essence, our procedure randomly converts a number of negative samples into positives and refits the models to test whether the failure to detect rare animals would have biased the results. This process is iterated for different probabilities of species detection, following the formula

$$N_{\mathrm{sim}} = (N_{\mathrm{pos}}/\mathrm{Pr}_{\mathrm{det}}) - N_{\mathrm{pos}}$$

where N_{sim} is the number of negative observations simulated as positive; N_{pos} is the number of presences detected in the original sample; and $\mathrm{Pr}_{\mathrm{det}}$ is the detection probability for absences. The number of "false negatives," N_{sim}, takes a zero value when the probability of correctly detecting an absence, $\mathrm{Pr}_{\mathrm{det}}$, is 1, and increases with lower detection probabilities. For each $\mathrm{Pr}_{\mathrm{det}}$, a random subsample of N_{sim} absences was converted into presences in the training data set. This modified data set was used to refit all hypothetical models and to recalculate the rank of each model and the associated selection uncertainty. The procedure was repeated 10 000 times and the probability of selecting each model was finally estimated for each detection probability.

Model fitting, calculation of selection statistics, and simulations were all performed using the S-Plus 2000 Professional statistical package (MathSoft 2000).

Model evaluation and habitat assessment

We first tested the classification accuracy of the most parsimonious model using the training data set. For this, we examined the model sensitivity (i.e., the probability of detecting all suitable habitats for the lynx) and the specificity (probability of detecting only true habitat) for the full range of habitat probability values obtained from the model (Pr). Sensitivity was calculated as the proportion of lynx positive hexagons classified as habitat at a given Pr value, and specificity as the proportion of negative hexagons classified as nonhabitat. Then, we selected the best cutoff probability score for habitat classification (Pr cutoff) as the midpoint between the probability where sensitivity equals specificity, and where the total proportion of correct prognoses is the highest. This cutoff was used to predict the distribution of lynx habitat in Sierra Morena and to test the model with new observations.

We used an independent data set on lynx distribution to evaluate the accuracy of habitat predictions. New data on lynx presence were obtained from a similar sampling protocol in subsequent surveys, which were carried out between summer 2001 and spring 2002 by the national and regional environmental agencies responsible for lynx monitoring and conservation. These surveys, based on a 5 × 5 km grid, covered a section of the Andújar Natural Park situated to the west of the original sampling area (Fig. 1). Feces collection and molecular analyses were consistent with the first sampling scheme, and therefore new hexagons with lynx could be identified from the UTM coordinates of positive feces. Because we could not ensure the reliability of negative hexagons in this case, the observations excluded from the training data set (one-third of all negatives) completed the evaluation sample.

We assessed predictive accuracy using two different methods. First, we calculated the area under a Receiver Operating Characteristic Curve (AUC). This is a cutoff-independent measure informing on the probability that, in randomly paired occurrences and nonoccurrences, the model-predicted occurrence will be classified with a higher Pr score than the nonoccurrence (Hanley and McNeil 1982). Because the rarity of Iberian lynx presence data may limit the robustness of AUC estimates, we tested confidence on these estimates using bootstrapping. We calculated mean bootstrap AUC scores and 95% bootstrap confidence intervals for both the training and the evaluation data sets ($N = 10\,000$ bootstrap repetitions).We then tested if bootstrapped AUCs significantly departed from random, and compared distributions for testing differences in predictions between training and evaluation data sets that could arise from model overfitting. Second, we evaluated the proportion of specific agreement between lynx distribution and model predictions under the Pr cutoff previously described. For this, we estimated the proportion of correct prognoses of lynx occurrences and nonoccurrences, and the Cohen's Kappa statistic, K_{C} (Fielding and Bell 1997). We finally calculated the proportion of correct prognoses for Pr scores above and below the cutoff, to obtain a range of cost estimations of false positive and negative errors when classifying habitat at different probabilities. Bootstrap mean and error statistics were estimated for both types of prognoses at each Pr score ($N = 10\,000$ bootstrap repetitions).

Predictions from the best model equation were translated into a map of lynx habitat probability in Sierra Morena. For this, the hexagonal grid used for sampling was expanded to the area covered by Cardeña-Montoro and Andújar Natural Parks, and the relevant habitat predictors were calculated for each hexagon. Habitat probability (Pr) was derived applying the logit-link formula from the binomial GLM. This prediction could be strongly influenced by the specific spatial arrangement of hexagons in the grid. Therefore, we improved this estimation using a moving-window routine, in which the original grid was displaced 20 times in regular intervals on all hexagon diagonals as well as on major and minor axes (Fernández et al. 2003). Habitat probability was recalculated for each of these displaced hexagons, and the resulting layers were intersected to obtain the average habitat probability from the overlying grids.

TABLE 3. Calibration results of the selected logistic regression model and the second-best model to predict Iberian lynx habitat in Sierra Morena, Spain.

Variable	df	Parameter estimate	SE	Standardized estimate	Wald χ^2	P
Best approximating model						
Intercept	1	−5.91	2.03		8.46	0.004
Mean cover of bushes (%)	1	5.42	2.33	1.00	5.39	0.020
Percentage of rocky places	1	1.07	0.35	1.80	9.05	0.002
Second-best model						
Intercept	1	−7.02	2.38		8.67	0.003
Percentage of dense shrub	1	8.5	3.53	0.97	5.81	0.016
Percentage of rocky places	1	1.13	0.36	1.91	9.68	0.002

Finally, we estimated habitat distribution using the Pr cutoff previously described, and measured the number and size of habitat patches and distances among them. In order to infer the capacity of predicted habitats for resident lynx, we calculated the potential number of nonoverlapping territories of mean size (4.1 km^2) and the number of territories of size at the lower and upper 95% bootstrap confidence limits of this mean (2.6 and 5.8 km^2, respectively; data are from 14 radio-tracked resident lynx females from Doñana).

RESULTS

From 149 feces collected around the Yeguas area, 79 were of lynx, as revealed by molecular analyses. These corresponded to 13 different hexagons, representing only 26% of the sampled area (6.1 ± 0.4 scats per hexagon [4.1 km^2], mean ± SE).

Univariate analyses

Only two landscape variables differed significantly ($P < 0.05$) between hexagons with and without lynx (Table 1). The percentage of habitat occupied by rocky patches showed the largest relative difference. Although they represented a relatively small portion of the overall area, these patches covered larger areas in landscapes with lynx, being present in all positive hexagons (compared with only 40% of negatives). Mean slope angles (SLO) were also significantly more pronounced in hexagons with lynx, indicating higher terrain complexity. A strong correlation was observed between dense shrub cover (%S) and mean cover of bushes (MB) ($r_S = 0.75$, $P < 0.01$). Moderate correlations existed between %S and the shrub/pasture ecotone (EDG) ($r_S = 0.42$, $P < 0.01$), %S and mean cover of pasture (MP) ($r_S = -0.37$, $P = 0.02$), MB and MP ($r_S = -0.48$, $P < 0.01$), and MP and EDG ($r_S = 0.42$, $P < 0.01$).

Model selection

The best approximating model included two variables, %RO (rock outcrops) and MB (Table 2). However, substantial model selection uncertainty was manifest from the Akaike weight, which was 0.38 for this model. The second-best model included %RO and %S (Akaike weight score 0.28). In addition, six models were needed to obtain a 95% confidence set on the best model (Table 2). In all these models, %RO was present, indicating its robustness as a model predictor. However, a model including exclusively %RO showed only 1% confidence in selection, indicating that the positive effect of this variable was manifest only in conjunction with other landscape attributes.

The fitted equation to predict lynx habitat was

$$\text{logit(PR)} = -5.91 + 1.07\%\ \text{RO} + 5.42\text{MB}.$$

Standard errors and significance tests of parameter estimates are shown in Table 3. A higher probability of lynx occurrence was predicted in landscapes with a greater percentage of granite outcrops and with higher abundance of bushes. The former predictor accounted for the major partial contribution to the model (see the standardized parameter estimates in Table 3). However, given similarities in AIC_c scores and the strong correlation between MB and %S, we could not reject the alternative second-best model. This predicted analogous positive effects of rocks and vegetation patches with dense shrub on lynx habitat probability (Table 3).

Sensitivity to imperfect detection of absences

Our simulation procedure showed that model selection results were robust to slight errors in the assignation of absences. For example, for a simulated detection probability of 0.93, the probability of selecting the best model was Pr = 0.49, and the probability of selecting this or the second-best alternative was Pr = 0.79. Moreover, these models showed Akaike weight scores $w_i > 0.05$ in all randomizations, i.e., above the threshold for model rejection. Although uncertainty of what constitutes the best model increased with error rates, detection probabilities ≥ 0.81 always resulted in model selection probabilities of Pr > 0.36 for the best model and Pr > 0.61 for the sum of this and the second; these values were comparable to selection probabilities obtained from the original data set (Table 3). Therefore, some degree of imperfect detection of absences is admissible without a significant effect on model results.

Predictive accuracy

According to the best model predictions for the training data set, the bootstrapped mean probability of correctly ranking occurrence–nonoccurrence pairs revealed a good model fit (AUC = 0.94 ± 0.06, mean and

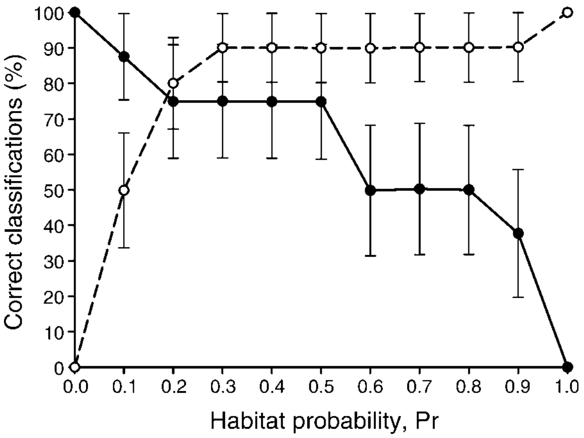

FIG. 2. Independent evaluation of the best approximating habitat model for the Iberian lynx in Sierra Morena, Spain. Black circles represent the bootstrapped mean accuracy of the best model for classifying lynx positives (sensitivity) at different probability (Pr) cutoffs, and open circles represent classification of negatives (specificity). Bars are bootstrap standard errors. The best probability cutoff from the training data set ($\mathrm{Pr} = 0.4$) revealed values for sensitivity of 74.9% and specificity of 90.0%.

CI). The probability value maximizing correct prognoses was $\mathrm{Pr} = 0.44$, and the probability of correctly classifying presences and absences coincided at $\mathrm{Pr} = 0.35$; therefore we selected the habitat probability cutoff at $\mathrm{Pr} = 0.4$. The classification accuracy at this cutoff was also high, classifying correctly 86.8% of all observations in the training set: 84.6% presences (sensitivity) and 88.0% absences (specificity); $K_{\mathrm{C}} = 0.71$.

We obtained eight new positive hexagons identified from the location of 43 lynx feces, which constituted the evaluation data set, together with 12 negatives. The classification of this new sample confirmed the high classification accuracy of the model, only slightly lower than for the training set (Fig. 2). The bootstrapped mean AUC was 0.81 ± 0.16, differing significantly from random ($P < 0.05$), but not from the training data set. With respect to habitat classification, correct prognoses at Pr cutoff = 0.4 were also high, accounting for 84% of the data. Bootstrapped mean sensitivity was 74.9% ± 15.9% (mean ± SE), specificity = 90.0% ± 9.7%, and $K_{\mathrm{C}} = 0.66 \pm 0.18$. The cost of enhancing model sensitivity above 80% (i.e., improving the classification of positives) was large in terms of specificity, and this occurred only at $\mathrm{Pr} \leq 0.15$. In addition, sensitivity strongly decreased at cutoffs of $\mathrm{Pr} > 0.5$ (Fig. 2).

Because of model selection uncertainty, we calculated the AUC estimates for the also-plausible second-best model, which showed slightly lower scores than the best, but not significant differences (mean AUC = 0.93 ± 0.06 CI and 0.79 ± 0.15 CI for the training and the evaluation data sets, respectively).

Habitat mapping

Translating model predictions into a map resulted in 175.8 km^2 of potential habitat for lynx (areas with mean $\mathrm{Pr} \geq 0.4$), representing 15.6% of the Natural Parks (Fig. 3). This habitat was distributed in several patches, mostly in two large ones accounting for 57.7% and 33.9% of total habitat, respectively (Table 4). The minimum distance separating both was only 2.2 km. Three smaller patches were predicted within the Natural Parks, two of them encompassing enough area to contain at least one female lynx territory. Minimum distances between small patches and the nearest large one were 5.4 km (northern to central Jándula) and 1.3 km (Lugar Nuevo to Central Jándula). All of these distances fall well below the mean distances of lynx dispersal in populations where this aspect has been studied (Ferreras et al. 2004). Changing the probability cutoff to $\mathrm{Pr} \geq 0.1$, which maximized model sensitivity above 85%, resulted in a mapped habitat area of 389 km^2, i.e., more than twice the area prediction at $\mathrm{Pr} \geq 0.4$.

Attending to the size and the spatial arrangement of predicted habitat, the estimated capacity for resident lynx in the two protected areas was 40 female territories, assuming mean territory size of 4.1 km^2, with a range of 28–68 km^2 for sizes in the upper and lower confidence limits, respectively.

DISCUSSION

Landscape structure and lynx distribution

The presence of the Iberian lynx in the Sierra Morena Mountains could be reliably predicted at the spatial scale of home ranges using a model that correctly classified ~85% of observations. This result showed the high potential for combining noninvasive molecular sampling with remote-sensing landscape data to model distribution of low-density, elusive species such as the Iberian lynx. The fecal DNA sampling method allowed us to accurately detect the species and collect distribution data required for habitat analyses. This represents a clear advantage over more traditional carnivore detection methods used in habitat studies, being appropriate for systematic sampling designs and applicable to many different environments, in contrast to sightings (e.g., Palma et al. 1999) or track census that are dependent on substrate (Palomares et al. 1998). In addition, our design represents a more cost-effective means to detect mammalian carnivores than other systematic methods such as camera trapping (e.g., Karanth and Nichols 1998), which require higher sampling efforts. We recognize that verifying perfect detection of absences is problematic in many species surveys (particularly of elusive species like many mammalian carnivores), which may represent a potential limitation of fecal molecular surveys and, more generally, of presence–absence data for habitat modeling. However, the easy detection of lynx positives in this study and the experience in a different well-known Iberian lynx population (e.g., Calzada 2000, Palomares et al. 2001) indicated that negative detections were also highly reliable. Moreover, our simulations suggested that some degree of imperfect detection of negatives

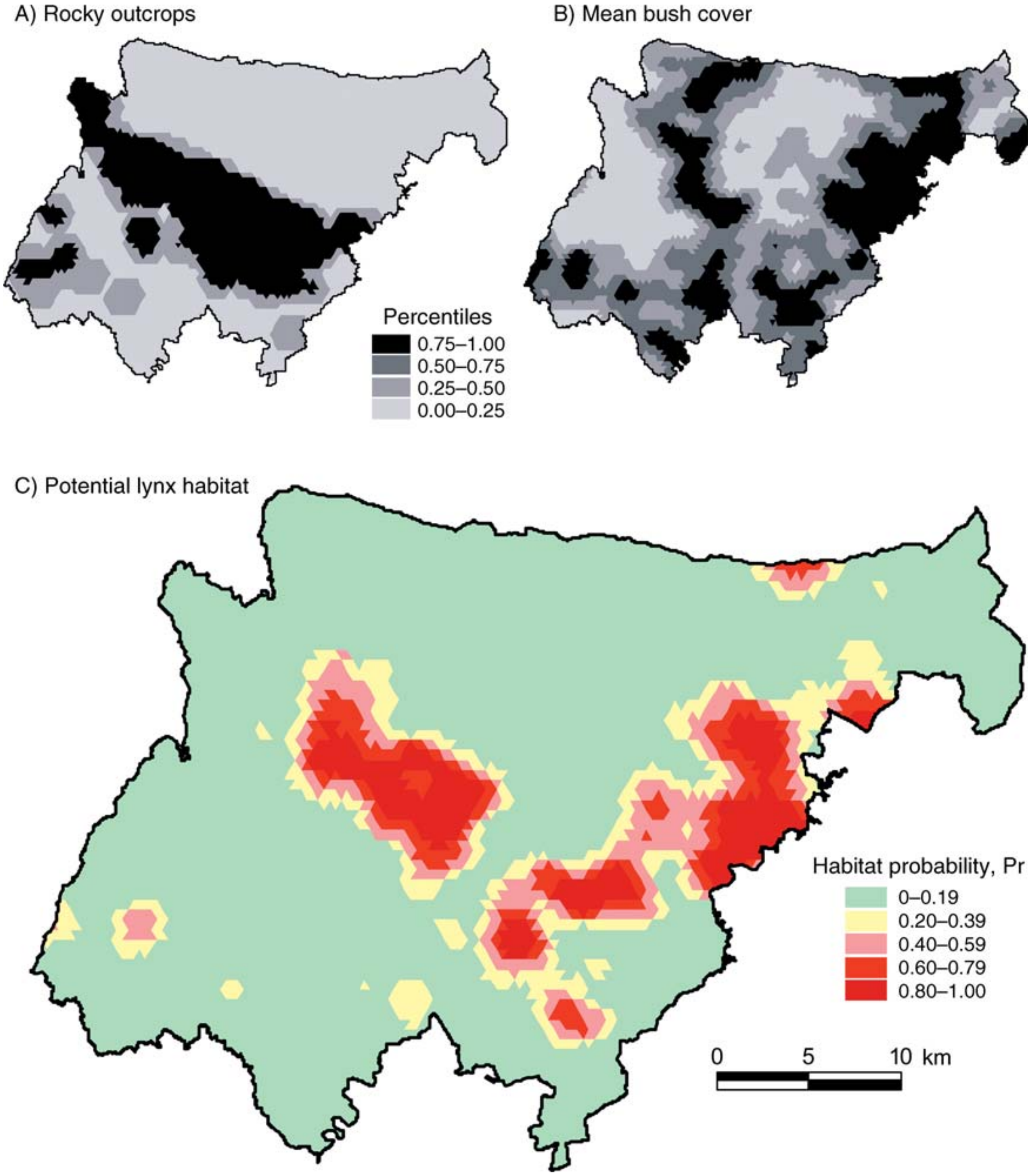

FIG. 3. Maps of predicted habitat probability for the Iberian lynx in Sierra Morena. Maps (A) and (B) show the percentile value for the partial probabilities contributed by each variable to model predictions of percentage occupied by granite outcrops and mean cover of bushes, respectively. Map (C) represents habitat probability values. Areas with Pr ≥ 0.4 were considered potential habitat.

(with errors $\leq$20%) was admissible and would not significantly affect model selection results.

A parsimony-based strategy for confronting different model hypotheses, founded on previous knowledge and biological plausibility, allowed us to assess the most relevant landscape attributes for lynx habitat conservation, with direct interpretation in terms of conservation planning. The most parsimonious model indicated that the species was associated with granite rocky outcrops and old-growth shrub vegetation typical of late-successional mediterranean communities, which were scarcely available in the study area. This suggested that population size and its spatial structure are dominated by a very restricted pattern of home range habitat selection, consistent with previous findings for the long-term radio-tracked population of the Iberian lynx in Doñana (Palomares et al. 2000, Fernández et al. 2003). In consequence, regional

TABLE 4. Estimated capacity for female Iberian lynx territories in the population of Sierra Morena, Spain.

Location	Area (km^2)	N_{mean}	N_{low}	N_{upp}
Jándula	99.8	24	37	17
Yeguas	58.6	14	22	10
Lugar Nuevo	6.3	1	2	1
Fontanarejo	5.7	1	1	0
Other	5.4	0	0	0
Total	175.8	40	62	28

Notes: Estimations correspond to the number of female territories of mean size (N_{mean}) and sizes in the lower (N_{low}) and upper (N_{upp}) 95% confidence limits of this mean. Place names are from Fig. 1.

planning for conservation of this species should seriously attend to these habitat needs.

Model predictions are probably related to the availability of prime resources for the Iberian lynx such as refuges and prey. Granite outcrops, the most significant landscape attribute, are rich in rocky cavities commonly used for refuge and breeding by the Iberian lynx and other felid species (e.g., Gashwiler et al. 1961, Rodríguez and Delibes 1990, Boutros 2002). Furthermore, felids are highly selective with respect to denning structures, and den availability is an important component of their habitats (Bailey 1981, Fernández and Palomares 2000, Boutros 2002). Therefore, it was not surprising that rocky outcrops were present in most areas with lynx: only one positive lynx hexagon from the evaluation data set, out of 21 total positives, contained no outcrops. However, the most important effect of landscape structure on lynx distribution was probably mediated by prey availability. Both granite soils and abundance of bushes are known to be related to the abundance of European rabbits (*Oryctolagus cuniculus*), the staple prey of lynx (Delibes 1980, Palomares et al. 2001, Fernández 2003). Granite formations in Sierra Morena include softer soils that favor rabbit burrowing, in contrast to the harder slaty formations of other parts of the mountain range. Rabbits currently are at low densities or absent in slate areas. Abundance of rocky outcrops in our models was also indicative of granite soils; our study does not clarify if lynx were strictly associated with outcrops, or with more general soil morphology. On the other hand, rabbits also attain higher densities in shrubland-dominated landscapes, particularly in those with old-growth bushes, where they take advantage of cover for increasing survival (Palomares et al. 2001, Lombardi et al. 2003, Fernández 2005).

The importance of shrub abundance to lynx habitat in Sierra Morena, particularly old-growth bushes, was consistent with previous findings on lynx home range selection elsewhere (Palomares 2001, Fernández et al. 2003). Nevertheless, other important landscape regulators of lynx distribution varied depending on the study region. Fernández et al. (2003) predicted for a population in Doñana that the distribution of lynx breeding territories responds to variations in the density of ecotones between shrubland and pastureland, which in turn favor prey abundance. However, this variable did not seem to limit lynx distribution in Sierra Morena; the average ecotone area in both occupied and unoccupied sites was similar to that for lynx habitats in Doñana (~2 km of ecotone/km^2; see Table 1). In Sierra Morena, current land management includes active promotion of pasture patches within shrubland habitats for favoring hunting and cattle raising, which generates a high amount of vegetation ecotones in landscapes. In contrast, the abandonment of these and other traditional practices in the region of Doñana has reduced ecotones favorable for rabbits and lynx (Moreno and Villafuerte 1995, Lombardi et al. 2003). An abiotic factor also influenced disparities: soils in Doñana are sandy and do not limit prey abundance, unlike Sierra Morena, where unfavorable slaty soils occupy >50% of the area. Therefore, differences in habitat correlates of lynx occurrence probably reflect disparities in landscape structure that influence the species within its current distribution range.

This outcome illustrates a rather frequent limitation of statistical habitat modeling for species conservation: differences in landscape composition may hinder extrapolation of model conclusions across different regions of the species' range (e.g., Flather and Sauer 1996, Rodríguez and Andrén 1999, Bakker et al. 2002, Reunanen et al. 2002). This discrepancy may be caused by region-specific patterns of association between landscape attributes and species' resources (such as prey and refuges in our study species). Therefore, a unique landscape model may not exist for predicting a species' habitat and designing strategies for its conservation. For example, it would make no sense to transfer the model from the present study to the Doñana population, where physiographic characteristics are not comparable, although it could help to predict potential habitat and its recovery over vast extensions of similar landform in southern Spain. Investigation of landscape factors regulating habitat availability in different regions is imperative for the management of endangered species, particularly of those with few populations and at high risk of extinction, such as the Iberian lynx.

Implications for conservation and future research

Both the amount of available habitat and its degree of fragmentation may greatly influence extinction in animal populations (Andrén 1994, Fahrig 2002). Our model predicted that 16% of the study area was potential habitat for the Iberian lynx. This represents a capacity for ~40 territories of average size (see Table 4), which roughly corresponds to 125 individuals in these territories if habitat were saturated (assuming an annual average of 3.2 individuals per territory; estimated from Palomares et al. [2001]). In addition, the spatial distribution of predicted habitat was highly clumped, with two large nuclei including 95% of this habitat. In comparison with the other persisting Iberian lynx population in Doñana (Palomares et al. 1991, Fernández et al. 2003), the estimated carrying capacity in Sierra Morena was 2–3 times higher. Distances between habitat patches were also shorter, and they were connected by covered habitats favorable for lynx dispersal, such as shrubland and pine forests (Palomares 2001). Therefore, Sierra Morena seems to provide the most promising situation of habitat quantity and spatial structure for the species' persistence. However, results also indicate that this "promising" population is critically small, and other lynx populations of similar sizes have become extinct during the last decades (Rodríguez and Delibes 2002). Therefore, urgent habitat management is required in Sierra Morena, not only for preserving the existing suitable areas for lynx, but also for restoring habitats to improve carrying capacity and expand the two main habitat patches detected in the present study.

Currently, in situ conservation of the Iberian lynx depends on acting on its habitat within natural protected areas where the species still exists. In Sierra Morena, these are mostly private lands dedicated to hunting (mainly of large ungulates). Therefore, high priority should be placed on making this activity compatible with lynx conservation. Hunting management includes reduction of native shrubland to provide pastures favorable to ungulates. Although the small pasture patches following shrubland reduction can improve lynx habitat, as previously discussed, demotion of shrubs has frequently been performed over large areas, conflicting with habitat requirements of the species. Our results show that dense shrub patches should be preserved for 40–50% of landscapes for use by lynx. However, shrubland may not be sufficient for preserving lynx habitat. Special efforts are needed to favor mature stages of this vegetation and guarantee >15% cover of old-growth bush species. This involves both active recovery of vegetation and control of disturbances such as fires and shrubland demotion for hunting.

Our model can be used to simulate the suitability of different landscape management scenarios for improving current habitat availability for the Iberian lynx. For example, the most favorable landscapes for lynx in Sierra Morena include granite rocky outcrops, and conservation strategies should largely focus on maintaining the ecological integrity of landscapes containing outcrops, with special attention to native vegetation. Furthermore, restoring demoted mediterranean shrubland in rocky areas would increase lynx habitat by 40%, mostly around the existing patches. Enlarging these habitat patches is recommended for sustaining endangered species in fragmented landscapes in general (Caughley and Gunn 1996), and the Iberian lynx in particular (Gaona et al. 1998, Ferreras et al. 2001). However, we acknowledge the difficulty of implementing this habitat restoration. Active recovery of mature shrubland is only possible at the long term; the few experiences at the spatial scale required by the Iberian lynx are very recent and do not allow evaluation of their success. Moreover, the hypothetical positive effects on prey abundance have not been tested yet. Therefore, a long-term adaptative habitat management scheme (Carroll and Meffe 1997) is required for lynx conservation, including investigation of the timing and magnitude of vegetation and prey recovery potential.

Although habitat selection models make an important contribution to species conservation, they also present evident limitations for addressing some important aspects of population structure. In particular, the manner in which habitats are structured in sources and sinks may greatly affect the most adequate actions for population conservation (e.g., Pulliam and Danielson 1991, Delibes et al. 2001). Findings of the present study already can be used for science-based management planning for lynx in Sierra Morena, but need to be followed by long-term population monitoring in order to evaluate aspects of demography that have important implications for conservation of the species. The habitat probability map obtained here can also be combined with population demography parameters in spatially explicit population models, to better understand threats to population persistence in landscapes of Sierra Morena (e.g., Dunning et al. 1995, Lima and Zollner 1996, Kramer-Schadt et al. 2005).

This study represents a significant contribution to understanding the role of landscape composition in the Iberian lynx habitat. Moreover, the method presented here can be translated easily to other situations with a scarcity of information for developing landscape-level conservation strategies, particularly for endangered mammalian carnivores. Once the molecular technique has been implemented, its application is straightforward and the economic cost is low (~15 euros per fecal sample in our study). It is suitable for extensive surveys or for tracking temporal changes in distributions that otherwise would be logistically difficult. Further refinements of the technique, such as analysis of microsatellite DNA variation, could be also used to identify individuals and therefore to improve population size estimates (e.g., Taberlet and Luikart 1999, Bellemain et al. 2005). Moreover, these methods, in combination with non-invasive surveys, also could provide very valuable information on population structure and gene flow among subpopulations of rare species. In addition, the highly detailed information on landscape structure used in this study, available from the combined analysis of airborne and satellite remote sensing, provided not only a sound basis for predicting habitat, but also criteria for recommending specific management actions. This fine-grained information is desirable (see Fernández et al. 2003), but rarely available. The more widely available broader scale satellite data can also be combined with the methods used here, in order to quickly provide significant results required for species conservation in rapidly changing landscapes (Soulé and Orians 2001).

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