Habitat-related heterogeneity in breeding in a metapopulation of the Iberian lynx

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Identifying attributes associated with good breeding habitat is critical for understanding animal population dynamics. However, the association between environmental heterogeneity and breeding probability has been often overlooked in habitat analyses. We evaluated habitat quality in a metapopulation of the endangered Iberian lynx *Lynx pardinus* by analyzing spatiotemporal patterns in breeding records. Data summarizing successful production of litters after emergence from dens over four years within 13 lynx territories were examined. We designed a set of generalized linear mixed models representing different hypotheses regarding how patterns in breeding records relate to environmental heterogeneity. Environmental heterogeneity was described by two characteristics: 1) a landscape index measured in lynx territories indicative of time-averaged prey availability and 2) yearly variability in prey abundance not captured with this index. By including the random effect of the lynx territory we also accounted for other territory-specific effects on reproduction. We found significant differences in yearly prey density dynamics among lynx territories. However, temporal variation in prey density contributed poorly to explaining lynx breeding. The most parsimonious model included the landscape structure as the only effect explaining breeding patterns. A multinomial-model-representation of the landscape hypothesis explained nearly 50% of variability in breeding records. Results pointed to the existence of a habitat quality gradient associated with particular landscape structures influencing lynx habitat selection and breeding performance. Underlying this gradient was time-averaged prey availability. Probably as a result of long-term fitness strategies in long-lived territorial species, the short-term fluctuations in prey availability had a minor influence. Our results illustrate how habitat inferences can be enhanced by incorporating the link between spatiotemporal patterns in reproduction and environmental heterogeneity.

Habitat selection is one of the most critical processes influencing individual fitness and population dynamics in animals (Wiens 1976, Pulliam and Danielson 1991). Recently, ecologists have relied on animal distribution data for the study of habitat selection and habitat-related population constraints (reviewed in Boyce and McDonald 1999, Guisan and Thuiller 2005). Landscape-oriented approaches, in which spatial heterogeneity in the environment is explicitly analyzed, have greatly contributed to our understanding of the habitat and distribution patterns of many animal species. Further, it has been argued that the relationship between patterns of species occurrence and landscape variables is a promising approach for describing the

environmental requirements for population and species persistence in the framework of niche theory and natural selection (Hirzel et al. 2002, Peterson et al. 2002, Guisan and Thuiller 2005).

The relationship between species distribution and environmental heterogeneity is only a limited descriptor of the necessary conditions for the persistence of populations, as habitat use does not always reflect habitat quality in terms of fitness (Pulliam 2000). For example, individuals may occasionally occur in low-quality habitats where they do not breed or they reproduce at low rates, whereas a minor fraction of higher quality habitats may be responsible for the major contribution to population productivity (Sergio et al.

2003, Penteriani et al. 2004). This variability implies spatially heterogeneous patterns in vital rates such as reproduction within habitats. Therefore, more rigorous habitat analyses require the study of breeding performance in different locations where individuals are found.

Recognizing that ecological patterns can show variability at a range of scales (Levin 1992), several studies have improved our ability to identify species habitats by incorporating a high degree of detail regarding spatial heterogeneity at different scales (Saab 1999, Manel et al. 2000, Fleishman et al. 2001, Johnson et al. 2004, Fernández 2005). However, most habitat studies still assume a constant environment and rely only on samples of animal distributions taken at one time-interval, therefore overlooking dynamic patterns. On the contrary, temporal heterogeneity may introduce an additional source of variability and exert an important influence on population dynamics (Southwood 1977, Korpimäki 1988). For example, breeding performance in territorial animals have been found to be regulated by landscape structure within the territory but also by short-term changes in the availability of resources such as food (Franklin et al. 2000). Therefore, the analysis and conservation of animal populations requires the explicit examination of patterns describing both spatial and temporal variability to characterize the species habitats and their quality for reproduction.

We investigated spatiotemporal patterns in reproduction in a metapopulation of a critically endangered carnivore, the Iberian lynx *Lynx pardinus*. Previous studies have shown that habitat selection in the Iberian lynx is strongly influenced by density of its staple prey, the European rabbit *Oryctolagus cuniculus*. Moreover, the distribution and size of lynx territories can be predicted from landscape variables influencing prey density (Fernández et al. 2003, Fernández et al. 2006). However, the factors that influence successful breeding by lynx are unclear. In the present study we aimed to test alternative hypotheses about the effects of environmental heterogeneity on spatiotemporal patterns in reproduction in the Iberian lynx. For this, we recorded the yearly production of litters after emergence from dens. We hypothesize that landscape variables indicative of time-averaged prey availability explain the frequency of these breeding records. A positive result would indicate that the landscape structure informs not only the suitable conditions for habitat selection but also the habitat quality for breeding. This hypothesis assumes constant environment effects on reproduction. However, local rabbit abundance within lynx habitats may largely vary among years (Palomares et al. 2001), which introduces a temporal dimension in environmental variability. Therefore, we also hypothesize that short-term variation in prey abundance influence

spatiotemporal patterns in breeding, implying that the quality of lynx territories varies from one breeding season to another. Prey availability may influence yearly breeding probability at different intervals, for example before the mating season, when the predator must defend a suitable territory to acquire an adequate physical condition for reproduction. Similarly, prey availability during and after the birth season, when nutritional requirements of females rising kittens are particularly high, may be important. To evaluate the importance of local spatiotemporal patterns of prey abundance on lynx breeding, we evaluated the fit of models using rabbit density during the year of reproduction and the year before reproduction. The landscape hypothesis, the short-term prey availability hypothesis and a combination of both were confronted using a theoretic-information approach.

Methods

The study population

The study was performed in Doñana, south-western Spain (37°0′N, 6°30′W), where a population of the Iberian lynx persists with a metapopulation structure. Several intensive radiotracking programs between 1984 and 2001 have allowed detailed descriptions of the metapopulation structure and the spatial distribution of breeding territories (Palomares et al. 2003). Resident individuals were detected in nineteen territories distributed among nine different nuclei, encompassing an area of ca 2000 km². The population size has remained stable throughout the last 15 yr. In the present work, we restricted the analyses to 13 resident female lynx territories distributed in five connected population nuclei with a high probability of territory occupancy (Revilla et al. 2004). Three of these nuclei were inside a highly-protected area in the Doñana National Park and two in the close surroundings (Fig. 1). The distribution and limits of lynx female territories have remained highly stable in these populations during the different radiotracking programs even though different individuals have occupied the same territories. We defined territory limits using 80%-fixed Kernel home range estimations from radiolocations of one representative resident lynx in each territory, for a total dataset of 2397 locations. Radiotracking and territory estimation procedures are fully described in Palomares et al. 2000 and Fernández et al. 2003.

Data collection

We carried out systematic track surveys to detect breeding within territories of the Iberian lynx every year from 2001 to 2004. Track censuses represent a
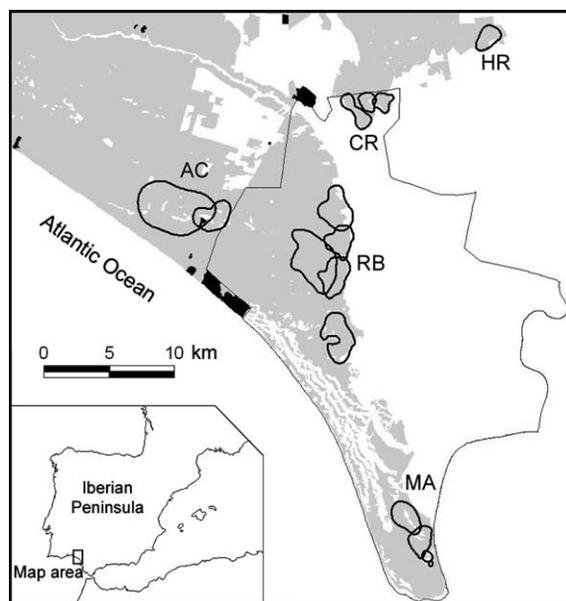
Fig. 1. Distribution of female Iberian lynx breeding territories in five subpopulations in Doñana, SW Spain. Thick lines represent lynx territories. Ten territories have been used for breeding within the Doñana National Park (thin line): three in Coto del Rey (CR), five in Reserva Biológica (RB) and two in Marismillas (MA). Three territories were located outside the Park, two in Acebuche (AC) and one in Hato Ratón (HR). Grey areas represent shrubland and forests favourable for lynx dispersal.

reliable and cost-effective method for the study of mammalian carnivores in areas like Doñana containing the appropriate sandy substrate. Three track surveys were performed in every territory each year between June and October, during the period when lynx kittens roam in their mother territories after emerging from their natal dens and before dispersing (Fernández et al. 2002). In each survey, one observer covered all sandy paths and trails inside the lynx territory. Lynx tracks reported the species presence, and kitten tracks, smaller and often together with adult tracks, indicated presence of kittens after the denning period. In addition, most breeding records (70%) could be also confirmed from cub tagging in their natal dens, from camera trapping, and from direct observations. We did not find any evidence for breeding outside areas detected from track surveys.

To examine whether spatiotemporal patterns in breeding were related to inter-annual variation in prey abundance, we estimated relative rabbit abundance for each territory every year from 2000 to 2004. This estimation was based on rabbit faecal pellet counts carried out between July and September in 246 fixed, randomly-distributed plots of 1 m^2 (Fernández 2005). It has been shown that rabbit pellet density is strongly

correlated with rabbit density and can be reliably used for monitoring rabbits throughout large areas (Palomares 2001a, b, Fernández 2005). All plots were sampled every year except in 2001, when we counted pellets in a random subsample of 160 plots. The number of sampled plots per territory-year ranged between 10 and 53. To evaluate the consistency of density estimates in relation to sample size we estimated the bootstrap distribution of differences in mean density using subsamples of 53 and 10 plots from the territory with the largest sample. Comparisons between simulated pairs of samples revealed no significant differences and the distribution of differences showed a small dispersion ($SD_{boot} = 0.059$ for standardized data between 0 and 1). This supported the reliability of mean density comparisons among samples of different size.

To test how landscape structure affects breeding we used predictions of a landscape-based habitat model of rabbit abundance (Appendix 1). This model was constructed for the northern area of the Doñana National and Natural parks, where spatial variations in rabbit abundance were closely linked to the landscape structure (Fernández 2005). The model predicts that the most favourable landscape mosaics for rabbits are those in the proximity to streams, ponds and lagoons and with a high cover of shrubs as well as ecotones between shrubland and pastureland. Moreover, it has been shown that the shrub density and the shrubland-pastureland ecotones are also the most important landscape features influencing habitat selection and size of territories in the Iberian lynx in Doñana (Fernández et al. 2003). Therefore, the rabbit habitat model can provide a static measure of the lynx habitat quality with clear biological meaning based on availability of prey. We mapped the predictions from the rabbit habitat model on a grid of 1-ha hexagonal cells, representing the spatial scale at which this model was built. Then, we estimated in every lynx territory a landscape index indicative of rabbit favourability as the average value of all cells within the territory boundaries.

Statistical analyses

We analyzed spatiotemporal variations in the European rabbit abundance within sampling plots in relation to the territory and the year, including their interaction. A significant interaction would indicate differences in the dynamics of rabbit abundance among the different lynx territories. This analysis was performed using a generalized linear model (GLM) with negative-binomial error distribution and log link (McCullagh and Nelder 1989).

Then, we tested whether breeding within territories was related to spatiotemporal variations in the density

of rabbits, to the landscape structure associated with time-averaged prey densities, or both. We compared breeding in a particular year Pr(B) as a function of different combinations of the average rabbit density within the territory during that year (i.e. parturition and kitten rising periods), the year before (previous to the mating period), and the landscape index described above. Since the same lynx territories were monitored across all years we used generalized linear mixed models (GLMM), an extension of GLM that allows modelling the covariance of random effects (Littell et al. 1996) We included the territory as a random term choosing the variance-components structure for modelling covariance. Pr(B) was coded as a binary response using binomial error distribution and logit link (McCullagh and Nelder 1989). We compared the explanatory strength of the different hypotheses confronting a set of competing models (Table 1) which included most combinations of variables except for some equations with rabbit density during the breeding year, because we considered this effect plausible only in combination with prey density before the breeding season.

Detection of the most parsimonious ecological hypothesis was based on model selection procedures using the Akaike's information criterion AIC (Burnham and Anderson 1998). AIC allows comparing multiple working hypotheses and weighting for their level of support in the data. The goal is to detect the best trade-off between model fit and number of parameters. We used a second-order derivation, AIC_c, which includes a correction for sample size, and selected the most parsimonious hypothesis according to the model with the lowest AIC_c. We also calculated the AIC_c weight (w_i) which reports the relative likelihood of every hypothesis normalized across the set of candidate models.

We additionally modelled the effect of the landscape structure on the number of breeding records per territory using multinomial GLM. In this analysis we ordered the response variable into five levels from 0 (no breeding during the study period) to 4 (breeding in all four years). Then, we modelled the probability that breeding is above a particular level as a function of the territory-averaged landscape index of rabbit

favourability. Model fit was compared with an analogous equation using the rabbit abundance in each territory averaged over the five years of data as the predictor. These two equations are non-exclusive model representations of the hypothesis that the most important habitat attributes influencing lynx habitat selection also affect breeding frequency.

All GLMs were performed using the GENMOD procedure in the SAS System for Windows v.8.02 (Anon. 1990). GLMMs were fit first using the GLIMMIX macro for SAS (Littell et al. 1996). Model selection procedures were coded using the R v. 2.01 free statistical software and the Lme4 package for mixed models (Anon. 2005, Bates and Sarkar 2006).

Results

The number of Iberian lynx breeding records ranged between 7 territories during 2002 (53.8%) and 4 during 2004 (30.8%). Seventy-seven percent of all territories showed evidence of breeding at least one year, whereas four years of reproduction occurred only in 2 territories (15.4%). In contrast, presence of adult lynx was recorded, on average, within 11 (84.6%) territories every breeding season, confirming the high rates of territory occupancy.

The correlation between the landscape index derived from rabbit habitat models and the time-averaged rabbit abundance was high ($r = 0.65$; $p = 0.019$; $DF = 11$), confirming the value of this index for describing prey availability within lynx territories. However, we also recorded substantial differences in prey density among years, dropping from of 43.3 ± 3.8 SE rabbit pellets m^{-2} in year 2000 to 11.6 ± 1.7 in year 2004. GLMs showed significant effects of the year, the territory and their interaction (Table 2), consistent with high spatiotemporal variations in rabbit abundance and indicating different dynamics among breeding territories (Fig. 2).

Table 1 shows the relative fit of the different GLMM in the lynx breeding data. Models including only variations in rabbit density as predictors had low support in the set, and their weighted likelihoods

Table 1. Set of generalized linear mixed models on breeding occurrence within female territories of the Iberian lynx. Models were fit using yearly binomial breeding data from 13 territories in Doñana during the period 2001–2004. The best approximating model is marked in bold.

Model	−2LogLik	AIC_c	Akaike w_i
0 Null model (no effect)	62.47	66.46	0.07
1 Prey abundance – previous year	59.70	65.70	0.09
2 Prey abundance – present and previous year	58.49	66.49	0.05
3 Landscape-only	**56.18**	**62.18**	**0.51**
4 Prey previous year and landscape	55.63	63.63	0.21
5 Full model (present and previous year, landscape)	55.23	65.23	0.07

Table 2. Negative-binomial generalized linear model for the European rabbit abundance within breeding territories of the Iberian lynx.

Model-effect	Type III tests		
	DF	χ^2	p
Year	3	65.90	<0.001
Territory	12	248.59	<0.001
Year × territory	24	122.72	<0.001

were not qualitatively different from a null model of no-effect. This indicated that, in spite of their large magnitude, yearly variations in prey availability did not explain breeding records. Type III tests also confirmed non-significant effects of prey density during the breeding year or the year before (GLMMs: all $\chi^2 \leq$ 0.29; p $\geq$ 0.14). In contrast, two hypotheses including the effect of the landscape accounted for >70% probability of selection in the model set (Tables 1 and 3). The landscape index as a single predictor was superior with 51% probability of selection, representing the best approximating model with the lowest number of parameters and the best relative fit to the data. The second model included also the rabbit abundance in the territory during the season before mating and showed a selection probability of 21%. Therefore, although some effect of short-term prey variation in combination with the landscape structure could not be entirely discarded, its relevance was low in comparison with the landscape.

The random effect of the territory was not significant in any model (Z $\leq$ 1.48; p $\geq$ 0.07).

Multinomial GLMs provided a better representation of landscape effects on lynx breeding (Table 3). The sole effect of the landscape index on the number of breeding records within the territory was significant and showed an acceptable fit to the data (adjusted generalized coefficient of determination $R^2 = 0.49$). The graphical representation of model effects illustrate the great impact of landscape structure on all breeding response levels and particularly on intermediate levels, with a maximum probability increase up to 0.8 for producing litters more than one year (Fig. 3). An alternative model showed that the effect of the rabbit abundance averaged over time was also significant (Type III test, $\chi^2 = 4.42$; p = 0.03) although model fit was lower in that case ($R^2 = 0.36$). This was not surprising given the correlation between time-averaged rabbit abundance and the landscape index reported above.

Discussion

We found that breeding records in the Iberian lynx were closely associated to landscape variables influencing the mean abundance of its prey. However, breeding did not show a clear correlation with yearly oscillations in prey availability within lynx territories. The hypotheses including only prey densities as
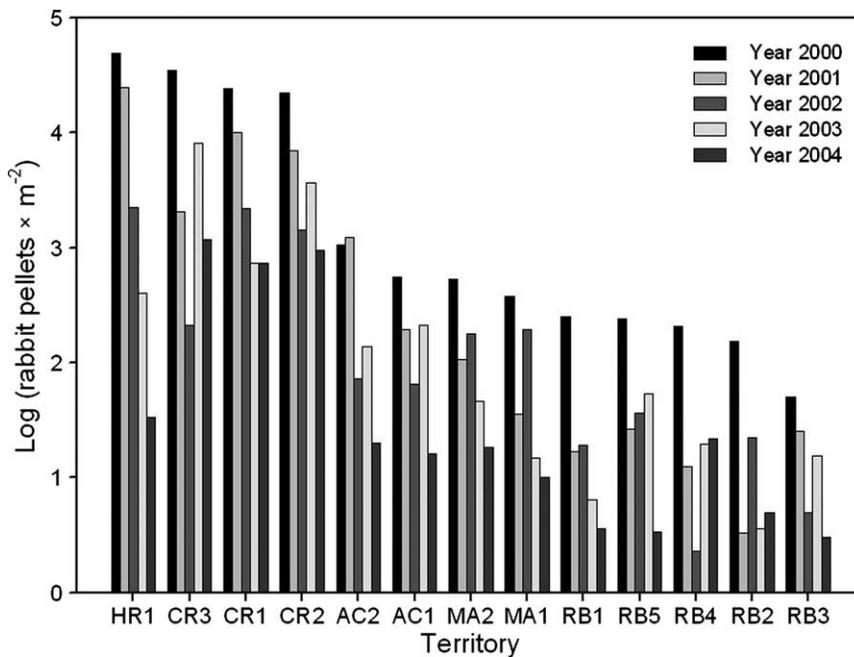

Fig. 2. Temporal variations in the European rabbit abundance within territories of the Iberian lynx between years 2000 and 2004. Territories are sorted on rabbit abundance in year 2000.

Table 3. The two best generalized linear mixed models (GLMM) for the yearly breeding probability and the multinomial model for breeding frequency in the Iberian lynx metapopulation of Doñana. The two GLMMs accounted for 72% probability of selection in the model set. The adjusted generalized coefficient of determination for the multinomial model was $R^2 = 0.49$.

Model-effect	Parameter estimate	SE	Type III tests		
			DF	χ^2	p
Best approximating GLMM:					
Intercept	−5.97	2.44			
Landscape index	0.08	0.04	1	5.36	0.021
Second best GLMM					
Intercept	−5.85	2.39			
Mean prey abundance (previous year)	0.22	0.40	1	0.31	0.583
Landscape index	0.07	0.04	1	3.73	0.061
Multinomial GLM					
Intercept 1	−4.72	2.06			
Intercept 2	−6.12	2.28			
Intercept 3	−6.94	2.43			
Intercept 4	−8.09	2.61			
Landscape index	0.09	0.033	1	6.33	0.012

predictors were not supported and only one model including both the landscape structure and prey abundance before reproduction could not be unequivocally discarded. This model was less parsimonious than the simpler nested hypothesis considering only landscape effects. In a previous study, Fernández et al. (2003) identified for the same lynx population the landscape factors influencing breeding habitat selection and territory size, and they concluded that the distribution and density of territories responded to the spatial structure of the vegetation. Noticeably, the significant landscape predictors were similar in the present study. Shrub cover (particularly shrubs typical of mature vegetation) and density of ecotones between shrubs and pastures were the most significant predictors
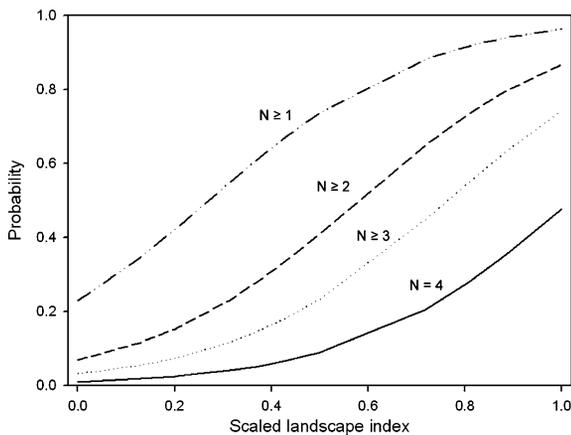

Fig. 3. Relationship between breeding frequency within female territories of the Iberian lynx and the landscape index predicted from the fitted multinomial model. The observed range for the landscape index was scaled from 0 to 1. N denotes the number of breeding records (levels) for each probability curve.

of habitat selection and constituted the landscape index associated to breeding records. According to these results, habitat selection and quality for breeding in the Iberian lynx can be observed as two aspects of a single gradient connected to the landscape structure and, ultimately, to the average prey availability. Indeed, the probability of finding a lynx breeding territory and the number of breeding records gradually increase with better vegetation conditions for rabbits. This supports the existence of a habitat quality gradient in the Iberian lynx associated to the landscape structure regulating territory selection, density and reproduction.

However, the amount of variability in breeding records explained by the landscape was only moderate (around 50% attending to the generalized coefficient of determination). There probably exist a complex variety of other factors not considered here that may affect breeding such as the individual quality for reproduction, female experience, probability of finding mates, etc. (Palomares et al. 2005). These effects are difficult to test in mammalian carnivores such as the Iberian lynx, where individual identification and monitoring is hampered by their secretive habits and rarity. The development of non-invasive methods for identification of individuals such as genetic typing from scats (Taberlet et al. 1999) may help to address these questions in the future.

Differences in breeding habitat quality observed in this study are directly related to opportunities for critical food resources in different landscapes. The Iberian lynx strongly relies on the availability of European rabbits to feed, a prey species that constitutes >80% of its diet (Delibes 1980) and limits the predator distribution (Palomares 2001a, b). In the present study, the association between the landscape structure and the availability of the European rabbit was

the basis for the landscape index that best explained breeding records. However, yearly changes in prey availability suggested that habitat quality for lynx was not only heterogeneous in space but also in time. Indeed, we confirmed significant differences among territories and years in the rabbit abundance, with a general declining trend over the years but with different dynamics in the different territories. Breeding occurred in some lynx territories with <5 rabbit pellets m^{-2}, a very low density which probably falls below the previously suggested threshold of one rabbit per hectare for lynx reproduction (Palomares et al. 2001). It has been suggested that short-term variations in food supply could modulate the suitable conditions for mating, pregnancy and kitten survival in other lynx species (Breitenmoser et al. 1993). Low prey density may also lead to reproductive failure caused by high postpartum kitten mortality, as shown for the Canada lynx and other felids subject to periods of prey declines (Brand et al. 1976, Packer et al. 1988, Mowat and Slough 1998). While fluctuations in rabbit abundance did not seem to influence successful litter emergence in the Iberian lynx at the short time, we can not reject other effects of food limitation such as reduced production of kittens, increased kitten mortality, etc. In addition, imperfect sampling of prey abundance could have hindered the detection of fine-tuning relationships between yearly prey variations and lynx breeding records.

There are several non-exclusive reasons why the hypothesis of short-term food-supply regulation was not adequate for predicting the spatiotemporal distribution of breeding records in the Iberian lynx. First, some territories have been occupied by resident females that did not breed during years of optimal prey availability (Palomares et al. 2005). Second, some females have not reproduced in some territories in years of relatively high prey abundance. For individuals selecting a habitat to breed, it may be difficult forecasting whether food levels in the next season will allow successful reproduction. Animals making habitat selection and breeding decisions often rely on indirect cues in their physical environment to anticipate the future state of the habitat (Cody 1981, Orians and Wittenberger 1991). This is consistent with the association of lynx breeding frequency with the more static landscape structure, which informs on the average rabbit abundance but reports imperfectly on yearly availability because stochastic variations in abundance are also large. Third, breeding may occur during years with low rabbit abundance when resident lynx attempt to optimize long-term territory holding. The alternative of searching for other breeding habitats during bad years is energetically costly and implies a high risk of mortality (Ferreras et al. 1992). Therefore, long-living animals like the Iberian lynx may benefit by staying in their territory and attempting to breed even during unfavourable periods of prey decline (Breitenmoser et al. 1993).

The present study also illustrates how the spatial analysis of a vital parameter can be used to understand the fitness consequences of habitat selection. Few studies have analyzed vital rates within different habitats in relation to spatial and temporal heterogeneity in the environment (Sergio et al. 2003, Muller et al. 2005), even though theoretical studies predict that spatial variation in vital rates have important demographic consequences for populations (Pulliam 2000). Resource selection functions, which are often used in spatial models of habitat selection (Boyce and McDonald 1999), can be easily expanded to address this relationship, as we have shown using GLMM. This information is particularly relevant for predicting the demographic consequences of habitat selection in metapopulations where the spatial heterogeneity in population parameters greatly influences their demography. Unfortunately, this type of assessment is limited by the lack of detailed spatial data on vital rates for many species, especially for elusive or rare animals such as the Iberian lynx. Yearly breeding data is one of the most useful parameters for evaluating the fitness consequences of habitat selection. Higher-quality data on breeding could also be used to improve habitat inferences; for example, if the number and survivorship of the offspring is also heterogeneous in space or time. The intensive monitoring program in the Iberian lynx provided exceptional information on the distribution of litters that emerged from dens, but more precise estimates of breeding success including offspring survival were difficult to obtain.

The identification of environmental variables related to spatiotemporal heterogeneity in reproduction represent an opportunity to improve demographic model projections and to manage breeding habitats in order to increase the probability of population persistence. Indeed, viability analyses suggest that increasing breeding rates in lynx territories is one of the most effective measures to assist the species conservation (Gaona et al. 1998). The strong dependence of lynx habitat selection and breeding on the time-averaged rabbit abundance implies that improving rabbit habitat is paramount to recover high-quality habitats for lynx. Our results indicate that increasing the interspersion of shrub-pasture patches will contribute to increase mean prey density and lynx reproduction in currently available habitats. One priority for lynx conservation is testing these predictions experimentally and quantifying the effect of landscape management on the species reproduction. Last, habitat quality can be also influenced by survival probability in different environments (Pease and Mattson 1999), another critical vital rate for population persistence. Future research should aim to

quantify habitat-specific reproduction and mortality simultaneously in order to account for critical population parameters in designing habitat management strategies.

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