

Research Article

Spatial patterns in European rabbit abundance after a population collapse

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Abstract

Assessing the associations between spatial patterns in population abundance and environmental heterogeneity is critical for understanding various population processes and for managing species and communities. This study evaluates responses in the abundance of the European rabbit (*Oryctolagus cuniculus*), an important prey for predators of conservation concern in Mediterranean ecosystems, to environmental heterogeneity at different spatial scales. Multi-scale habitat models of rabbit abundance in three areas of Doñana, south-western Spain, were developed using a spatially extensive dataset of faecal pellet counts as an abundance index. The best models included habitat variables at the three spatial scales examined: distance from lagoons (broad scale), mean landscape shrub coverage and interspersion of pastures (home-range scale), and shrub and pasture cover (microhabitat scale). These variables may well have been related to the availability of food and refuge for the species at the different scales. However, the models' fit to data and their predictive accuracy for an independent sample varied among the study regions. Accurate predictions in some areas showed that the combination of variables at various spatial scales can provide a reliable method for assessing the abundance of ecologically complex species such as the European rabbit over large areas. On the other hand, the models failed to identify abundance patterns in a population that suffered the strongest demographic collapse after viral epidemics, underlining the difficulty of generalizing this approach. In the latter case, factors difficult to implement in static models such as disease history and prevalence, predator regulation and others may underlie the lack of association. Habitat models can provide useful guidelines for the management of landscape attributes relevant to rabbits and help improve the conservation of Mediterranean communities. However, other influential factors not obviously related to environmental heterogeneity should also be analyzed in more detail.

Introduction

The distributions of abundance in animal populations are spatially heterogeneous (Brown et al. 1995, Ives and Klopfer 1997, Keitt et al. 2002). This heterogeneity can greatly influence population dynamics through parameters such as

breeding performance, survival rates and dispersal (Aars and Ims 2000; Paradis et al. 2002). Moreover, patterns in the abundance of one or a small number of species may have crucial effects on the structure and functioning of many communities through density-dependent interactions with other species and large-scale alterations of the structure

of vegetation (e.g. Paine 1992; Palomares et al. 1995; Weltzin et al. 1997; Kotliar 2000). Therefore, identifying factors influencing spatial heterogeneity in abundance is critical for an ecological understanding of populations and has important implications for species management and conservation (e.g. Coops and Catling 2002; Fisher et al. 2002; Lichstein et al. 2002).

Recent research suggests that patterns in population abundance are a product of the distribution of resources necessary to satisfy the species' niche requirements (Brown et al. 1995). This implies that animal abundance could be predicted by analyzing habitat and landscape variables related to environmental conditions and resources relevant to the species (e.g. Micol et al. 1994; Flather and Sauer 1996). However, pattern prediction is a complex topic – for several reasons. Firstly, it is a multifactorial problem involving the ways in which resource availability, predation, competition, diseases and other factors affect various population parameters. Secondly, the intervening factors may operate at various spatial scales (e.g. Wiens et al. 1987; Kotliar and Wiens 1990; Bissonette et al. 1997; Saab 1999; Schweiger et al. 1999). For example, relevant scales for many animals may include the microhabitat where individuals obtain resources (e.g. food and refuge), the landscape mosaic used by individuals or groups within more or less stable home ranges, and the landscape context surrounding home ranges that may influence population-level processes.

Empirical habitat modeling can provide an effective means of evaluating and predicting responses in population abundance to environmental heterogeneity at multiple spatial scales (e.g. Boyce and McDonald 1999; Guisan and Zimmermann 2000). This approach may greatly benefit the study of populations over large areas, where more traditional methods such as experimental control and testing individual effects are often unfeasible. Moreover, model extrapolation can help address practical issues such as identifying 'hotspots' of high population abundance, selecting the most promising areas for planning reserves, and assessing habitat management strategies for species restoration. However, the reliability of habitat models may be challenged when other factors, such as demographics or history, have an additional impact on population abundance (e.g. Rushton et al. 1994; Bustamante 1997; Pearce and Ferrier

2001). Therefore, multi-scale habitat modeling requires further investigation to assess associations between environmental variables and population abundance, and to evaluate how these associations may vary among populations of the same species that may be affected by different constraints.

The European rabbit (*Oryctolagus cuniculus*) is a prey species of key importance in Mediterranean ecosystems. It constitutes the diet of more than 30 predators in southern Europe, and also exerts a strong influence on the habitats of other species through vegetation consumption, seed dispersal and burrowing (Delibes and Hiraldo 1981; Sorriquer 1986; Gómez-Sal et al. 1999). During the last five decades, the species has suffered widespread population collapses throughout the Mediterranean as a result of two different epidemics: myxomatosis and Rabbit Hemorrhagic Disease, RHD (Thompson and King 1994; Villafuerte et al. 1995). This resulted in the extinction of many populations of Mediterranean predators, such as the critically endangered Iberian lynx (*Lynx pardinus*) and the Spanish Imperial Eagle (*Aquila adalberti*) (Rodríguez and Delibes 1992; Ferrer 1993). Consequently, strong conservation concerns have arisen regarding the identification of current broad-scale patterns in European rabbit abundance and how they are related to the distribution of resources.

In this study, the abundance of the European rabbit is analyzed in relation to habitat variables at the scales of microhabitat, home-range landscape composition, and landscape context. The main aim was to establish whether, after a long history of dramatic population declines, current abundance follows any predictable pattern related to the spatial distribution of resources. Habitat models developed in different regions ought to predict abundance well if the current regulation of rabbit populations were governed by patterns in environmental heterogeneity. Moreover, these models could be used to assess the relative importance of environmental variables measured at different scales for predicting abundance, and hence provide management guidelines at scales favoring rabbit populations.

Methods

Study area

The study was performed in the Doñana National and Natural Parks (Figure 1) in south-western

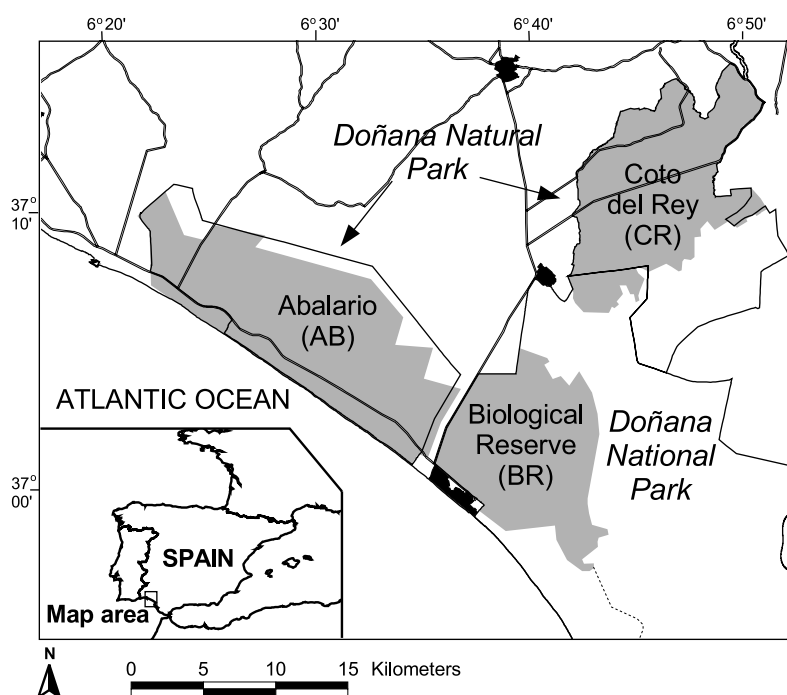


Figure 1. Map of the study area in Doñana (south-western Spain) with roads, towns and limits of protected areas. Shaded areas represent partial study domains.

Spain (37°0' N, 6°30' W). This is a flat region of sandy soils bordering on the Atlantic Ocean, with a maximum elevation of 106 m. The climate is Mediterranean sub-humid with marked seasons. Doñana National Park is one of the most important natural reserves in Europe in terms of the richness of its fauna, and is vital to vertebrate predator diversity. Human access is restricted and management is carried out by National Conservation authorities. The surrounding Doñana National Park has a less strict protection status that allows the exploitation of some natural resources, such as logging, hunting and cattle raising (see Fernández-Delgado 1997 for more detailed descriptions of Doñana).

Three different geographic areas can be identified in fixed dunes where rabbits are found. To the north, Coto del Rey (CR) is isolated from the other two areas by marsh and crops; about 10% is encompassed by the National Park, and the rest by the Natural Park. CR has a diversity of vegetation types; pine forests with variable understory vegetation are dominant, although there are also some areas of autochthonous Mediterranean scrubland vegetation of *Myrtus communis*, *Pistacia lentiscus*, *Halimium halimifolium* and *Cistus* spp. Abalarío

(AB) makes up the western portion of the Natural Park. Vegetation here is dominated by pine and eucalyptus plantations, which were cultivated from the 1940s to the late 1980s, resulting in landscape transformations that reduced the original heterogeneity (Sousa and García-Murillo 2001). Understorey vegetation is composed of short scrubs of *Halimium halimifolium* and *Ulex* spp. in xerophytic areas, and *Erica scoparia* and *Ulex minor* in moister soils. At the centre, Doñana Biological Reserve and its surroundings (BR) include the heart of the National Park. The vegetation is mainly heterogeneous Mediterranean shrubland, a product of more traditional land usage by humans, dominated by *Halimium halimifolium*, *Ulex* spp. *Erica* spp. and *Juniperus phoenicea*.

Rabbit data collection

A rabbit abundance survey was conducted in Doñana during the year 2000 based on rabbit pellet collection. Pellet counts provide a good approximation of rabbit density and are adequate for broad-scale studies (Palomares 2001a). The survey was carried out on an area of 388 km²:

Table 1. Environmental variables at the three spatial scales used for modeling European rabbit abundance in Doñana, Spain.

Code	Type	Definition	DO (<i>n</i> = 750)	AB	CR	BR
Landscape context						
<i>L·Lc</i>	Discrete	Land cover type	–	–	–	–
<i>L·DMar</i>	Continuous	Distance to the marsh (m)	8397 ± 264	16,933 ± 140	4581 ± 217	3678 ± 167
<i>L·DLag</i>	Continuous	Distance to nearest pond > 1 ha (m)	807 ± 25	860 ± 52	566 ± 25.5	994 ± 44
<i>L·DUrb</i>	Continuous	Distance to urban areas with > 100 inhabitants (m)	6234 ± 95	7196 ± 192	5723 ± 140	5728 ± 143
<i>L·Pro</i>	Discrete	Protection status	–	–	–	–
Home-range landscape composition						
<i>Hr·Bush</i>	Continuous	Mean landscape bushy vegetation cover (index ranging 0–4)	0.4 ± 0.02	0.1 ± 0.02	0.4 ± 0.04	0.6 ± 0.05
<i>Hr·Shr</i>	Continuous	Mean landscape shrub cover (0–4)	2.3 ± 0.03	2.2 ± 0.05	2.0 ± 0.07	2.8 ± 0.06
<i>Hr·Pas</i>	Continuous	Mean landscape pasture cover (0–4)	0.5 ± 0.03	0.2 ± 0.02	0.8 ± 0.06	0.4 ± 0.05
<i>Hr·%Inu</i>	Continuous	Landscape proportion of flooding patches	2.6 ± 0.4	2.2 ± 0.5	2.1 ± 0.5	3.7 ± 0.9
<i>Hr·Edge</i>	Continuous	Density of shrub-pasture ecotones (m/ha)	5.8 ± 0.7	2.6 ± 0.0	7.4 ± 1.5	7.5 ± 1.4
<i>Hr·DomVeg</i>	Discrete	Predominant vegetation class	–	–	–	–
<i>Hr·NVeg</i>	Continuous	Number of different vegetation classes (max. <i>n</i> = 9).	2.0 ± 0.03	1.9 ± 0.06	1.8 ± 0.05	2.2 ± 0.06
<i>Hr·Awd</i>	Continuous	Landscape average weighted fractal dimension	1.0 ± 0.01	1.0 ± 0.01	1.0 ± 0.01	1.0 ± 0.01
Microhabitat						
<i>M·Shr</i>	Continuous	Mean shrub cover (%)	44.4 ± 1.0	43.6 ± 1.4	33.2 ± 1.9	56.6 ± 1.6
<i>M·Bush</i>	Continuous	Mean bushy vegetation cover	9.2 ± 0.7	1.74 ± 0.6	13.3 ± 1.3	12.5 ± 1.5
<i>M·Pas</i>	Continuous	Mean pasture cover	15.2 ± 0.9	7.24 ± 0.9	25.6 ± 1.9	12.8 ± 1.3
<i>M·Hshr</i>	Continuous	Mean shrub height (m)	0.8 ± 0.04	0.9 ± 0.02	0.7 ± 0.1	0.9 ± 0.03
<i>M·DomShr</i>	Discrete	Predominant shrub species	–	–	–	–
<i>M·DomPas</i>	Discrete	Type of predominant pasture	–	–	–	–

Mean values of continuous variables and their standard errors are shown for each study domain: the global domain of Doñana (DO) and partial domains of Abalario (AB), Coto del Rey (CR) and Biological Reserve (BR).

116 km² in CR, 163 km² in AB and 109 km² in BR. Sampling was concentrated between mid-July and mid-September, after the annual peak of maximum abundance following reproduction, and when the persistence of fecal pellets in the field is higher and abundance estimates from pellets are more reliable (Villafuerte et al. 1997; Palomares 2001a). The sample consisted of 750 plots (250 per area) identified using randomly generated UTM coordinates with a minimum spacing of 200 m and at least 100 m from the study area borders. Plots were located using a Global Positioning System (Garmin GPS III Pilot, Garmin Corp., Olathe, Kansas, USA). In each plot, pellets were counted in two 0.5 m² circles 5 m apart. Rabbit abundance was indexed as the sum of these two counts.

Description of scales and variables

A multiple-scale modeling approach was adopted to analyze relationships between patterns in rabbit abundance and the composition and configuration

of resources. This involved both study domains of different sizes and environmental variables measured at different scales. Rabbit abundance was modeled in four study domains: the whole study area of Doñana (referred to below as the global study domain model), and three sub-regions within this area (partial study domain models of CR, AB and BR, respectively). With respect to habitat metrics, variables were selected at three different spatial scales (Table 1): (1) the landscape context above the home-range scale, which included proximity and geographic location metrics potentially related to abundance regulation at the population level; (2) the structure of landscape mosaics at the home-range scale, related to resource availability for rabbit groups within home ranges; and (3) microhabitat attributes at a lower scale, related more closely to resource usage within home ranges (e.g. Johnson 1980).

At the landscape context scale, five variables were measured using a geographic information system (GIS). These were selected taking into account factors that may regulate rabbit populations

over broad areas, such as land use history, current human impact or exposure to different predators (Rogers and Myers 1979; Palomares et al. 1995; Fernández-Delgado 1997; Travaini et al. 1997). (1) Land cover divided into the three broad vegetation units that differ in land-use history: Shrubland, Pastureland and Pine forests. Plots were assigned to each of these units using 1:50,000 land cover maps (Moreira and Fernández-Palacios 1995). (2) Distance from the border of the marsh was also measured from this digital map. (3) Distance from lagoons of more than 1 ha (either seasonal or permanent) was calculated from 1:40,000 and 1:15,000 digital cartography (Montes et al. 1998; C. Montes et al., unpublished map; author, unpublished map). (4) Distance from urban areas, including towns and villages with a population of more than 100 (Instituto de Cartografía de Andalucía 1999). (5) Protection status was either National Park (more protected) or Natural Park (less protected).

At the home-range scale, landscape composition variables were measured within a circular area with a 100 m radius around rabbit sampling plots. This area is equivalent to the largest mean home-range size observed for a rabbit population in Doñana (= 3.0 ha; Villafuerte et al. 1994). Variables were selected depending on their potential association with essential rabbit resources at this scale, such as protective vegetation against predators, feeding pastures or exposure to warren flooding (Moreno and Villafuerte 1995; Lombardi et al. 2003; Palomares 2003). Eight variables were measured: (1) Mean cover of bushy vegetation, referring solely to the more sheltering tall shrubs and thickets (>1.5 m, mainly *Myrtus communis*, *Pistacia lentiscus*, *Erica* spp. and *Juniperus phoenicea*), whereas (2) mean shrub coverage referred to short shrubs (<1.5 m; *Halimium halimifolium*, *Ulex* spp., *Stauracanthus genistoides*, *Erica* spp., etc). Both variables were calculated using the formula $Hr\text{-veg} = \sum (A_{patch} * \delta_{veg}) / A_{hr}$, where $Hr\text{-veg}$ = mean cover of vegetation type veg; A_{patch} = patch area; δ_{veg} = index of patch cover density for veg, measured to the nearest 25%; and A_{hr} = 3 ha. (3) Mean pasture coverage was calculated similarly for grasses. (4) The proportion of landscape occupied by flooding patches included permanent and seasonal ponds and other occasionally flooded patches with hydrophilic vegetation. (5) The density of ecotones between shrubs and pastures was

calculated for edges between patches with shrub or pasture cover > 50%. (6) Dominant vegetation was introduced as a categorical variable providing information about the most abundant vegetation class in the circle and subdivided into ten classes: mature Mediterranean shrubland, xerophytic scrub formations, heaths and peat bogs, grassland, juniper formations of *Juniperus phoenicea*, eucalyptus plantations, pine forests, recent pine plantations, hydrophilic vegetation and seasonal pools, and bare soils. These patch classes were also used to calculate: (7) the number of vegetation types as a vegetation richness measure; and (8) a weighted fractal dimension index as a landscape pattern complexity measure. All these variables were estimated using a GIS and a digital vector map of the structure of vegetation, which was assembled from the interpretation of 1:15,000 color + infrared aerial photographs (see Fernández et al. 2003 for more details). This was a fine-grained map with 4874 vegetation polygons covering the study area, which had a minimum size of 0.05 ha and a mode of 2.5 ha.

At the microhabitat scale, six vegetation variables were measured *in situ* during the rabbit survey within a circular area of 25 m radii around sampling plots. These included the percentage of the area covered by (1) shrub vegetation, (2) bushy vegetation and (3) pastures, respectively; (4) mean shrub height; (5) dominant shrub species and (6) dominant pastures family (Asteraceae or Poaceae). Percentages were estimated visually to the nearest 10% by comparison with template drawings of known coverage, and heights to the nearest 0.1 m.

Most GIS routines and calculations were performed in ArcInfo 8.0 (ESRI, Inc., Redlands, CA, USA), except for proximity and fractal dimension metrics, which were calculated using two scripts in ArcView 3.1 (ESRI, Inc., Redlands, CA, USA): Nearest Features 3.5 (Jenness Enterprises, Flagstaff, AZ, USA) and Patch Analyst 2.2 (by R. Rempel, Lakehead University, Ontario, Canada).

Habitat modeling

The modeling approach was based on the specification *a priori* of an exploratory set of competing models, and their subsequent comparison to select a best approximating model explaining the abundance patterns observed. This best model

represented a compromise between data fitting and a low number of parameters in the model (Burnham and Anderson 1998).

The set of *a priori* exploratory models was specified under criteria of biological plausibility based on previous information on rabbit ecology. These models included habitat variables at three scales, combinations of two adjacent scales, and individual scales. Correlation among predictors was checked beforehand using Spearman's rank coefficient (ρ), and only non-correlated variables or those with weak correlation ($\rho < 0.4$) were included in the same models. The *a priori* models were identical for all study domains except for the inclusion of *Protection* in the global study domain and CR. A total of 140 *a priori* models were set for the global domain and CR, and 100 for AB and RB.

Next, the *a priori* models were fitted in the framework of generalized linear models (GLMs; McCullagh and Nelder 1989), using in each study domain a 2/3 random subset of the original sample (i.e. $n = 500$ for the global and $n = 167$ for each partial domain). The remaining 1/3 of the sample was reserved for model evaluation purposes (see below). GLMs were fitted using a negative binomial variance function, which is appropriate for skewed count data distributions, and a logarithmic link (White and Bennetts 1996). Some predictors were non-linearly related to rabbit abundance and these were modeled using parametric natural spline terms with 3 degrees of freedom (Chambers and Hastie 1993). GLMs were fitted using `glm.nb` function in MASS library for S-Plus V. 2000 Professional (Venables and Ripley 1997; MathSoft, Inc., Seattle, Washington, USA).

A bias-corrected Akaike's Information Criterion (AIC_c) was calculated for each fitted model, and the model with the lowest AIC_c was selected as the most parsimonious (Akaike 1973; Hurvich and Tsay 1991). A weighted AIC_c score index (w_i) was also calculated to estimate the uncertainty of actually selecting the best approximating model from the set under consideration (Burnham and Anderson 1998). Although only the best model was selected for latter predictions, a 'confidence set' of models with $w_i > 0.05$ (i.e. with a $> 5\%$ chance of being selected as the best approximating model) was explored as alternative pattern-hypotheses that could not be rejected. Model selection statistics were also compared with a null model including only the intercept.

Finally, model fit to rabbit abundance data was estimated using the Spearman's rank correlation coefficient (ρ_m) between the log-transformed numbers of pellets observed and model-predicted scores (e.g. Guisan and Zimmermann 2000).

Model evaluation

The capacity of best approximating model functions for predicting rabbit abundance was evaluated for the different study domains using the random subset of 1/3 of observations reserved for this purpose. For each partial sub-region, both the global model of Doñana and the specific sub-region model were evaluated using two coefficients. The Spearman correlation coefficient between observed abundance and model predictions was calculated first (ρ_t). This statistic provided a measure of the association between observed and predicted abundances over the continuous range of abundances. Secondly, each observation was assigned to categories of high and low rabbit abundance using an arbitrary cut-off at the 75% percentile of the pellet count sample ($= 33$ rabbit pellets m^{-1}). Then, an index of categorical coincidence between counts and model predictions was estimated using Cohen's *Kappa* (e.g. Manel et al. 2001). This index provided an estimation of model capacity for predicting a minority of locations with high relative rabbit abundance, useful for many management purposes.

Results

Rabbits showed widespread distribution in the study regions and only 6% of the plots surveyed had zero counts. Based on pellet counts, the mean relative rabbit abundance was 32.5 pellets $m^{-2} \pm 1.9$ SE in the entire Doñana study domain ($n = 750$), with a maximum of 465 pellets m^{-2} . CR showed the largest mean relative abundance (50.9 ± 4.5 pellets m^{-2} ; $n = 250$), followed by AB (26.9 ± 2.0 pellets m^{-2} ; $n = 250$) and BR (19.9 ± 2.4 pellets m^{-2} ; $n = 250$). Abundance distributions in all study domains were highly skewed towards low values, with only a few 'hot-spots' of higher rabbit abundance in several orders of magnitude (Figure 2).

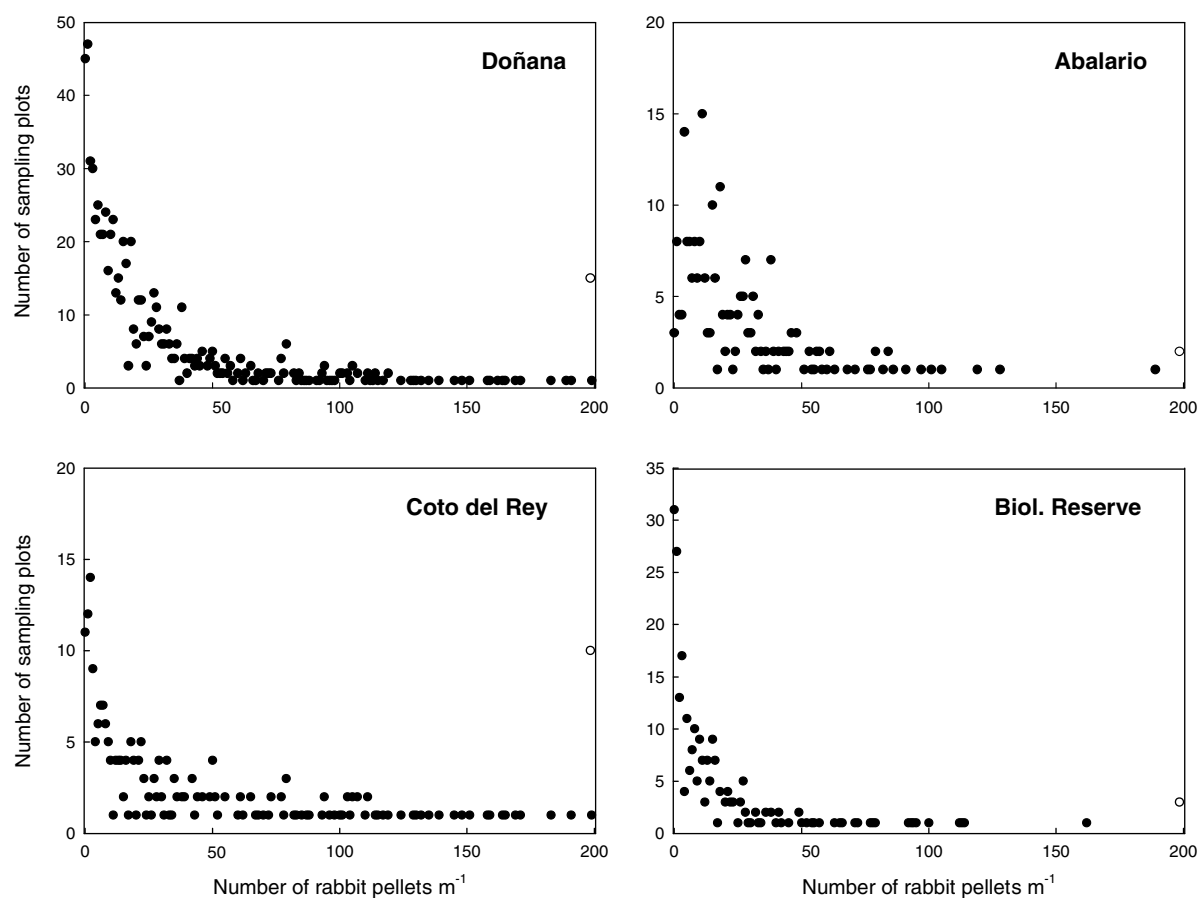


Figure 2. Frequency distributions of relative abundance of the European rabbit in four study domains, measured through pellet counts. Black dots represent frequencies of sampling plots with ≤ 200 pellets m^{-1} . White dots at $X = 200$ represent the number of plots with > 200 pellets m^{-1} in each study domain.

Global study domain model

Model selection results indicated that patterns in rabbit abundance were associated with habitat variables at all the spatial scales under consideration: the landscape context, home-range landscape composition and microhabitat. Protection status at the context scale, mean cover of shrubs at the scale of home ranges, and shrub and pasture cover at microhabitats were consistently present in three models, constituting a 95% confidence set on the best approximating one. In addition, the most parsimonious of these models (Table 2) included density of ecotones between shrub and pasture patches at the home-range scale. As shown in Figure 3, this model predicted higher rabbit density in locations within the less

protected Natural Park, regardless of other landscape and microhabitat characteristics. Rabbit abundance was positively associated with shrub cover, which provides shelter against predators, at both the home-range and the microhabitat scales. It was also associated with shrub interspersion with pastures providing food, which was reflected in the positive effect of shrub–pasture ecotones at the home-range scale and of pasture cover in microhabitats. The best approximating model showed a moderate correlation between observed and predicted pellet counts (Table 2), indicating an acceptable fit to the original data. Two alternative models constituting the confidence model set differed from the best in the inclusion of distance from ponds and lagoons as a predictor.

Table 2. Best approximating models for European rabbit abundance in Doñana, Spain.

Predictors	AIC _c	w _i	ρ _m
Doñana – global study domain			
Null model	–86311.6	<0.001	–
<i>L-Pro</i> , <i>ns(Hr-Shr)</i> , <i>Hr-Edge</i> , <i>S-Shr</i> , <i>S-Pas</i>	–86424.1	0.512	0.421**
Abalarío (AB)			
Null model	–28068.0	<0.001	–
<i>ns (L-DLag)</i> , <i>ns (Hr-Shr)</i> , <i>ns(M-Shr)</i> , <i>M-Pas</i>	–28126.4	0.373	0.528**
Coto del Rey (CR)			
Null model	–46116.5	<0.001	–
<i>L-DLag</i> , <i>ns(Hr-Shr)</i> , <i>Hr-Edge</i> , <i>M-Shr</i> , <i>M-Pas</i>	–46190.1	0.301	0.640**
Biological Reserve (BR)			
Null model	–18978.8	0.001	–
<i>Hr-Shr</i> , <i>M-Pas</i>	–18988.7	<0.175	0.126

Variable codes are from Table 1; *ns* before a code notates natural spline terms (*d.f.* = 3). For comparison purposes, Akaike's information criterion scores (AIC_c) from intercept-only null models are also presented. *w_i* informs on AIC weights, and *ρ_m* is the Spearman rank correlation coefficient between model predictions and the observed abundance. Dispersion parameters for the best models were as follows: Doñana: $\theta = 0.83 \pm 0.05$ SE; Abalarío: $\theta = 1.78 \pm 0.19$ SE; Coto Rey: $\theta = 0.92 \pm 0.09$ SE; Biological Reserve: $\theta = 0.55 \pm 0.06$ SE.

***p* < 0.001.

Partial study domain models

All the best approximating models for CR and AB confirmed that variables at three spatial scales influenced patterns in rabbit abundance (Table 2).

The best model for CR revealed a positive effect of distance to lagoons and streams on rabbit abundance. This result suggested that rabbits benefited from moister areas with a higher water table. Predictions at the home-range and micro-habitat scales were similar to the global domain model described above (Figure 3). Three other candidate models with a >5% chance of being selected differed from the former by either including the protection status, excluding the density of shrub–pasture ecotones, or both.

A similar best approximating model was obtained for AB, although some predictors were non-linearly related to rabbit abundance (Figure 3). In contrast to other study domains, the best model here did not include shrub–pasture

ecotones. These ecotones were scarcely present in the AB data set (5% of the sample), which impeded obtaining reliable parameter estimates for this variable. Overall *ρ_m* scores indicated good model fit to the original rabbit abundance data, particularly in the region of CR (Table 2).

Conversely, analyses in BR did not provide a satisfactory approximating model to identify patterns in rabbit abundance. Selection uncertainty was high and 37 models were needed to obtain a 95% confidence set on the best approximating one. In addition, output predictions from the best model correlated poorly with data on rabbit abundance used for model building (Table 2).

Model evaluation

The global domain model was found to be moderately accurate when confronted with independent evaluation data ($\rho_t = 0.417$; $p < 0.001$). However, this accuracy varied considerably among the three study regions. The global model satisfactorily predicted variations in rabbit abundance within CR, where correlation between predictions and independent data was $\rho_t = 0.655$; $p < 0.001$. This correlation was also significant in AB, albeit weaker ($\rho_t = 0.238$; $p = 0.015$). Conversely, predictions in BR were inaccurate ($\rho_t = 0.085$; $p = 0.504$). The evaluation of specific models for their corresponding partial domains produced similar results. Correlation in CR was $\rho_t = 0.601$; $p < 0.001$; in AB, $\rho_t = 0.259$; $p = 0.019$; and in BR, $\rho_t = 0.087$; $p = 0.42$.

Model accuracy for categorical predictions of abundance is best represented in Figure 4. As shown, the global domain model accurately classified both high-density and low-density plots from the evaluation sample in CR (Cohen's Kappa = 0.60). This accuracy tended to be less precise for high than low densities in AB (Kappa = 0.27), and the model was completely unable to predict high densities in BR (Kappa = 0.10). Accordingly, the overall accuracy for Doñana was influenced by lower rates of correct classification for high rabbit density locations (Kappa = 0.41). Cohen's Kappa scores derived from the application of partial study domains were similar to those reported for the global model (results not shown).

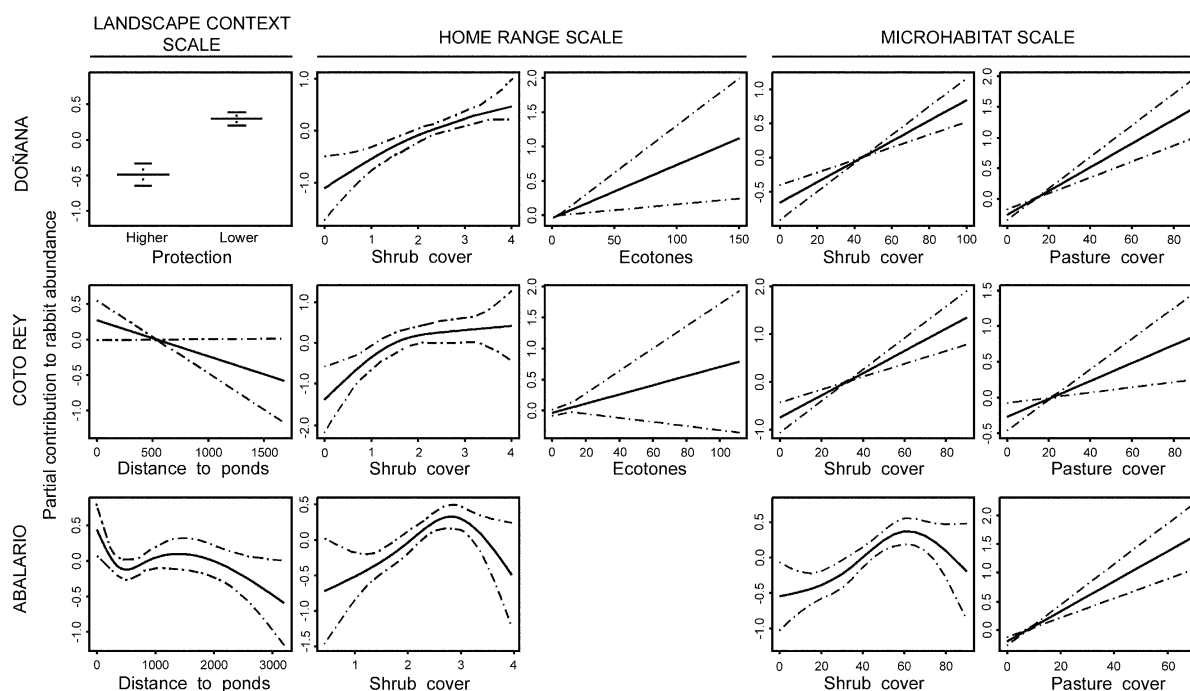


Figure 3. Best approximating GLMs of European rabbit abundance in relation to habitat heterogeneity in three study domains in Doñana, Spain. Solid lines represent the partial contribution of individual model variables to predicted abundance, and dashed lines are standard errors. Non-linear predictions were modeled using natural spline terms with three degrees of freedom.

Discussion

One key objective of this research was to assess the extent of association between spatial patterns in European rabbit abundance and environmental heterogeneity. Model selection results in two different regions of Doñana revealed high concordance among the attributes of the physical environment influencing rabbit abundance, helping to understand the species' habitat requirements at different spatial scales. Models based on landscape, habitat and microhabitat attributes largely explained spatial variations of rabbit abundance in the northern region of Coto del Rey, supporting the initial hypothesis. Moreover, these patterns were to a great extent predictable with new high-density locations being accurately predicted by the model in >80% of cases and low densities in >75%. A similar relationship between abundance patterns and environmental variation was observed in the western region of Abalarío, albeit with less accurate model predictions.

By contrast, habitat models did not help understand spatial variations in rabbit abundance

in the Biological Reserve, meaning the generalization of this approach for predictive purposes must be treated with a degree of caution. In this region, European rabbit declines have been particularly dramatic since the eruption of the RHD epidemic. Populations suffered two-thirds declines in abundance shortly after the outbreak of the disease a decade ago (Villafuerte et al. 1995), and the low abundance levels obtained in the present study indicate that this tendency continued later. The severity of the population collapse may well have caused sharp imbalances between spatial patterns in rabbit abundance and the configuration and abundance of resources; this is supported by evidence of associations between abundance and some landscape characteristics previous to the RHD outbreak (Rogers and Myers 1979). After the eruption of epidemics, the interactions between diseases and host populations can result in the spatial patterning of host densities not necessarily related to habitat heterogeneity, such as in the Biological Reserve, but rather to spatial mosaics of virulence and resistance (Thompson 1996). The existence of some

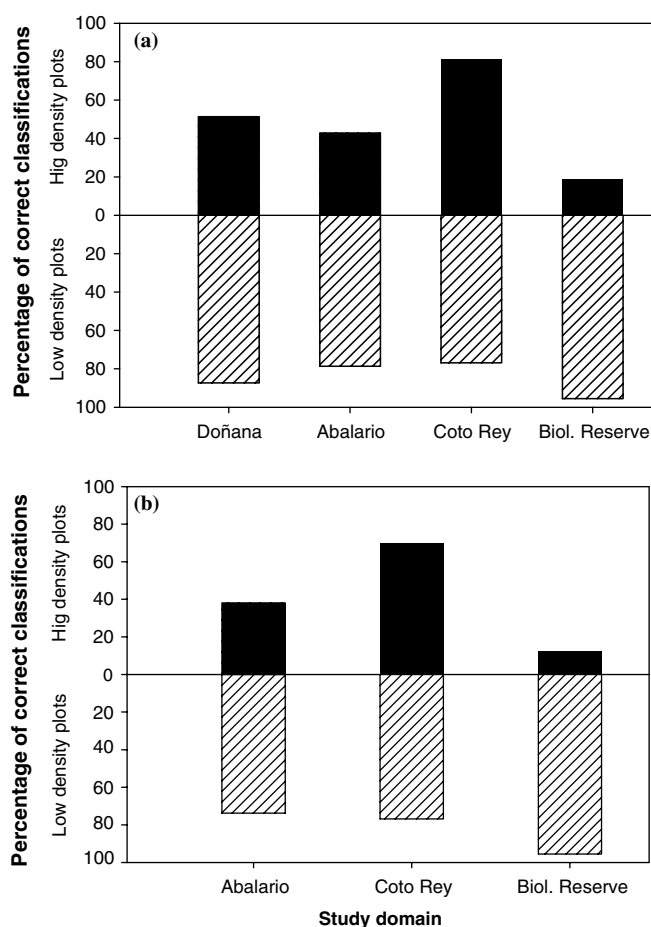


Figure 4. Predictive accuracy of the best GLMs on rabbit abundance, estimated using an independent evaluation sample. (a) represents the percentage of occasions in which the best model for the global study domain of Doñana correctly classified plots of high rabbit pellet density (≥ 33 pellets m^{-2}) and low density (< 33 pellets m^{-2}). Similarly, (b) represents correct prognoses from partial study domain models.

isolated hotspots of high rabbit abundance in the Biological Reserve is also consistent with the prediction that rabbits may locally overcome disease regulation (Calvete 1999), while viral prevalence and interaction with predators can largely prevent rabbit populations from recovering over larger areas, even in highly favorable habitats (Dwyer et al. 1990; Pech et al. 1992; Calvete 1999). Our understanding of spatial dynamics in European rabbit diseases is far from comprehensive (Fa et al. 2001; Cooke 2002), and both empirical evidence and spatially explicit epidemiological models are needed in order to better understand the relationships between abundance and environmental heterogeneity in the context of disease history and prevalence.

Habitat correlates of rabbit abundance

Combining variables at different spatial scales provided better approximating habitat models for identifying and predicting patterns in abundance: the best models for Doñana and two sub-regions consistently included habitat descriptors above, at and below the scale of home ranges. The issue of the spatial scale in regional studies of population abundance has sometimes been addressed as an 'either-or' decision of selecting the best scale to improve predictive model accuracy (Orrock et al. 2000). However, a combination of different scales in GLMs may improve predictions, as shown in the present study, and is more realistic in attempts to reflect patterns that are a product of species'

hierarchical responses to habitat heterogeneity (e.g. Kotliar and Wiens 1990; Mazerolle and Villard 1999).

The ecological significance of the resulting models is best explained by the capacity of landscapes to provide basic rabbit resources. Rabbits benefit from shorter distances from streams and lagoons, where water table levels are lower and green pastures endure longer during droughts. In Mediterranean environments, the maintenance of moist pastures during the dry season enhances rabbit productivity, given that reproduction is largely affected by the availability of moist grass high in protein (Villafuerte et al. 1997). The positive effect of ponds and lagoons on rabbit abundance was observed beyond the scale of home ranges. A similar pattern was observed by Palomares et al. (2001) for moist pastures bordering on the marsh in a smaller area of Doñana, which favored rabbit abundance up to 300 m apart within the shrubland. On the other hand, rabbit abundance was linearly correlated with the density of shrubland–pastureland ecotones and non-linearly with mean landscape shrub cover at the home-range scale. Shrub-dominated landscapes favor rabbit predator avoidance and diminish the risk of mortality (Lombardi et al. 2003), but this cover is also to the detriment of pastures to feed on (Moreno and Villafuerte 1995). Therefore, areas with interspersed patches of shrubland and pastureland provide a favorable combination of food and refuge, which is reflected in the broad-scale positive effects of ecotones on abundance. Rabbit association with shrub and pasture cover at the micro-habitat scale was largely consistent with findings at the home-range scale.

Implications for conservation

Spatial variation in European rabbit abundance greatly influences terrestrial communities in Mediterranean ecosystems as many vertebrate predators, including some highly endangered species, depend on this prey (e.g. Ferrer 1993; Palomares 2001b; Fernández et al. 2003). Nevertheless, the few existing studies evaluating methods to revive rabbit populations have mostly been performed at small spatial scales relative to predator spatial requirements (Moreno and Villafuerte 1995; Calvete et al. 1997; Letty et al. 2000). The present

study may provide useful guidelines for developing landscape-oriented management strategies for the recovery of rabbits over broader areas. For instance, vegetation should be managed to increase shrub–pasture interspersion at the scale of rabbit home ranges, and this strategy should involve large areas so that rabbit abundance can be influenced at the spatial scale required by predator populations. This is supported by local experiments that have demonstrated the effectiveness of small burnings within shrubland (a traditional management approach that has been abandoned in many areas) to increase pasture availability and rabbit abundance (Moreno and Villafuerte 1995). In addition, rabbit recovery efforts should be focused on landscapes close to lagoons and ponds with higher pasture growth.

However, this study also identifies potential difficulties that may arise in rabbit population management. The results indicate that in Doñana, a critically important area for conservation in southern Europe (Fernández-Delgado 1997), rabbits were less abundant in the strictly protected National Park than in the surroundings. This conservation paradox could be explained by the higher abundance of rabbit predators inside the park as a result of protection (Travaini et al. 1997). High predator density, particularly of generalist predators, is an important factor regulating rabbit populations at low densities (Pech et al. 1992; Palomares et al. 1995). Moreover, predators can greatly undermine rabbit recovery after epidemic-related population declines through low-prey-density stable equilibrium states and predation pit effects. Therefore, protection and landscape management may be insufficient for the recovery of rabbits in some situations of weak association between population abundance and landscape structure, particularly where other potential regulating factors may be involved.

Conclusion

The present study shows that, even for the same species in nearby regions with similar habitat characteristics, habitat models can properly predict broad-scale spatial variations in abundance in some areas, but may provide little insight in others. In the first case, models revealed their ability to provide information about landscape and

microhabitat attributes important for the abundance of the species. Resource availability may well underlie the relationship outlined in these models. In the second case, historical and dynamic population processes, which are difficult to incorporate into static habitat models, may have resulted in imbalances in the spatial relationships between rabbit abundance and habitat heterogeneity. Although the conservation of biodiversity in Mediterranean areas would benefit from broad-scale habitat analyses of rabbit abundance as presented here, further integrated research is needed to better understand the spatial effects of landscape structure, predators and epidemics on rabbit abundance. This is crucial to deriving solutions to current conservation problems stemming from rabbit population collapse in Mediterranean ecosystems.

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