Vegetation structure and prey abundance requirements of the Iberian lynx: implications for the design of reserves and corridors

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Summary

1. Habitat alteration and fragmentation are two of the greatest threats to biodiversity. The conservation of most species in highly encroached areas requires reserves that are connected by suitable habitat corridors to increase the effectiveness of the area under protection. However, the quality required for such corridors is still debated. This study investigated the habitat characteristics (vegetation structure and prey abundance) of sites used by resident and dispersing Iberian lynx in south-western Spain.

2. Vegetation structure and an index of rabbit abundance (the staple prey of lynx) were measured at sites used by radio-collared lynx in 1996 and 1997. Data from 128 plots used by resident lynx and 310 plots used by dispersing individuals were compared with data from 162 randomly located plots in sites considered to be unused by lynx.

3. Resident sites had a lower percentage of tree cover, shorter tree height, higher percentage of tall shrub cover, higher percentage of overall understorey and higher number of rabbit pellets than both dispersal and unused sites. The height of the short shrub layer was taller and the rabbit abundance index was higher in dispersing sites than in unused sites.

4. Gender did not affect habitat selection by lynx. During dispersal, lynx frequently (50% of cases) used vegetation patches narrower than 300 m. In these cases, sites used by lynx had higher understorey cover and taller shrub height than adjacent unused sites. The percentage of short shrub cover used by lynx increased with the length of time taken to disperse; this was the only variable that changed over time.

5. Range size of resident individuals declined significantly with the index of rabbit abundance but increased with the percentage of short shrub cover. Both variables were good predictors of range size.

6. The study shows that corridors connecting reserves do not have to be prime habitats; they can even support moderate habitat degradation due to human activity. This result has implications both for the conservation of existing corridors, and for the restoration of the many corridors between reserves that have been lost.

Key-words: dispersal, European rabbit, fragmentation, habitat selection, *Lynx pardinus*, Mediterranean scrubland, *Oryctolagus cuniculus*, resident areas.

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Introduction

Alteration and fragmentation of pristine habitats by human activities are two of the greatest threats to the maintenance of biodiversity (Diamond 1989; Myers 1994). Because of these modifications, well-conserved natural areas are rare and animal species have had either to adapt or, more frequently, to move to remnants of former natural areas. This situation is particularly pro-

nounced in western Europe, where there is a long history of human settlement (Fernández-Delgado 1997).

The preservation of biodiversity requires the protection of remaining fragmented natural areas. However, these areas are often small and, for example, there are only 19 nature reserves larger than 100 km^2 in Europe (Wallis de Vries 1995). To counter the effects of fragmentation, managers must consider enlarging or linking protected areas. Possible strategies include restoring surrounding semi-natural low-quality areas, setting aside former cultivated areas, and connecting reserves by effective corridors through which species can move freely

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(Meffe & Carroll 1994). Whether the areas used effectively as corridors must have the same characteristics as high-quality patches used by resident individuals is not known (Loney & Hobbs 1991; Harrison 1992), in spite of the important management considerations this has for practical conservation. For example, if corridors of human-modified low-quality habitats are suitable for species dispersal, then it would be possible to connect natural patches or reserves of high conservation value with low-quality habitats that can undergo controlled human exploitation.

Medium and large carnivorous mammals are some of the most suitable species to study the habitat requirements of resident and dispersing individuals (Noss *et al*. 1996), and hence to determine if habitats within corridors need to have the same characteristics as prime habitats. These mammals range over large areas and need a large enough area to ensure viability of their populations (Beier 1993). So, in highly fragmented landscapes, they need to move between suitable patches to ensure gene flow and recolonization after local extinctions (Gaona, Ferreras & Delibes 1998).

In this study, the characteristics of the areas used by resident and dispersing Iberian lynx *Lynx pardinus* Temminck in the Doñana region, Spain, an area highly modified by humans throughout history, were examined (Fernández-Delgado 1997). In Doñana, remnant patches of natural vegetation are interspersed across a landscape dominated by agriculture and forestry (Moreira & Fernández-Palacios 1995). Specifically, the roles of vegetation structure and prey abundance in habitats selected by both resident and dispersing radio-tracked Iberian lynx were studied. These data were compared with data from randomly selected sites that were probably never or rarely used by lynx, even though they had access to them (see the Methods for details). Whether the range size of resident lynx was correlated with any of the measured vegetation variables or with an index of rabbit abundance (the basic prey of lynx; Delibes 1980) was also examined, and whether dispersing lynx became more selective in their habitat choice when dispersal took a long time.

The Iberian lynx is a medium-sized carnivore, endemic to south-western Europe (Spain and Portugal; Delibes 1979), with probably less than 1100 individuals remaining (Rodríguez & Delibes 1992). Due to its low population level, it has been listed by the International Union for the Conservation of Nature as the most globally endangered felid species (Nowell & Jackson 1996). This cat is specific to Mediterranean scrubland (Palomares *et al*. 1991, 1998; Palma, Beja & Rodrigues 1999) and in the Doñana area it survives in a metapopulation where dispersal is vital for its persistence (Gaona, Ferreras & Delibes 1998).

Methods

STUDY AREA

Surveys of vegetation structure and rabbit abundance were conducted in the Doñana area (approximately 3500 km²). This area is bordered to the south and west by the Atlantic Ocean, to the east by the Guadalquivir River, and to the north by the foothills of the Sierra Morena. It is a flat region predominately composed of sandy soils of aeolian deposits of marine origin with marshland to the east. The landscape is highly fragmented with a diversity of vegetation types. Forty-nine per cent of the area is cropland. Vegetation in the remaining area is a mixture of Mediterranean shrubs dominated by *Halimium* sp., *Cistus* sp. and *Pistacia lentiscus* L., plantations of pines *Pinus pinea* L. and eucalyptus *Eucalyptus* sp., and areas of pastureland. The south-easternmost part of the study area is protected by the Doñana National Park (550 km²). Inside the National Park a dune system borders the Atlantic Ocean. Lynx used in this study were captured in Coto del Rey, one of the lynx subpopulations found within the Park (for details see Palomares *et al*. 1991).

The climate is Mediterranean subhumid, with mild rainy winters and dry hot summers. More information on the Doñana region, the Doñana National Park and the lynx subpopulation that was the focus of this study can be found in Palomares *et al*. (1991, 1996b) and Ferreras *et al*. (1997).

RADIO-TELEMETRY AND SELECTION OF STUDY AREA

Thirteen radio-tagged lynx, captured with box-traps and padded foothold traps between autumn/winter 1995 and winter 1997, were used to select the sites used by dispersing and resident lynx. On first capture, nine lynx were young (< 12 months old on 1 April), three were subadults (12–24 months old) and one an adult (> 24 months old). All lynx except the adult, which was dispersing, were living in their natal ranges when captured.

Resident lynx were ground-located usually between two and four times a week, while dispersing individuals were located daily. Spatial position of the animals was determined mainly by walking to (homing) the actual position (73% of times), or from two signal bearings, usually < 500 m from the animal, to decrease triangulation error. During homing, a global positioning system (GPS; model Garmin 75, Garmin Corp., Olathe, Kansas, USA) was used to record lynx positions. About 60% of locations were determined in daylight, the remainder at night or twilight. GPS error was estimated at < 50 m in 72% of the recordings, and < 100 m in 97% (E. Revilla & F. Palomares, unpublished data).

Lynx were considered resident if (i) they had not left the subpopulation where they were born (*n* = 11) or (ii) they had already settled after dispersal (*n* = 4). Lynx were considered dispersing if they had left the sub-population where they were born for > 1 week and up to the time at which they became residents. The end of dispersal was identified by operationally measuring site fidelity in short time intervals (Palomares *et al*. 2000).

Characteristics (i.e. vegetation structure and rabbit abundance) of sites both used and unused by lynx were surveyed in September/October 1996 and 1997 (autumn surveys). Between January 1996 and October 1997 a survey was also conducted once a week on the same day or on the day after a lynx was radio-located (simultaneous surveys). This ensured sampling confidence about actual used sites for every radio-located lynx during this period.

A total of 438 plots was sampled in areas used by lynx: 128 and 310 plots where 11 resident and 10 dispersing lynx had been radio-located, respectively. Autumn surveys were undertaken in 132 plots in 1996 and 183 in 1997. Autumn surveys were undertaken at least 15 days after a lynx had been located. The remaining 123 plots consisted of simultaneous surveys.

Sites for the autumn surveys were selected randomly from a database of all available radio-locations taken between January 1995 and 15 August 1996 ($n = 1008$) for the 1996 survey, and September 1996 and 15 August 1997 ($n = 900$) for the 1997 survey. Sites sampled in 1997 had not been sampled in 1996. Sites within resident areas were selected from home ranges (hereafter ranges) of mothers of pre-dispersing juveniles ($n = 3$ ranges) or within home ranges of post-dispersing individuals ($n = 2$ ranges). Ranges were delineated by the minimum convex polygon method (excluding 10% of locations), using the Ranges software package (Kenward & Hodder 1996). Simultaneous surveys were carried out once a week between January 1996 and October 1997, provided that animals allowed the observer to approach within 20–30 m of their actual position without fleeing.

Lynx were frequently located in the same areas. Thus, to avoid repeating surveys, all sites selected were at least 400 m away from the centre of any surveyed plot. This also ensured no overlap with the rabbit pellet plots.

Unused sites were randomly selected within a buffer zone between 400 m and 1500 m away from any known lynx location. Habitats within this zone could potentially be selected by lynx (lynx rarely go further than 1500 m into unsuitable habitats; Ferreras 1994). So the zone maximized the possibility of surveying unused sites that might be used, while guarding against overlaps between sites known to be used. In determining the above buffer zone, all lynx locations taken during this study ($n = 1908$) and > 21 000 locations of 66 individuals taken throughout the last 15 years in the Doñana area were taken into account. This large data set increased confidence in the assumption that unused areas had really not been used. A total of 162 plots (83 in 1996 and 79 in 1997) was surveyed as unused sites. Plots sampled in 1997 were different from those sampled in 1996. Unused sites were located in the field using GPS.

Survey plots for both used and unused sites were always within scrubland or forested habitats. Previous analyses on habitat use of dispersing and resident lynx have shown that crops and open habitats are always avoided (Palomares *et al.* 2000). Therefore, surveys were restricted to potentially used habitats to determine

further the specific characteristics of used and non-used sites.

VEGETATION STRUCTURE AND RABBIT ABUNDANCE

Seven vegetation variables were measured on 100-m diameter plots at each selected site: tree height, percentage of tree cover, tall shrub height, percentage of tall shrub cover, short shrub height, percentage of short shrub cover, and percentage of understorey cover (i.e. tall and short shrub cover combined). The shrub species formed two clearly defined layers according to their growth potential. So, the tall shrub layer included species such as *Pistacia lentiscus*, which reached between 2·5 and 4 m, whereas other species, such as *Halimium halimifolium* L., only reached 1·5 m. In some plots there were small trees structurally more similar to tall shrubs (usually < 15 cm diameter at chest height with stems close to the ground) that were considered as components of the tall shrub layer. Heights were measured to the nearest 0·5 m for trees and 0·1 m for shrubs or plants considered to represent the most common height of each layer. Percentage cover was estimated visually to the nearest 5% aided by drawings of plots with known percentages of cover.

In autumn surveys, variables were measured over the entire surface area of the plots. In simultaneous surveys, measurements were only taken from the actual vegetation patches where animals were found, taking into account situations where (i) animals were inside or close to the edge of homogeneous vegetation patches larger than 300 m in any of their main axes, and (ii) animals were inside homogeneous vegetation patches where one or two of the main axes were shorter than 300 m. Figure 1 shows which areas of the plot were measured in each case. When lynx were in patches with one or both of their main axes shorter than 300 m, the same vegetation measurements were recorded for another 100-m diameter plot, 100 m away from the edge of the patch where the lynx was located. Thus, it was possible to check lynx preferences on a small scale by comparing the characteristics of habitat patches where lynx were with the surrounding habitat conditions. Three hundred metres were chosen for axes because larger distances were logistically difficult to estimate in the field. The position of the extra plot was randomly chosen from any of the four cardinal directions, when the patch was shorter than 300 m for both axes, or any of the two perpendicular directions to the longest patch axis when only one of the two axes was shorter than 300 m (Fig. 1). A patch was considered as different from the surrounding habitat when the overstorey, understorey or both were different.

Abundance of rabbits was indexed by counting faecal pellets in 40-cm diameter subplots. Previous studies have shown that rabbit pellets may be an acceptable indicator of rabbit abundance in Doñana for large-scale surveys (Palomares, in press). For each site used by
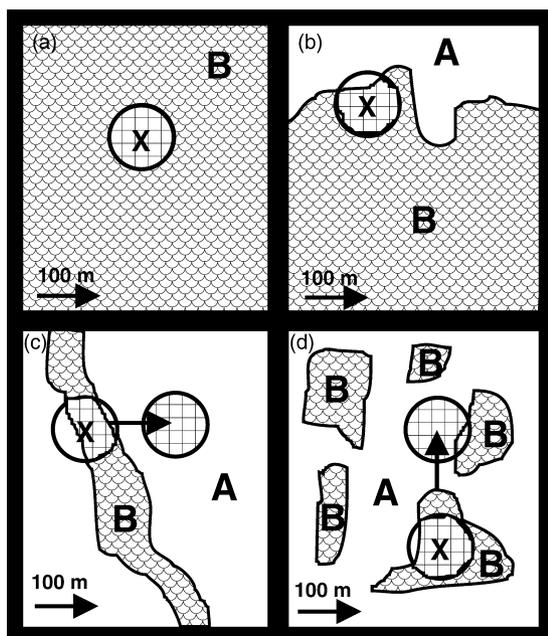
Fig. 1. Four different cases encountered during simultaneous surveys of vegetation structure: (a) lynx (cross on figure) was located within a large patch of a given homogeneous habitat type (A and B are habitat types); (b) lynx is within a large patch of habitat but close to the edge of another habitat type; (c) lynx is within a patch longer than 300 m but narrower than 300 m; (d) lynx is within an irregular habitat patch shorter than 300 m in its two main axes. Circles are 100 m in diameter and the squared areas indicate where vegetation structure was surveyed in each case. In cases (a) and (b) no other surveys of vegetation structure were conducted. In cases (c) and (d) other randomly chosen plots were surveyed to within 100 m from the edge of the patch where lynx were located.

lynx, pellets were counted in nine subplots distributed as follows: one on the supposed lynx position, and another situated at points north, south, east and west of this central subplot at distances of 50 and 100 m. Therefore, the area covered was an imaginary circle of 200 m diameter, which maximized the possibility of detecting good rabbit patches because it accounted for their uneven distribution patterns (Rogers & Myers 1979; Soriguer & Rogers 1981; Palomares, Calzada & Revilla 1996a).

Rabbit abundance fluctuates widely throughout the year (Soriguer 1981; Beltrán 1991). Therefore, all rabbit pellet counts were carried out during autumn to standardize results.

DATA ANALYSIS

Differences in vegetation structure and the index of rabbit abundance (average and maximum number of pellets) in unused sites, sites used during dispersal, and sites used by resident individuals were tested by nested univariate analyses of variance (ANOVA). To test for overall differences in the characteristics of these sites, it would have been more appropriate to perform a multivariate analysis of variance (MANOVA) in which all

dependent variables would be included in a single analysis (Scheiner 1993). However, height variables of the different vegetation layers could not be recorded in all plots because on some occasions one or more layers were absent. This would have reduced the sample size from 600 to 330 and would have greatly reduced the power of the MANOVA. Instead, ANOVAs were used with a standard Bonferroni correction to set the probability level at which an effect was deemed to be statistically significant (Scheiner 1993). There was a further problem with the ANOVAs. Data on sites used by lynx came from areas used by different individuals, many of them living on the same ranges as residents. To avoid pseudoreplication, individuals were considered as the sampling unit for the data on dispersing lynx. This, however, was not a solution for resident lynx because sometimes more than one individual lived in the same range. In this case, the range was considered to be the sampling unit. Because different sample sizes were available for each individual/range, an unbalanced nested ANOVA with a random statement was performed. The individual/range variable was nested within the type of site. When overall differences were found for any variable, pairwise differences between types of sites were tested by least squares means.

As stated, some of the vegetation layers and rabbit pellets were occasionally absent in the sampled plots, so chi-square tests were used to determine if there were differences between types of sites in the number of surveys without the presence of any particular layer or pellets.

Differences in vegetation structure between autumn and simultaneous surveys were tested with two-way ANOVAs and standard Bonferroni corrections where the independent variables were the type of site (dispersal and resident) and the type of survey. However, differences between used and unused sites when dispersing lynx were in patches smaller than 300 m in either of their two axes were tested using paired *t*-tests and standard Bonferroni corrections.

The effect of gender was tested by ANOVAs with standard Bonferroni corrections in a model considering three independent variables: type of site (dispersal and resident), gender, and individual/range nested within the two previous variables.

The effect of the length of time since the start of dispersal on characteristics of the sites used by dispersing lynx was tested by analysis of covariance (ANCOVA) with standard Bonferroni corrections. The independent variables were individuals and days since the start of dispersal (the covariate). Finally, Pearson product moment correlations and standard linear regressions were used to examine the effect of vegetation structure and rabbit abundance on range size (estimated as minimum convex polygon areas excluding 10% of locations). At least 59 independent locations (i.e. separated by at least 24-h) were used to estimate range sizes using radio-tracking data from the three mothers of pre-dispersing individuals, and from dispersing individuals

Table 1. Vegetation structure and rabbit abundance within home ranges of resident lynx (*n* = 5 ranges), during dispersal phase (*n* = 9 lynx) and in unused sites (*n* = 162 plots). Both autumn and simultaneous surveys were used for dispersal and resident individuals. Asterisks indicate cases where significant differences were found once the Bonferroni correction was applied

Variable	Mean ± SE			Univariate analysis of variance		
	Non-used sites (1)	Dispersal (2)	Resident (3)	*F*-value	*P*-value	Significant pairwise comparisons (*P* < 0·05)
Percentage tree cover	39·1 ± 1·98	31·9 ± 3·35	14·2 ± 4·45	38·56	< 0·0001*	1–3, 2–3
Tree height (m)	9·8 ± 0·40	10·5 ± 1·32	6·8 ± 0·88	7·86	0·0004*	1–3, 2–3
Percentage tall shrub cover	10·1 ± 1·36	13·4 ± 1·16	20·4 ± 3·52	17·69	< 0·0001*	1–3, 2–3
Tall shrub height (m)	2·1 ± 0·07	2·2 ± 0·10	2·5 ± 0·14	0·75	0·4721	–
Percentage short shrub cover	28·0 ± 1·72	31·7 ± 5·26	35·4 ± 9·48	1·21	0·2983	–
Short shrub height (m)	0·8 ± 0·03	1·0 ± 0·06	1·0 ± 0·06	11·60	< 0·0001*	1–2, 1–3
Percentage overall understorey cover	38·1 ± 2·05	45·2 ± 6·06	55·8 ± 7·10	11·95	< 0·0001*	1–3, 2–3
Average rabbits (pellets m^{-2})	31·6 ± 3·31	35·3 ± 3·85	79·7 ± 14·69	26·28	< 0·0001*	1–2, 1–3, 2–3
Maximum rabbits (pellets m^{-2})	87·5 ± 7·68	122·3 ± 12·69	243·0 ± 37·64	20·47	< 0·0001*	1–2, 1–3, 2–3

that settled. In the latter case, four lynx (one female and three males) settled in two different areas (two on each). However, data were used only for the female in one of the ranges, and the two males in the second range. Because lynx male ranges tend to be larger than female ranges, in the case where there was only information for two males, female range size was inferred by multiplying male range (i.e. the average range size of the two radio-tracked males) by the ratio female/male ranges found for 17 adult resident lynx in Doñana area through the last 15 years of study (Ferreras *et al*. 1997; Palomares, in press).

SAS (SAS Institute Inc. 1990a, 1990b) and Sigma-Stat® (Jandel Scientific Software 1995) software packages were used for statistical analyses, and significant differences were considered if $P \leq 0·05$, except for Bonferroni corrections where a conservative judgement was taken: *P* equalled $0·05/2 \times k$, where *k* was the number of dependent variables considered (Byers & Steinhorst 1984). To normalize data, all variables were transformed as the arcsine of the square root for percentages, or log-transformed for heights, number of pellets, range size and number of days since beginning of dispersal.

Results

A total of 128 plots (1152 subplots for rabbit pellets) was surveyed within lynx territories. The number of plots surveyed for each of five lynx territories was between 19 and 42. These five lynx territories were used by 11 different non-dispersing individuals (six males and five females), which resulted in a sample size of between two and 32 plots. During dispersal, 310 plots (2790 subplots for rabbit pellets) were surveyed corresponding to 10 different lynx (six males and four females). The numbers of plots surveyed for these 10 lynx were one for one individual, between seven and 12 for five lynx, between 26 and 41 for three lynx, and 163 for one lynx. The plot of the lynx sampled only once during dispersal was not used in further analyses.

DIFFERENCES IN VEGETATION STRUCTURE BETWEEN TYPES OF SITES

Vegetation structure was different between unused, dispersal and resident sites (autumn and simultaneous surveys combined; Table 1). No significant differences between sites were detected for tall shrub height (range 2·1–2·5 m) and percentage of short shrub cover (28·0–35·4%). Between-site comparisons showed that resident areas were significantly different from both unused and dispersal sites for percentage of tree cover, tree height, percentage of tall shrub cover and percentage of overall understorey cover (Table 1). The only vegetation structure variable that differed between unused and dispersal sites was the height of the short shrub layer, which was the same for dispersal and resident sites (Table 1). Resident sites had, on average, lower tree cover, shorter trees, higher percentage of understorey cover, and slightly taller shrubs, than dispersal and unused sites (Table 1). Values for all vegetation variables for dispersal sites were between those values of resident and unused sites (Table 1). This was also the case for survey plots that did not have these vegetation layers (Fig. 2). In resident sites there were more plots without trees and fewer plots without a shrub layer than in unused sites. In dispersal sites, there were more plots without trees than in resident sites (although the difference was not significant), but the number of plots without shrubs was higher (Fig. 2).

Gender did not affect results (all *F*s < 4·2, all *P*s > 0·04; the Bonferroni corrections advises a threshold *P*-value of > 0·0031).

Simultaneous surveys of vegetation structure were carried out 123 times. Autumn surveys numbered 256. The two-way ANOVA found significant differences only between both types of surveys for tree and short shrub height. Mean tree heights of dispersal and resident sites were 10·0 ± 0·43 m (*n* = 174) and 7·3 ± 0·78 m (*n* = 34) during the autumn, and 6·8 ± 0·44 m (*n* = 81) and 6·6 ± 0·85 m (*n* = 24) for simultaneous surveys. Mean short shrub heights were 0·9 ± 0·02 m (*n* = 208) and
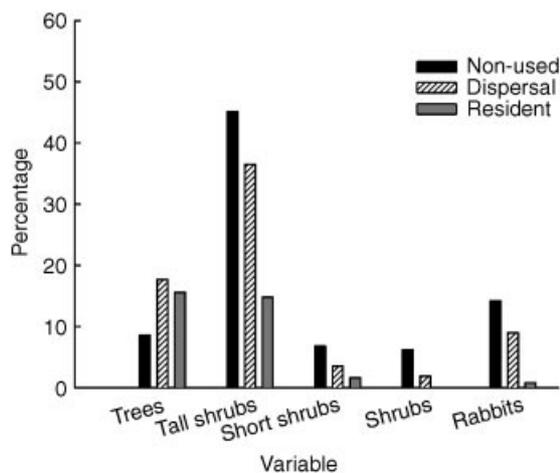
Fig. 2. Percentage of occasions in which trees, tall shrub layer, short shrub layer, any shrub layer, and rabbit pellets were not found within the plots sampled in ranges of resident lynx (*n* = 128 plots), dispersal sites (*n* = 310 plots) and in unused sites (*n* = 162 plots). Results of chi-square tests to analyse significant differences between categories of use, and among each pair of categories of use (significance is presented for the pair groupings of unused/dispersal sites, unused/resident sites, and dispersal/resident sites, respectively; NS = not significant, *$P < 0.05$) are as follows. Trees: $\chi^2 = 7.1$, d.f. = 2, $P = 0.029$, *, NS, NS; tall shrubs: $\chi^2 = 30.5$, d.f. = 2, $P < 0.001$, NS, *, *; short shrubs: $\chi^2 = 5.4$, d.f. = 2, $P = 0.066$; shrubs: $\chi^2 = 11.8$, d.f. = 2, $P = 0.003$, *, *, NS; rabbits: $\chi^2 = 16.4$, d.f. = 2, $P < 0.001$, NS, *, *. Chi-square tests between pairs were not performed for short shrubs because significant overall differences were not found.

1.1 ± 0.07 m (*n* = 38) for autumn dispersal and resident sites, and 1.1 ± 0.04 m (*n* = 91) and 1.3 ± 0.06 m (*n* = 31) for the simultaneous surveys.

In 96 simultaneous surveys of dispersing lynx, six individuals were located a total of 48 times within patches that had at least one of their main two axes shorter than 300 m (i.e. 50% of times). In these cases, vegetation structure was also sampled at random points. Sites used by dispersing lynx had a higher percentage of shrub cover and taller shrub height (mainly of the short shrub layer; Table 2). Tree cover or tree height was not significantly different between used and unused sites (Table 2).

DIFFERENCES IN THE INDEX OF RABBIT ABUNDANCE BETWEEN TYPES OF SITES
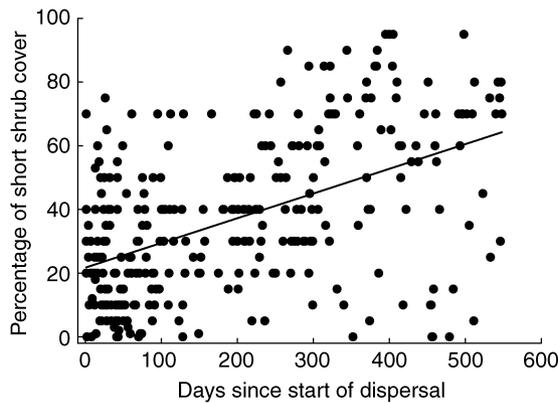
Both the mean number and maximum number of rabbit pellets were different between unused, dispersal and resident sites (Table 1). Differences between types of sites were statistically significant for all pairwise comparisons (Table 1). Numbers of pellets in resident sites were 2·0–2·3 and 2·5–2·8 times higher than in dispersal and unused sites, respectively. Numbers of pellets in dispersal sites were only between 1·1 and 1·4 times higher than in unused sites, although differences were statistically significant (Table 1). Only in one resident plot was no rabbit pellets found (*n* = 128), whereas the number of plots without pellets was considerably higher for both unused and dispersal sites (Fig. 2). Number of rabbit pellets was not statistically different in plots used by male and female lynx for either average number of pellets ($F = 1.62$, d.f. = 1, $P = 0.3529$) or maximum number of pellets ($F = 0.77$, d.f. = 1, $P = 0.3799$).

DISPERSAL SPAN AND CHARACTERISTICS OF THE SITES USED

ANCOVA showed that the only characteristic that clearly varied through the dispersal period was the percentage of short shrub cover ($F = 9.21$, d.f. = 9, $P < 0.0001$ for the model, and $F = 13.74$, d.f. = 1, $P = 0.0003$ for the covariate). This variable tended to increase with the number of days of dispersal (Fig. 3). For none of the remaining variables was *P* lower than the threshold of 0·0031.

SIZE AND CHARACTERISTICS OF RANGES

For the five ranges measured, range size was significantly and negatively correlated with the mean number of rabbit pellets ($r = -0.995$, $P = 0.0004$) and positively correlated with the mean percentage of short shrub cover ($r = 0.994$, $P = 0.0005$) and the average percentage of understorey cover ($r = 0.959$, $P = 0.0098$). Range size was not significantly correlated with any of the remaining variables (all *P*s > 0·0772). Of particular

Table 2. Differences in vegetation structure between sites where dispersing lynx were located and unused sites when animals were in vegetation patches smaller than 300 m in any of their main two axes. For height variables, only plots where the layer was present were considered. Asterisks indicate cases where significant differences were found once the Bonferroni correction was applied

				t-tests		
Variable	*n*	Used sites (mean ± SE)	Random sites (mean ± SE)	*t*-value	d.f.	*P*-value
Percentage tree cover	48	33·8 ± 3·47	30·8 ± 3·42	0·83	94	0·4079
Tree height (m)	40	9·7 ± 0·65	9·3 ± 0·72	0·70	83	0·4802
Percentage tall shrub cover	48	21·1 ± 3·51	6·4 ± 1·93	3·73	94	0·0003*
Tall shrub height (m)	27	2·35 ± 0·13	2·1 ± 0·18	1·51	59	0·1353
Percentage short shrub cover	48	30·7 ± 3·75	17·6 ± 2·86	2·75	94	0·0071
Short shrub height (m)	42	1·1 ± 0·06	0·8 ± 0·06	3·06	84	0·0028*
Percentage overall understorey cover	48	51·8 ± 4·62	24·0 ± 3·34	4·21	94	< 0·0001*

Fig. 3. Percentage of the short shrub cover in the sites used by lynx during dispersal in relation to time since the beginning of dispersal. The line indicates the trend.

Fig. 4. Relationship between range size and (a) number of rabbit pellets ($y = 5\cdot72 - 1\cdot61x$, Adj $R^2 = 0\cdot986$, $F = 288$, $P = 0\cdot0004$) and (b) percentage of short shrub cover ($y = 2\cdot17 + 0\cdot03x$, Adj $R^2 = 0\cdot985$, $F = 266$, $P = 0\cdot0005$).

interest was the negative correlation found between range size and percentage of tall shrub cover ($r = -0\cdot779$), when the former was positively correlated with percentage of short shrub cover. The correlation between number of rabbit pellets and the percentage of tall shrub cover was positive ($r = 0\cdot764$, $P = 0\cdot133$) but negative for short shrub cover ($r = -0\cdot979$, $P = 0\cdot0036$). These results suggest that the height of the shrub layer has an effect on rabbits (they favour tall shrubs but avoid high cover in short shrubs) and therefore size of lynx range (see below).

The size of the lynx ranges could be predicted from data on the number of rabbit pellets (Fig. 4a) and percentage of short shrub cover (Fig. 4b). This result was expected as both independent variables were highly correlated ($r = -0\cdot979$, $P = 0\cdot0036$, $n = 5$). There was one point on Fig. 4 that seemed to be influencing the results of both correlations (Cook's distances > 5·8), therefore the regressions were run again to check for the influence of this point. The significance and the predictive value of the relationship remained unchanged in both cases once the influencing point had been removed ($F > 26$, $P < 0\cdot02$, Adj $R^2 > 89\%$). To test further for any multiple effect of the variables measured on range size, a forward stepwise regression was performed where three variables (average number of rabbit pellets, percentage of tree cover, and percentage of tall shrub cover) were entered if $F = 4\cdot0$. Only the first two variables entered into the model, which was significant ($F = 411$, $P = 0\cdot002$) and accounted for most of the variation in range size (Adj $R^2 = 0\cdot995$). However, whereas the number of rabbit pellets explained 99% of variation in range size, percentage of tree cover only explained the remaining 1%. Similar results were obtained when the average number of rabbit pellets was replaced in the stepwise regression by percentage of short shrub cover ($F = 266$, $P < 0\cdot0001$, Adj $R^2 = 0\cdot985$). The only difference was that percentage of tree cover did not enter the model in this case ($F = 3\cdot09$). Therefore, either the number of rabbit pellets or the percentage of short shrub cover was an adequate predictor of range size.
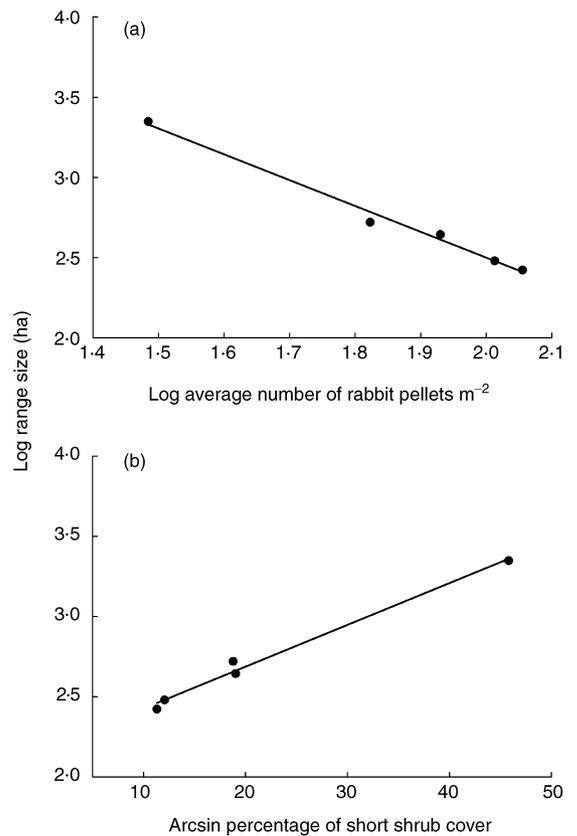
Discussion

HABITAT SELECTION BY IBERIAN LYNX

Vegetation structure and the index of prey abundance in sites used by dispersing and resident lynx and sites that were probably not used by lynx were compared. The results are valid only if a high degree of confidence exists in the classification of these areas. However, GPS, with an expected mean error of 50 m, was used both to record lynx positions and to relocate points during the autumn surveys. So error could not be avoided. Surveys had to be carried out in autumn to standardize results, mainly for the index of rabbit abundance. Nevertheless, to control for any potential error associated with lynx positions, simultaneous surveys were also undertaken during the same day, or the following day after, a lynx was located. In these cases, the exact location of the animal was surveyed. Comparison of the results obtained on vegetation structure during the autumn and simultaneous surveys indicated that only tree and short shrub layer heights were significantly different, which suggests that, in general, results obtained during autumn sampling were also representative of the areas used by lynx. In addition, there was a distance of 200 m between the furthest 40-cm diameter subplots surveyed for rabbit pellets for each point, thus pellets were counted at actual locations of lynx. Differences in tree height

between autumn and simultaneous surveys cannot be clearly accounted for. However, the taller shrub heights recorded during the simultaneous surveys may be a result of the timing of surveys during daylight when lynx are expected to be resting (Beltrán & Delibes 1994) and therefore favouring sites with slightly more protection and cover.

It is reasonable to assume that the sites considered as unused had been determined accurately as a large data set of lynx locations collected over 15 years exists for the study area. The GPS error should not affect results because the sites were at least 400 m from any known lynx location.

One clear fact emerged regarding the characteristics of the habitats used by lynx: sites used by resident lynx were very different from sites used during dispersal and from unused sites. However, there was little difference between sites used during dispersal and unused sites, even though unused sites were within scrubland and plantation habitats (i.e. habitats potentially suitable for lynx). Sites used by resident individuals had less tree cover, shorter trees, higher percentage of understorey cover, taller shrubs and higher rabbit abundance. A lower percentage of tree cover and higher of understorey vegetation cover were expected because lynx prefer areas of Mediterranean scrubland in their home ranges (Palomares *et al.* 2000). Trees were shorter because the species in resident areas were predominantly *Quercus* sp. and *Olea europaea* L. as opposed to the taller pines and eucalyptus. As expected, more rabbit pellets were found in resident areas because rabbits thrive best in Mediterranean scrubland in Doñana (Palomares, Calzada & Revilla 1996a). Rabbits are the main prey of lynx (Delibes 1980) and, therefore, they are vital for the survival of resident lynx. Conversely, during dispersal lynx can cope with lower rabbit densities. Results also showed that rabbits were more evenly distributed in resident areas than in dispersal areas. Rabbit pellets were only absent in one resident plot, whereas about 10% of dispersal plots had no pellets. Although the number of plots without pellets was higher for unused sites, differences were not significant, indicating that, in general, rabbit abundance was not much higher in dispersal sites than in unused sites. Height of short shrub layer was the only other variable of vegetation structure that differed between dispersal and unused sites, suggesting that lynx look for sites that provide higher protection while dispersing.

Simultaneous surveys can provide good insights into the characteristics of the areas used by dispersing lynx during rest. On half of the occasions, lynx used small vegetation patches (one or two axes shorter than 300 m) within a varied habitat mosaic characterized by higher cover and taller shrubs than that recorded in unused sites. This result clearly suggested the necessity of patches of vegetation with high understorey cover for resting. This necessity is further influenced by that fact that dispersing lynx must move through habitats with a high human presence, carrying a high risk of mortality (Ferreras *et al.* 1992).

Dispersing lynx increased their use of sites with a higher percentage of shrub cover the longer dispersal lasted. This result suggests that, after an exploratory phase, lynx concentrate on the more suitable areas where they try to acquire territory.

Vegetation structure and prey abundance clearly affected range size. Sandell (1989) predicted that female range size should correlate negatively with food abundance in solitary carnivores. However, empirical data are scarce on the subject, and only in a few cases could the relationship be verified with relative accuracy (Ward & Krebs 1985; Litvaitis, Sherburne & Bissonette 1986; White & Garrott 1997). In Iberian lynx, territories with more rabbits and lower shrub cover were smaller. Both variables were a measure of range quality. However, it was not clear which variable best explained range size because a high negative correlation was found between shrub cover and the index of rabbit abundance. As stated, rabbits thrive best in habitats adjacent to patches of shrub and grassland, or on the edge of shrubland and grassland habitats (Rogers & Myers 1979; Rogers 1981; Soriguer & Rogers 1981; Beltrán 1991; Palomares, Calzada & Revilla 1996a; Palomares & Delibes 1997). Thus, one variable is clearly dependent on the other. However, it was interesting to find a positive correlation between tall shrub cover and the index of rabbit abundance, and a negative one with short shrub cover. Tall shrub cover could be favoured because it provides rabbits with more adequate protection from predators and better substratum for warrens. When tall shrubs such as *Pistacia lentiscus* are present, more than 70% of warrens are built below the protection of these shrubs, and very few beneath short shrubs (F. Palomares, unpublished data). Conversely, if understorey cover provided by short shrubs is very dense, the area available for grass would decrease, and so would the carrying capacity of rabbits.

MANAGEMENT IMPLICATIONS

Medium and large carnivorous mammals are considered as key and umbrella species because of their role in shaping community structure, their need for large areas to survive, and their specific habitat requirements (Noss *et al.* 1996). Because of this, management plans focused on these species, or the design of reserves to protect them, may also help to preserve many other species and the overall health of natural ecosystems.

The Iberian lynx is the largest predator (with the exception of wolves *Canis lupus* L. in a small part of its distribution area) of the Mediterranean ecosystem in south-western Europe (Delibes 1983). It is a keystone species that regulates the community structure of this ecosystem with strong direct and indirect effects on other species (Palomares *et al.* 1995, 1996b, 1998). Lynx are effective killers of smaller carnivores such as domestic cats *Felis catus* L., red foxes *Vulpes vulpes* L., Egyptian mongooses *Herpestes ichneumon* L. and European genets *Genetta genetta* L. In areas with high lynx densities, it has been shown that densities of

mongooses and genets are between 10 and 20 times lower than in areas without lynx. This, in turn, has strong positive effects on species at lower trophic levels, such as rabbits, which probably also affects primary producers (McLaren & Peterson 1994). The positive effect of lynx on rabbits is particularly important for the conservation of the predator community because rabbits are preyed upon by more that 30 species in south-western Europe (Delibes & Hiraldo 1981; Jaksic & Soriguer 1981), many of them threatened or endangered species. In addition, rabbits are an important game species in the area (Rogers, Arthur & Soriguer 1994), therefore any positive effect on this prey species is likely to have a positive impact on both human and non-human communities.

Conservation of the Iberian lynx requires good-quality habitats where individuals can settle and breed, and adequate corridors connecting these areas, because lynx presently exhibit a metapopulation structure (Rodríguez & Delibes 1992; Gaona, Ferreras & Delibes 1998) that is unlikely to return to a continuous distribution area. General characteristics of habitats sustaining stable lynx populations should include isolated trees and, ideally, 40% cover of understorey vegetation (half of which should be tall shrubs). Rabbits should also be abundant in resident areas, with autumn mean number of rabbit pellets being around 80 pellets m^{-2}. In areas with 114 pellets m^{-2} lynx density may be higher due to the decrease in range size. Estimations of absolute rabbit abundance in part of the study area indicate that an average of 114 pellets m^{-2} represents mean rabbit densities of about 4·6 rabbits ha^{-1} [95% confidence interval (CI) = 3·85–5·91] in spring, and about 1·0 rabbits ha^{-1} (95% CI = 0·78–1·13) in autumn (Palomares, in press).

The landscape of the Doñana area has been historically modified by fire, which has degraded the climax vegetation of the area into a few species of shrubs (Granados-Corona, Martín-Vicente & García-Novo 1986). Rabbits seem to benefit from fires as they increase their activity on burned areas (Moreno & Villafuerte 1995). Thus, controlled fires have been recommended as a useful tool for the maintenance of good lynx habitat (Moreno & Villafuerte 1995), by decreasing understorey cover and so increasing rabbit density. Nevertheless, fire would also destroy tall shrubs that are beneficial to lynx and rabbits. Therefore, fire or other types of selective clearing focused on short shrubs should be applied to small areas avoiding tall shrubs.

Dispersing animals often use lower quality habitats from which they tend to select areas with higher understorey cover and rabbit abundance within patches of forested habitats. These results stress the importance of small patches of natural vegetation consisting of 50% understorey cover and between 2 and 2·5 times fewer rabbit pellets than resident areas. Plantations are very frequently used by dispersing lynx (Palomares *et al.* 2000). Understorey vegetation of plantations is frequently removed by humans, thus decreasing their suitability to dispersing lynx. If plantations are to be an adequate transition habitat for lynx, the preservation of small patches with enough understorey vegetation should be considered.

An interesting result from this study indicates that areas suitable as corridors had lower habitat quality than areas suitable for resident individuals. This result allows for some relaxation in the design of reserves connected by corridors. Corridors might also be moderately exploited by humans (pine seed harvesting and forestry, in the case of the Iberian lynx). A problem often arising with some corridor proposals is the enormous cost requirement for their implementation (Simberloff *et al.* 1992). Thus proposals with economically self-sustaining corridors with less critical design than core areas are desirable and recommended.

Acknowledgements

References

Beier, P. (1993) Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology*, **7**, 94–108.

Beltrán, J.F. (1991) Temporal abundance pattern of the wild rabbit in Doñana, SW Spain. *Mammalia*, **55**, 591–599.

Beltrán, J. & Delibes, M. (1994) Environmental determinants of circadian activity of free-ranging Iberian lynx. *Journal of Mammalogy*, **75**, 382–393.

Byers, C.R. & Steinhorst, R.K. (1984) Clarification of a technique for analysis of utilization–availability data. *Journal of Wildlife Management*, **48**, 1050–1053.

Delibes, M. (1979) Le lynx dans la Péninsule Ibérique: répartition et régresion. *Bulletin Mensuel de l'Office National de la Chasse. Numéro Spécial Scientifique et Technique LE LYNX*, 41–46.

Delibes, M. (1980) Feeding ecology of the Spanish lynx in the Coto Doñana. *Acta Theriologica*, **25**, 309–324.

Delibes, M. (1983) Distribution and ecology of Iberian carnivores: a short review. *XV Congreso Internacional de Fauna Cinegetica y Silvestre, Trujillo 1981*. Estación Biológica de Doñana y Federación Española de Caza.

Delibes, M. & Hiraldo, F. (1981) The rabbit as prey in the Iberian Mediterranean ecosystem. *Proceedings of the World Lagomorph Conference 1979* (eds K. Myers & C.D. Innes), pp. 614–622. University of Guelph, Ontario, Canada.

Diamond, J. (1989) Overview of recent extinctions. *Conservation for the Twenty-First Century* (eds D. Western & M.C. Pearl). pp. 37–41. Oxford University Press, New York, NY.

Fernández-Delgado, C. (1997) Conservation management of an European natural area: Doñana National Park, Spain. *Principles of Conservation Biology* (eds G.K. Meffe & C.R. Carroll), pp. 458–467. Sinauer Associates Inc., Sunderland, MA.

Ferreras, P. (1994) *Patrones de dispersión del Lince ibérico (Lynx pardina) en Doñana e implicaciones para su conservación*. PhD Thesis. Universidad Autónoma de Madrid, Madrid, Spain.

Ferreras, P., Aldama, J.J., Beltrán, J.F. & Delibes, M. (1992) Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* (Temminck). *Biological Conservation*, **61**, 197–202.

Ferreras, P., Beltrán, J.F., Aldama, J.J. & Delibes, M. (1997) Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*, Temminck, 1824). *Journal of Zoology*, **243**, 163–189.

Gaona, P., Ferreras, P. & Delibes, M. (1998) Dynamics and viability of a metapopulation of the endangered Iberian Lynx (*Lynx pardinus*). *Ecological Monographs*, **68**, 349–370.

Granados-Corona, M., Martín-Vicente, A. & García-Novo, F. (1986) El papel del fuego en los ecosistemas de Doñana. *Boletin de la Estación Central de Ecología*, **15**, 17–28.

Harrison, R.L. (1992) Toward a theory of inter-refuge corridor design. *Conservation Biology*, **6**, 293–295.

Jaksic, F.M. & Soriguer, R.C. (1981) Predation upon the European rabbit (*Oryctolagus cuniculus*) in mediterranean habitats of Chile and Spain: a comparative analysis. *Journal of Animal Ecology*, **50**, 269–281.

Jandel Scientific Software (1995) *SigmaStat® Statistical Software. User's Manual*. Jandel Corporation, San Rafael, CA, USA.

Kenward, R.E. & Hodder, K.H. (1996) *Ranges. V. An Analysis System for Biological Location Data*. Institute of Terrestrial Ecology, Wareham, UK.

Litvaitis, J.A., Sherburne, J.A. & Bissonette, J.A. (1986) Bobcat habitat use and home range size in relation to prey density. *Journal of Wildlife Management*, **50**, 110–117.

Loney, B. & Hobbs, R.J. (1991) Management of vegetation corridors: maintenance, rehabilitation and establishment. *Nature Conservation 2: The Role of Corridors* (eds D.A. Saunders & R.J. Hobbs), pp. 299–311. Surrey Beatty & Sons, Chipping Norton, Australia.

McLaren, B.E. & Peterson, R.O. (1994) Wolves, moose, and tree rings on Isle Royale. *Science*, **266**, 1555–1558.

Meffe, G.K. & Carroll, C.R. (1994) The design of conservation reserves. *Principles of Conservation Biology* (eds G.K. Meffe & C.R. Carroll). pp. 265–304. Sinauer Associates Inc., Sunderland, MA.

Moreira, J.M. & Fernández-Palacios, A. (1995) *Usos y Coberturas Vegetales Del Suelo En Andalucía. Seguimiento a Través de Imágenes de Satélite*. Junta de Andalucía, Consejería de Medio Ambiente, Sevilla, Spain.

Moreno, S. & Villafuerte, R. (1995) Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biological Conservation*, **72**, 1–5.

Myers, N. (1994) Global biodiversity. II. Losses. *Principles of Conservation Biology* (eds G.K. Meffe & C.R. Carroll). pp. 110–140. Sinauer Associates Inc., Sunderland, MA.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T. & Paquet, P.C. (1996) Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, **10**, 949–963.

Nowell, K. & Jackson, P. (1996) *Wild Cats*. IUCN Publications, The Burlington Press, Cambridge, UK.

Palma, L., Beja, P. & Rodrigues, M. (1999) The use of sighting data to analyse Iberian lynx habitat and distribution. *Journal of Applied Ecology*, **36**, 812–824.

Palomares, F. (in press) Comparison of 3 methods to estimate rabbit abundance in a Mediterranean environment. *Wildlife Society Bulletin*.

Palomares, F. & Delibes, M. (1997) Predation upon European rabbits and their use of open and closed patches in Mediterranean habitats. *Oikos*, **80**, 407–410.

Palomares, F., Calzada, J. & Revilla, E. (1996a) El manejo del hábitat y la abundancia de conejos: diferencias entre dos áreas potenciales identicas. *Revista Forestal*, **9**, 201–210.

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J.M., Calzada, J. & Revilla, E. (2000) Iberian lynx in a fragmented landscape: pre-dispersal, dispersal and post-dispersal habitats. *Conservation Biology*, **14**, 809–818.

Palomares, F., Delibes, M., Revilla, E., Calzada, J. & Fedriani, J.M. (in press) Spatial ecology of Iberian lynx and abundance of European rabbit in southwestern Spain. *Wildlife Monographs*.

Palomares, F., Ferreras, P., Fedriani, J.M. & Delibes, M. (1996b) Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. *Journal of Applied Ecology*, **33**, 5–13.

Palomares, F., Ferreras, P., Travaini, A. & Delibes, M. (1998) Coexistence between Iberian lynx and Egyptian mongooses: estimating interaction strength by structural equation modelling and testing by an observational study. *Journal of Animal Ecology*, **67**, 967–978.

Palomares, F., Gaona, P., Ferreras, P. & Delibes, M. (1995) Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Conservation Biology*, **9**, 295–305.

Palomares, F., Rodríguez, A., Laffitte, R. & Delibes, M. (1991) The status and distribution of the Iberian lynx *Felis pardina* (Temminck) in Coto Doñana area, SW Spain. *Biological Conservation*, **57**, 159–169.

Rodríguez, A. & Delibes, M. (1992) Current range and status of the Iberian lynx *Felis pardina* Temminck 1824 in Spain. *Conservation Biology*, **61**, 189–196.

Rogers, P.M. (1981) Ecology of the European wild rabbit *Oryctolagus cuniculus* (L.) in Mediterranean habitats. II. Distribution in the landscape of the Camargue, S. France. *Journal of Applied Ecology*, **18**, 355–371.

Rogers, P.M. & Myers, K. (1979) Ecology of the European wild rabbit, *Oryctolagus cuniculus* (L.), in Mediterranean habitats. I. Distribution in the landscape of the Coto Doñana, S. Spain. *Journal of Applied Ecology*, **16**, 691–703.

Rogers, P.M., Arthur, C.P. & Soriguer, C. (1994) The rabbit in continental Europe. *The European Rabbit. History and Biology of a Successful Colonizer* (eds H.V. Thompson & C.M. King). pp. 22–63. Oxford University Press, Oxford, UK.

Sandell, M. (1989) The mating tactics and spacing patterns of solitary carnivores. *Carnivore, Ecology and Evolution* (ed. J.L. Gittleman). pp. 164–182. Cornell University Press, Ithaca, NY.

SAS Institute Inc. (1990a) *SAS/STAT User's Guide. Vol. 1*. SAS Institute, Cary, NC.

SAS Institute Inc. (1990b) *SAS/STAT User's Guide. Vol. 2*. SAS Institute, Cary, NC.

Scheiner, S.M. (1993) MANOVA: multiple response variables and multispecies interactions. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch). pp. 94–112. Chapman & Hall, New York, NY.

Simberloff, D., Farr, J.A., Cox, J. & Mehlman, D.W. (1992) Movement corridors: conservation bargains or poor investment? *Conservation Biology*, **6**, 493–504.

Soriguer, R.C. (1981) Biología y dinámica de una población de conejos (*Oryctolagus cuniculus* L.) en Andalucía Occidental. *Doñana Acta Vertebrata*, **8**, 1–379.

Soriguer, R.C. & Rogers, P.M. (1981) The European wild rabbit in Mediterranean Spain. *Proceedings of the World Lagomorph Conference, 1979* (eds K. Myers & C.D. MacInnes), pp. 600–603. University of Guelph, Ontario, Canada.

Wallis de Vries, M.F. (1995) Large herbivores and the design of large-scale nature reserves in Western Europe. *Conservation Biology*, **9**, 25–33.

Ward, R.M.P. & Krebs, J. (1985) Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology*, **63**, 2817–2824.

White, P.J. & Garrott, R.A. (1997) Factors regulating kit fox populations. *Canadian Journal of Zoology*, **75**, 1982–1988.