

The selection of breeding dens by the endangered Iberian lynx (*Lynx pardinus*): implications for its conservation

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Abstract

We investigated the preferences shown by Iberian lynx (*Lynx pardinus*) for structures and sites for denning in Doñana National Park. Lynx proved to be highly selective regarding the features of the natural structures selected, but their preferences concerning the characteristics of the habitat for the denning sites were not so evident. All located litters were born inside hollow trunks with very large cavities (mean area = 0.40 m²). Later, they were moved into bushes characterised by their large size (mean area = 201.7 m²) and protective capabilities. We used logistic regressions to explore the relative strength of association between the selection of dens, the characteristics of their structure and those of the habitat around dens. The regressions indicated that the physical nature of dens was more important for breeding lynxes than habitat features (like prey densities or structure of vegetation). Preserving old growth habitats is important for the conservation of the endangered Iberian lynx because they provide suitable breeding structures. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Suitable structures and sites for denning are essential resources for many mammals during their breeding period, if the requirements of females and their newborn are to be met (e.g. Rabinowitz and Pelton, 1986; Reichman and Smith, 1990; Laurenson, 1993). Mammal dens fulfil at least two functions essential for cub survival: providing refuge against predators, and microclimatic stability and shelter against harsh weather conditions (Hellgren and Vaughan, 1989; Reichman and Smith, 1990; Endres and Smith, 1993; Laurenson, 1994; Magoun and Copeland, 1998). Clearly, the structural characteristics of dens and denning sites determine their ability to satisfy these functions. Under certain situations, such as high predator pressure or climatic stress, the possibility of having access to safe dens may affect individual and/or overall population productivity (Alt, 1984; Laurenson, 1993; Oli et al., 1997; Magoun and Copeland, 1998).

On the other hand, in carnivores the need for breeding dens may affect the ecological behaviour of individuals in

several ways. First, dens can influence the spatial configuration of territory borders (Doncaster and Woodroffe, 1993). Second, by regulating the abundance and distribution of individuals, they act as a limiting resource (Neal, 1986; Weber, 1989; Halliwell and MacDonald, 1996; Ruggiero et al., 1998). Third, they lead females into changing their spatial behaviour during the denning period by enlarging or displacing their home ranges in order to access suitable structures for denning (Bailey, 1981). Therefore, the presence of suitable dens is one of the key factors that make a habitat suitable for carnivore species.

The Iberian lynx (*Lynx pardinus*) is a rare and endangered endemic carnivore of the Iberian Peninsula (Rodríguez and Delibes, 1992). Recently classified as the most endangered felid species in the world (Nowell and Jackson, 1996), its total number is around 1000 individuals, distributed among several isolated populations (Rodríguez and Delibes, 1992). It is a food and habitat specialist species, highly dependent on the quality and structure of the vegetation for establishing territories and for breeding (Palomares et al., 1991; Ferreras et al., 1997). Lynx females breed once a year, giving birth to one to four cubs which are totally dependent on their

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mother at least until their third month of life (Aldama, 1993; Fernández and Palomares, own observations). Like most cat species, lynx do not construct breeding dens, but rather occupy natural structures as lairs for their cubs. Little is known about denning in the Iberian lynx, although they are thought to be highly selective regarding the characteristics of the structures they choose for this purpose. Also, little is known about denning in other felids, and only a few aspects of the characteristics and use of dens by some species have been described (e.g. Bailey, 1981; Laurenson, 1993; Schmidt, 1998).

Our main goals in the present study were to identify which factors determine the selection of dens by the Iberian lynx and to propose management strategies designed to improve denning conditions for the species. We studied two types of dens: (a) Natal dens (Bailey, 1981) used by the female for giving birth; (b) Auxiliary dens (Bailey, 1981) to which cubs are moved afterwards. There can be several of these until the end of the denning period (about 2 months).

We considered several factors as being the determinants of den selection: protective advantages against predators, microclimatic stability, proximity to food resources, proximity to the core zone of the territory and distance to the neighbour territory. With this aim in mind, we approached the analysis of den selection in two ways. First, we analysed the physical structure of the den and its protective capabilities (i.e. preventing detection and access by predators, and maintaining stable internal thermal conditions); and second, we investigated den site selection in relationship to environmental factors (structure of the vegetation, territories and prey availability).

2. Study area and methods

2.1. Study area

The study was carried out in Coto del Rey, an area in the north of Doñana National Park, south-western Spain (37°9'N 6°26'W; Fig. 1). It is a sandy, flat terrain at sea level. The climate is Mediterranean subhumid with Atlantic influence and has marked seasons: winters are mild and wet, and summers, hot and dry. Annual rainfall is 500–600 mm. General descriptions of Doñana can be found in Rogers and Myers (1980) and Castroviejo (1993).

Vegetation in Coto del Rey is characterised by autochthonous Mediterranean scrubland formations, where *Pistacia lentiscus* bushes and *Halimium halimifolium* shrubs predominate, with scattered trees in between, mainly *Quercus suber* and *Olea europaea*. The area is crossed by seasonal streams flanked by small stands of ash (*Fraxinus angustifolius*), riparian bushes (*Tamarix africana*, *Rubus ulmifolius*), and abundant *P. lentiscus*. Surrounding these habitats are both cultivated forests

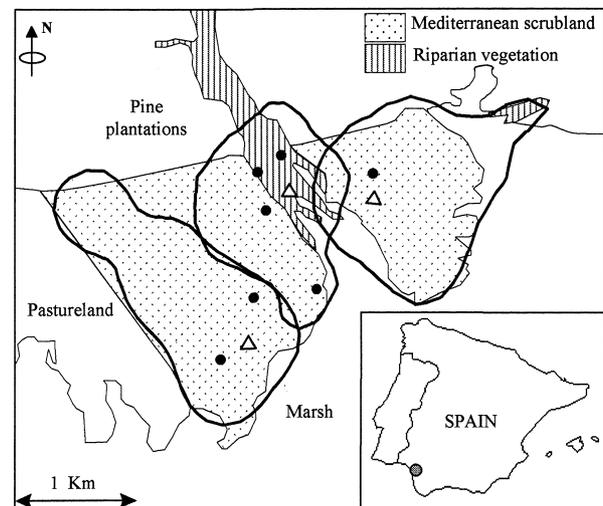


Fig. 1. Map of the study area and female territory borders. Thick black lines represent territories, defined by the 80%-fixed Kernel method. Black circles indicate the location of natal dens. Triangles indicate the winter activity centres (i.e. Kernel centres) of female territories.

(*Pinus pinea* or *Eucalyptus* sp.) with low understory coverage, and marshland (Fig. 1). The ecotone — locally called ‘La Vera’ — which occurs between the scrubland and the marshland, is a particularly productive ecosystem, where refuge and grass availability favour the highest rabbit densities in the Doñana area (Villafuerte and Moreno, 1997). Rabbits are the staple prey for lynx and many other predators in Iberian Mediterranean ecosystems (Delibes, 1980; Delibes and Hiraldo, 1981).

Most of the area is under full protection, and human access is highly restricted. Coto del Rey is a highly productive area inhabited by the subpopulation of lynx with the highest density in the Doñana area (Palomares et al., 1996).

2.2. Den location

Location of natal dens was carried out by radio-tracking adult females between 1993 and 1997, in the framework of a wider research into the behaviour and ecology of the Iberian lynx (for details see Palomares et al., 1995, 1996). During this period, all suspected litters were searched for by locating the female in its natal den with the ‘homing’ technique (Mech, 1983). Direct contact with cubs confirmed their presence.

The auxiliary dens were used by three litters closely monitored in 1997 plus another two litters fortuitously found in previous years. During the 1997 breeding period, females were radio-tracked at least once per day by short triangulation (< 300 m from the animal) during the hottest hours of the day, when females usually rest in or near their den. This allowed us to detect changes in the location of the litter and identify new auxiliary dens by homing. Sites were flagged and mapped in 1:5000

aerial photographs, and their UTM co-ordinates registered. After the females had left, we returned to suspected dens and searched for signs (cub footprints and faeces, prey remains eaten by cubs, etc.) to confirm whether litters had been there or not. Monitoring was continued until the cubs emerged and began to walk with their mothers.

2.3. Sampling procedures

Structure variables of dens were measured after the 1997 breeding season. As explained below, all natal dens were holes in trees, and auxiliary dens were bushes. Thus, we designed a specific set of variables for each type of structure (Table 1). All lengths and diameters were measured with a measuring tape. Areas were calculated as ellipses, using the longest longitudinal and transverse axes. The variable *visibility of the bush's interior* (IVI) was calculated as the ratio between average visible length (d) at 0.5 and 1.5 m high from both extremes of the longitudinal and transverse axes, and average axis length (D): $IVI = (\Sigma d_{0.5} + d_{1.5}/8)/(D_1 + D_2)/2$. Visible length was measured with a coloured, graduated pole like a surveyor's pole. Two ranked variables measuring the degree of cub protection inside auxiliary dens were estimated using ordinal scales of integer values arranged in tables designed specifically for this study. These variables were: (a) *inside refuge*, which describes refuge availability inside the bush (e.g. dead wood, burrows, dense stems) and ranked from 1 = without any of these, to 5 = a lot of oak bark, dense stems and/or rabbit burrows everywhere within the bush; and (b) *access to bush interior* (i.e. the degree of difficulty for the observer to reach the centre of the bush), which ranked from 1 = easy to reach the centre of the bush, to 4 = impenetrable.

Ten environment variables, including some descriptive ones of microhabitat and lynx space use (Table 1), were also measured in each natal and auxiliary den site, within a 50-m-radius circle whose centre was the den. Flora

composition and *scrub* and *tree layer cover* were visually estimated. *Bush layer cover* was measured from aerial photographs using SigmaScan Pro 4.0 Image Analysis Software (Jandel Scientific Co.). Layer average heights were measured with measuring tapes and graduated poles. Estimated *rabbit densities* for spring 1996 came from 50-m-precision maps of predicted rabbit density generated throughout the study area using a GIS (Palomares et al., unpublished). Since the greatest rabbit densities are found in "La Vera" and lynxes searching for food frequent this zone, we also measured the distance between den location and this ecotone band.

Female territories were defined by the 80%-fixed Kernel calculation (KE80) choosing the reference bandwidth (Kenward and Hodder, 1996; Seaman and Powell, 1996), and using all the locations recorded between 1993 and 1996 ($n=1755$). This method was used because it was the one that best defined the territory borders of females minimising the overlap between them (Palomares et al., unpublished). The *distance* from dens to the *neighbour territory border* was used to test if denning lynxes avoided these areas, where it is likely that there are higher probabilities of encountering other lynxes due to boundary-walking patrolling (Emmons, 1988). The *distance* from dens to the *winter activity centre* of each female was used to test if there was any relationship between the core point of the territory and den placement (see a similar approach in Ciucci and Mech, 1992). Winter activity centres were measured as the Kernel centre (Kc) (Worton, 1989) of all recorded locations between 1992 and 1996, outside the breeding period (i.e. August–December). Only autumn and winter locations were utilised in order to avoid the influence of den use in the calculation of Kc. Territory boundaries and Kcs were calculated with Ranges V software (Kenward and Hodder, 1996). All distance variables were calculated using FoxPro (Microsoft Inc).

For the selection analysis, we designed two different availability samplings. The first one consisted of two microsite samples, constituted by the 10 closest trees to

Table 1
Sets of variables measured in natal and auxiliary dens

Structure variables		Environment variables
Natal dens	Auxiliary dens	
Trunk height	Bush area	Shrub cover
Diameter at the breath height (dbh)	Bush height	Bush cover
Number of holes in the trunk	Widest stalk diameter	Tree cover
Percentage of living branches	Inside refuge	Shrub average height
Hole bottom area	Accessibility to the interior	Bush average height
Hole entry area	Visibility of the bush's interior	Tree average height
Height to hole entry		Rabbit density
Percentage of hole visible from the entry		Distance to ecotone marsh–scrubland (La Vera)
		Distance to winter activity centre
		Distance to neighbour territory border

each natal den and the 10 closest bushes to each auxiliary den, respectively. This allowed comparison of each den type with similar structures available nearby and enabled us to isolate the analyses of structure selection from the influence of spatial variations that could occur in the area under study. The second one consisted of a random sample of the whole study area, carried out by generating 100 random UTM co-ordinates. Sampling was restricted to the autochthonous Mediterranean scrubland and riparian formations, as being the preferred habitats of lynx (Palomares et al., in press) and the only one used for denning. Points were systematically searched with a GPS, and then the closest tree and the closest bush to each point were characterised in order to obtain a structure sample for the whole area under study. We imposed restrictions on items belonging to the samples: young trees and bushes too small to shelter an adult lynx were not taken into account.

The environment sample was constituted by environment measurements within 50-m circles around each random co-ordinate, which we denominate as random circles. For the analysis of *distance to the activity centre* and *distance to the neighbouring territory*, we assume that each female has exclusive access to the random co-ordinates inside its territory; that is, each random co-ordinate was assigned to one female lynx.

Thermal oscillations inside dens were also compared to other similar structures and to other nearby shaded sites. We measured maximum and minimum temperatures in 21 points simultaneously (i.e. seven points allocated to each type of site) and during four periods: three 24-h periods and one 7-day period. This procedure was repeated for both types of dens, i.e. natal and auxiliary ones. All thermal measurements were taken between October and November 1997.

2.4. Data analysis

Statistical comparisons between dens and their respective microsite samples were made with Paired *t*-tests and Wilcoxon Rank Sum Tests (Sokal and Rohlf, 1995). In the analyses, each den was paired with the average (continuous variables) or mode (ranked variables) value calculated from the microsite sample. Comparisons between dens and randomly chosen circles and structures were carried out with *t*-tests and Mann–Whitney rank sum tests. Thermal differences between inside dens, the inside of similar structures and outside sites were analysed using a single classification anova (Sokal and Rohlf, 1995). Only differences with $P < 0.05$ were considered statistically significant. Tests were performed using Sigma-Stat 2.0 Statistical Software (Jandel Scientific Co.).

To explore which features are associated with the selection of dens, three stepwise logistic regressions (SAS Institute, 1990) were developed, including different sets of variables. Dens were ‘occurrences’ in the

binary response variable, and items of the random sample were considered equal to ‘non occurrences’. First, the response variable was regressed on structure variables. Then it was regressed on environment variables. Finally, structure and environment variables were grouped into the same analysis. The goodness of fit of the models was assessed calculating log-likelihood statistics and using chi square (Tabachnick and Fidell, 1996). The predictive ability of each model was assessed by its concordance score (SAS Institute, 1990), which is a measure of the correlation between the predicted probability of belonging to one group and actually belonging to it. Analyses were done using the LOGISTIC procedure of the SAS software package (SAS Institute, 1990).

3. Results

In Coto del Rey, four Iberian lynx females successfully bred between 1993 and 1997, in three different territories. One of the territories was occupied by two different females in different years. We were able to find 10 out of the 11 litters which ongoing intensive research had revealed as being born in the study area (i.e. not all females bred every year; Table 2). Two remaining litters could not be located because the females did not have active radio-collars at the time. The litters found were born in seven different natal dens. Two dens were re-utilised, one of them three times by two different females. During spring and summer of 1997 we located 13 auxiliary dens, and another two in previous years.

3.1. Structure selection

3.1.1. Natal dens

All natal dens were natural hollow trees, *Q. suber* ($n=5$) and *F. angustifolius* ($n=2$). Paired comparisons between natal den trees and other trees nearby revealed that den trees were significantly wider, presented a lower proportion of living branches, and had more holes in the trunk (Fig. 2). Trunk height, however, did not show significant differences ($t=0.20$; $df=6$; $P=0.85$; $n=77$). Comparisons between randomly chosen trees in the study area and den trees showed identical results (Table 3).

Table 2
Lynx litters recorded and number of natal dens located in each of the three territories in Coto del Rey

Territory	Breeding years	<i>n</i> of natal dens
Eastern (1 female)	1993, 1995, 1997	2
Central (1 female)	1993, 1994, 1995, 1996, ^a 1997	4
Western (2 females)	1994 (1st female), 1996, 1997 (2nd female)	1

^a Non-located litter.

Trees with holes were scarce in the study area and thus in our samples and so we had to carry out another sample of trees with measurable holes ($n=40$). There were 12 hollow trees from the microsite sample, 11 from the random sample, and 17 specifically searched for in

random surveys. We restricted sampling to trees with holes with a 15-cm minimum diameter entrance, considered to be the minimum space through which an adult lynx could pass (based on cranial zygomatic width, which is < 10 cm in adult females). Den holes differed from other available holes only in their dimensions (Table 4): *bottom area* and *hole entry area* were significantly larger in dens. Variables measuring protection capability did not show significant differences.

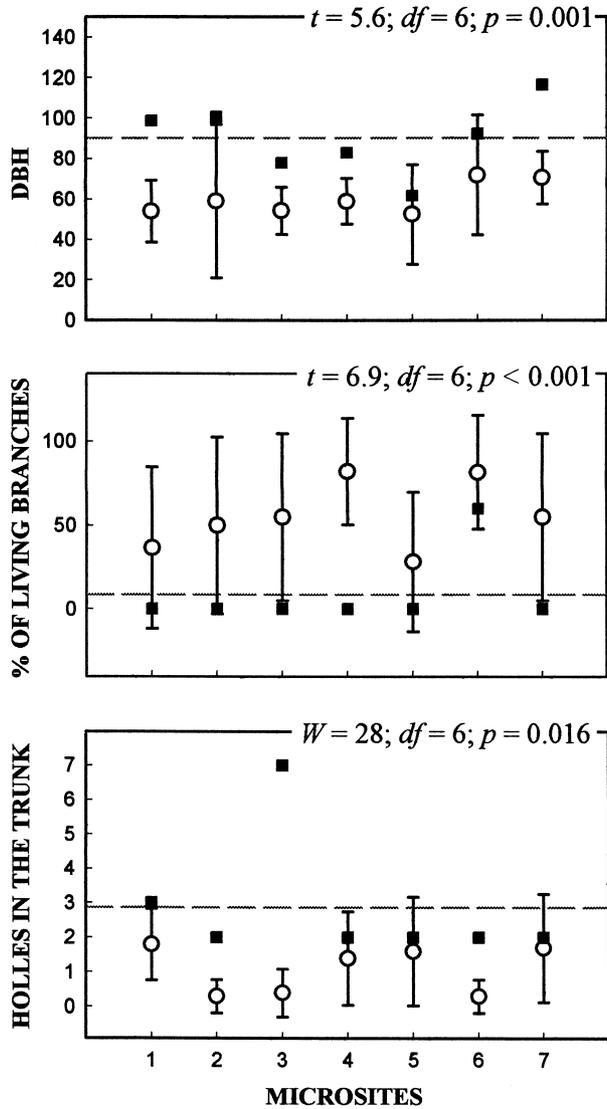


Fig. 2. Significant differences between natal dens and microsite sample. Black squares represent den values, dashed lines the average values for dens, and white circles with bars represent the average values of each microsite sample and 95% confidence intervals for the mean. All $n=77$.

3.1.2. Auxiliary dens

After 2–3 weeks, natal dens were left and cubs moved to a different type of structure. All initial and subsequent auxiliary dens consisted of bush complexes, generally *P. lentiscus*. Several relevant differences were found between bush dens and nearby bushes (Fig. 3). *Bush areas* were significantly larger in dens, but no significant differences were found in *bush height* (dens: $\bar{X}_d = 350.3 \pm 21.0$ cm; microsite sample: $\bar{X}_m = 310.4 \pm 9.9$ cm; $t=2.2$; $df=14$; $P=0.06$) or the *widest stalk diameter* ($\bar{X}_d = 16.1 \pm 1.6$ cm; $\bar{X}_m = 14.9 \pm 1.0$ cm; $t=0.59$; $df=14$; $P=0.57$). Sixty-seven percent of den bushes had rabbit warrens inside, and there was also an abundance of other elements giving shelter to cubs such as bark and cork, dense stalks or intertwined brambles. On the other hand, microsite bushes had little potential for refuge inside as compared to den bushes. Also the inside of the dens was less accessible and the index of *visibility of the bush's interior* was lower than in nearby bushes.

Bushes in the random sample were quite homogeneous in their appearance, and differed significantly from auxiliary dens in the same variables as microsites (Table 5).

3.2. Thermal characteristics

Daily oscillation in temperature outside dens was between 65 and 95% higher than inside dens. Analyses of variance showed significant differences in the mean *thermal oscillation* during the 24-h periods studied between natal dens, similar structures and nearest outside settings ($F=34.7$; $df=18, 2$; $P<0.001$). The same results were obtained regarding auxiliary dens ($F=21.8$; $df=18, 2$; $P<0.001$). Similarly, 7-day periods for both types of dens yielded the same results (all $F>6.2$; all $df=18, 2$; all $P<0.001$). Tukey tests always showed

Table 3
Characteristics of natal dens in comparison with random sample^a

Variable	Random sample ($n=100$)	Natal dens ($n=7$)	Statistic ($df=105$)	P
dbh	56.5 ± 2.5	90.1 ± 6.7	$t=3.60$	<0.01
% of living branches	82.9 ± 3.5	8.6 ± 8.6	$T=85.5$	<0.01
No. of holes in the trunk	0.26 ± 0.06	2.86 ± 0.7	$T=710$	<0.01
Trunk height	211 ± 6.3	255 ± 18.8	$T=495.5$	0.14

^a Mean values are given with standard errors.

Table 4
Characteristics of natal den holes in comparison with holes sample^a

Variable	Hole sample ($n = 400$)	Natal dens ($n = 7$)	Statistic ($df = 45$)	P
Hole bottom area (m ²)	0.097 ± 0.01	0.403 ± 0.06	$t = 6.70$	< 0.01
Hole entry area (m ²)	0.056 ± 0.01	0.16 ± 0.03	$t = 4.98$	< 0.01
Height to hole entry (cm)	114 ± 17	174 ± 28	$T = 225.5$	0.09
% of hole visible from the entry	97.1 ± 1.3	95.0 ± 2.2	$T = 116.5$	0.13

^a Mean values are given with standard errors.

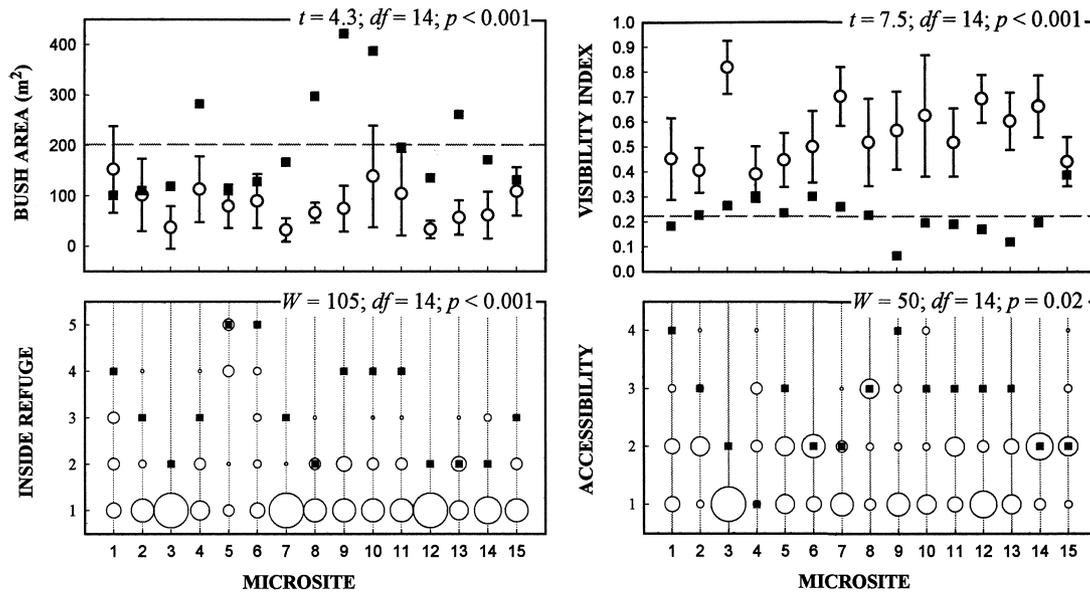


Fig. 3. Significant differences between auxiliary dens and microsite samples. In the upper two graphs, black squares represent den values, dashed lines the average values for dens, and white circles with bars represent the average values of each microsite sample and 95% confidence intervals for the mean. In the lower graphs, black squares represent recorded values for dens estimated using ordinal scales, and balloons represent the proportional number of observations inside each microsite taking a given value (i.e. larger balloons, higher number of observations taking that value). Higher values for *inside refuge* mean more refuges, and higher values for *accessibility* mean more difficult accessibility. All $n = 165$.

Table 5
Characteristics of auxiliary dens in comparison with random sample^a

Variable	Random sample ($n = 100$)	Auxiliary dens ($n = 15$)	Statistic ($df = 105$)	P
Bush area (m ²)	58.5 ± 6.7	201.7 ± 26.9	$T = 1523$	< 0.01
Bush height (cm)	308.6 ± 7.6	350.3 ± 21.0	$t = 1.88$	0.06
Widest stalk diameter (cm)	15.74 ± 0.97	16.07 ± 1.62	$t = 0.46$	0.65
Inside refuge	1 (1/2)	3 (2/4)	$T = 1446$	< 0.01
Accessibility to the interior	2 (1/2)	3 (2/3)	$T = 1247$	< 0.01
Visibility of bush's interior	0.61 ± 0.02	0.22 ± 0.02	$t = 6.58$	< 0.01

^a Mean values are given with standard errors. In ranked variables, mode values are given with 25 and 75 percentiles.

differences between dens and outside sites, and between similar structures and outside sites (all $q > 3.7$; all $P < 0.05$), but not between dens and similar structures (all $q < 1.3$; all $P > 0.05$).

3.3. Environment selection

Natal and auxiliary den sites showed some differences in the characteristics of vegetation structure when compared to random circles (Table 6). Natal den sites presented

higher *bush* and *tree cover*. By contrast, auxiliary den sites only differed in *tree cover*. The heights of the three layers were very similar in all the samples, although a significant but small difference was found in *tree average height* in natal den sites and random circles.

Predicted *rabbit densities* inside circles did not statistically differ between dens (either natal or auxiliary) and the random sample (Table 6). Similarly, *distance to 'La Vera'* did not present significant differences with respect to random co-ordinates (Table 6).

Table 6
Environment characteristics of natal and auxiliary dens sites, and comparison with random sample^a

Variable	Random sample (n = 100)	Natal dens (n = 7)	Statistic (df = 105)	P	Auxiliary dens (n = 15)	Statistic (df = 123)	P
Shrub cover (%)	25 ± 2	23 ± 7	T = 344.0	0.67	26 ± 4	T = 890	0.87
Bush cover (%)	24 ± 1	39 ± 6	t = 3.07	< 0.01	29 ± 0.3	t = 1.61	0.11
Tree cover (%)	15 ± 1	28 ± 5	T = 573.5	0.01	23 ± 3	T = 1187	< 0.01
Shrub average height (cm)	85 ± 2.2	86 ± 9.0	T = 448.0	0.85	92 ± 4.4	T = 1005	0.23
Bush average height (cm)	311 ± 16.4	329 ± 13	T = 513.0	0.34	303 ± 11	T = 784	0.52
Tree average height (cm)	807 ± 16	1000 ± 49	T = 651.5	< 0.01	786 ± 30	T = 692	0.41
Rabbit density (individual/ha)	7.77 ± 0.59	4.77 ± 0.82	T = 359	0.82	5.72 ± 1.2	T = 856	0.91
Distance to 'La Vera' (m)	701 ± 52	510 ± 56	t = 0.56	0.57	579 ± 90	t = 0.55	0.58
Distance to activity centre (m)	754 ± 40	389 ± 93	t = 2.84	< 0.01	617 ± 81	t = 1.31	0.19
Distance to neighbour territory (m)	458 ± 34	335 ± 74	T = 323	0.49	469 ± 73	T = 891	0.86

^a Mean values are given with standard errors. In ranked variables, mode values are given with 25 and 75 percentiles.

Distances from both natal and auxiliary dens to neighbour territory borders were not statistically different from random co-ordinates distances to the borders (Table 6). Some of the natal dens were as close to neighbour isoline as 150 m, and one auxiliary den was inside the small overlapping zone of two territories.

For the analysis of the distance to winter activity centre the natal den used by the two females was considered twice, given that they had different activity centres. Natal dens were significantly closer to centres than random co-ordinates, but this was not the case for auxiliary dens (Table 6). We explored in two different ways the possible influence of underlying habitat variables on the result of natal dens being placed near activity centres. First, we studied correlations between distance to winter activity centre and tree cover, shrub cover and rabbit density. Only tree cover showed a significant correlation with distance to winter activity centre ($P = 0.043$; $n = 100$) although weak ($r_s = 0.20$). We also analysed habitat differences between random circles 200 m from each winter centre ($n = 15$) and other circles outside that distance ($n = 85$). Layers cover, rabbit density, tree dbh (all $t > 0.8$) and the relative number of trees with dead branches or holes ($\chi^2 = 0.41$) all showed non-significant differences (all $P > 0.05$). Thus, no underlying factors were detected.

3.4. Logistic regression models

All models obtained, both for natal and auxiliary dens, and for all sets of variables, showed significant goodness of fit, although their predictive value differed considerably.

3.4.1. Natal dens

The best structure model for natal dens ($n = 107$) included the variables dbh and % of living branches. The best environment model, in which the den used by two different females was introduced twice (see above), included the variables tree cover and distance to winter activity centre ($n = 108$). When environment and structure

descriptors were combined, the best model obtained was identical to the structure model, which presented higher concordance scores than the environment model (Table 7).

As holes were not considered for developing the structure model, we developed an additional analysis with the holes sample ($n = 47$; see above). A significant model was obtained which only included the variable hole diameter. Concordance scores for this model were the highest obtained in all natal den regressions (Table 7).

3.4.2. Auxiliary dens

The structure model ($n = 165$) included the variables inside refuge and visibility of the bush's interior. The environment model only included tree cover, and had a low predictive value. As in natal dens, the model combining structure and environment variables was identical to the structure model (Table 7). We observed that the protective capacity of bushes was lower in the latest dens used by each litter, and they showed the smallest P values in the logistic equations. Thus, all the auxiliary dens which sheltered litters younger than 50 days-old showed P values higher than 0.50 ($\bar{X} = 0.77 \pm 0.07$), while the remaining ones showed values lower than this ($\bar{X} = 0.37 \pm 0.09$).

4. Discussion

Conservation of endangered species is often regarded at a coarse level, and usually does not account for local 'subtle' elements of the habitats, like the ones we are concerned with here. However, some authors have shown the importance of these kinds of subtle resources for many animals (see, for example, Johnson and Pelton, 1981; Forsman et al., 1984; Walters, 1991; Newton, 1994; Schlesinger and Shine, 1994). Effective action for the conservation of lynx may need to take these kinds of features into account, in addition to other conventional habitat management.

Table 7
Results of stepwise logistic regression analyses

Model	Model χ^2 ^a	df	Intercept	1st variable entered	Parameter estimate	2nd variable entered	Parameter estimate	Concordance (%)
<i>Structure model</i> ^b								
Natal dens — trees model	28.88***	2	−4.97	dbh	0.06	% Living branches	−4.88	97.4
Natal dens — holes model	36.50***	2	−17.06	Hole diameter	0.0002			99.7
Auxiliary dens	55.84***	2	−0.15	Refuges inside	1.27	Visibility of interior	−13.4	96.9
<i>Environment model</i>								
Natal dens	19.01***	2	−4.06	Bush cover	0.11	Distance to Kc	0.004	86.9
Auxiliary dens	4.50*	2	−2.63	Tree cover	0.04			66.5

^a * $P < 0.05$; *** $P < 0.001$.

^b The models including structure and environmental variables are identical to the structure models.

We studied the selection of breeding dens in the Iberian lynx, analysing their availability using two different approaches: the immediate surroundings of dens and the females' entire potential breeding area. The first one allowed us to isolate the assessment of den structures from potential correlations with environment characteristics if a previous site selection had occurred. The second one allowed us to investigate the environment characteristics of den sites as well as structure selection in a wider context, and was also used to compare the explanatory capability of each group of variables regarding den selection.

We are aware of the limitations imposed by the sample size on defining a selection pattern. However, we stress the impossibility of having large samples in a species as scarce and secretive as the Iberian lynx. From 1993 to 1997 all female lynxes established in the north of Doñana National Park were captured and marked with radio-collars; all litters born in the area in that period have been registered, and 10 out of the 11 could be located in their natal den. During 1997, 13 out of no more than 17 auxiliary dens used by the litters of that year were also identified. In spite of the difficulties, our sample reliably shows the selection of dens by Iberian lynx in one of the populations that still exist.

4.1. What do female lynx select?

The selection of particular breeding dens is, in theory, influenced by their ability to satisfy the demands of cubs during their development, and of lactating females. Thus, the placement of litters in felids has been related to a combination of factors, including security for cubs and energy economy for the females (Laurenson, 1995a). On that latter point, a widely accepted hypothesis deals with the demands of feeding optimisation. The 'central place foraging' (Orians and Pearson, 1979) pattern of the search for food by females during denning, together with strong energetic stress and higher requirements due to breeding (Aldman, 1993), would constrain females to den in sites with optimal access to

food. In addition, nutritional status and energy acquisition rates could determine reproductive rates as suggested in other works of felid species (Emmons, 1988; Maehr et al., 1989; Laurenson, 1995b). Feeding optimisation has been proposed as an influential factor in the location of dens in several studies with carnivores (Hewson, 1986; Ciucci and Mech, 1992; Aldama, 1993; Laurenson, 1995a), although such a relationship has not been objectively demonstrated. Our results did not reflect such a preference, as dens were situated in zones of relatively low prey-density. However, female lynx territories in the area under study are small (between 1.86 and 3.22 km²) in comparison with those used by Iberian lynx females in the South of Doñana (Ferrerias et al., 1997). So, they do not need to walk a long way to reach the higher prey-density zones inside their territories, whereby any influence of prey distribution on selection would be masked by high availability (Johnson, 1980).

The tendency to place dens in the surroundings of activity centres has been interpreted as an effort to optimise daily movements of the mother and to decrease the interaction with conspecific neighbouring territories (Ciucci and Mech, 1992). Our results show that female lynxes selected natal dens around territory centres, but it is not evident that there is a relationship between selection and avoiding neighbouring lynxes: several dens, natal or auxiliary, were inside the influence area of other territories, near their boundaries or even inside the intersection areas between both territories.

Natal den trunks did not show intrinsic features that made them specially safe, although hollow trunks are protective structures per se. Natal den surroundings usually presented high bush cover, which is a further protective advantage. However, given that hollow trees are preferred by females for parturition, the possibilities of choice are reduced. The selection of hollow trunks is conditioned by the animal's size (Lindenmayer et al., 1991), which in the case of lynx corresponds to large hollow trunks, which are very scarce in Coto del Rey. The use of hollow trunks for parturition is a constant in all the births of our study and all others previously

recorded in Doñana (Valverde, 1957; Aldama, 1993; P. Ferreras, pers. com.). This leads to an obvious question: what are the critical characteristics that make hollow trunks so worthy as natal dens? A possible explanation is that hollow trunks are capable of holding the body heat given off by the animal (Stains, 1961). Females stay inside the hole for hours at least during the first few days after giving birth, and we registered great differences between the thermal stability inside empty hollow trunks and outside them. These two factors in combination would provide an important advantage for the thermoregulation of the vulnerable new-born cubs. Tree holes would also be advantageous because they would allow the litter to be easily gathered by the female, and may affect other behavioural characteristics related to giving birth and suckling cubs.

In our study auxiliary den selection appears to be closely associated with their protective and hiding power, suitable bushes being characterised by their large area, thickness and abundance of protective elements inside them such as rabbit warrens, cork and tangled stalks. A good protective bush seems specially important for the cubs' survival while they develop mobility and as they become more easily detected than in natal dens but are still unable to defend themselves. Around the second month of life, females appear to be less selective regarding the protective characteristics of the bushes for denning, as cubs begin to leave dens soon after this period.

In conclusion, the selection hypothesis that better suits our results is the necessity to protect cubs against enemies by means of the specific properties of the structure of the breeding dens. We must point out that some habitat features which were not different in breeding dens and random sites within female lynx's home ranges, particularly prey availability, are probably influencing habitat selection at lower orders of selection (Johnson, 1980).

4.2. Implications for conservation

Preferred breeding structures can be limiting resources for animals, and, therefore, their importance in conservation strategies must be recognised and considered (see, for example, Forsman et al., 1984; Meffe and Carroll, 1994; Lidenmayer, 1995; Marsden and Jones, 1997). For the Iberian lynx, we believe that availability of suitable breeding dens may influence the use of space by a female to ensure it has access to dens, and this could be the most likely way to limit lynx densities.

Preservation of large hollow trees is highly important for this species, at least for the Doñana population, where other structures, also probably suitable for breeding, such as rock crevices and caves, are not present. But it also may benefit all kinds of vertebrates in Mediterranean ecosystems that use these cavities for

breeding or resting, such as other carnivore species (genets: Palomares and Delibes, 1994; badgers: Revilla, 1998; wild cats: Fernández, 1997; many corvid and owl species: Valverde, 1967; Mikkola, 1983; bats: Ibáñez, 1995, etc.). In our study area, hollow trees, mainly those with wide holes, are very scarce, as our samplings showed. On the other hand, two of the natal dens known in Coto del Rey have deteriorated during the study years, which means an index of disappearance of 7.3% dens per year.

The appearance of tree cavities is a slow process in slow-growing stands like cork oak forests, which are also under stress in Doñana due to low regeneration rates of the forest. In the medium and long term, managing and promoting mature stands, which provide hollow trees for lynx breeding, must take into account balanced regeneration and optimum ageing of the forest. Higher numbers of old trees means higher probabilities of large hollows appearing, but dense forests do not favour lynx because they reduce the growth of bushes and pastures that provide refuge for the lynx and food for its prey (Moreno and Villafuerte, 1995; Palomares et al., unpublished). Large dead trees and their remains should be left in the field as dens.

With respect to auxiliary dens, bushes must be fostered, specially large, thick and protective old-growth species like *Pistacia lentiscus*, *Rubus ulmifolius* or *Quercus coccifera*. The management of Mediterranean habitats to favour livestock usually brings the destruction of this layer of the vegetation, which is to the detriment of the Iberian lynx (Rodríguez and Delibes, 1992). Such management policies must be modified in order to guarantee the existence of sufficient coverage to encourage the presence and breeding of lynx. From our results we can establish that 25–30% of bush cover with at least 10% of bushes > 100 m² could be appropriate for providing potential auxiliary dens inside suitable lynx areas.

A productive approach in the future may be the introduction of suitable, artificial structures as natal dens in areas where natural dens are very limited as in the south of Doñana, which might serve to increase the productivity of the population.

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