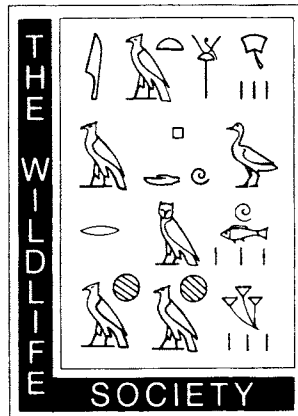


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SPATIAL ECOLOGY OF IBERIAN LYNX AND ABUNDANCE OF EUROPEAN RABBITS IN SOUTHWESTERN SPAIN

by

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AND JOSE MARÍA FEDRIANI



FRONTISPIECE. Adult female Iberian lynx in pastureland habitat in Doñana National Park, southwestern Spain (Photo by Antonio Sabater).

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Abstract: Spatial ecology and diet of Iberian lynx (*Lynx pardinus*) and the abundance of its main prey, the European rabbit (*Oryctolagus cuniculus*), were studied in southwestern Spain from December 1992 to December 1996 when a decline in rabbit populations occurred. Our objectives were to relate spatial ecology of lynx to rabbit abundance, water availability, and protection from human disturbance. Rabbits were almost the sole prey of lynx; rabbit remains were present in 99.2% ($n = 1,171$) of feces analyzed.

Rabbit abundance and density in 6 different habitats were estimated by line transect sampling. Rabbits were more abundant in Mediterranean scrubland, closely followed by ash stands. Pastureland and lentiscus in plantations had 4.5 times fewer rabbits, and pine plantations 15–20 times fewer rabbits, than the Mediterranean scrubland. Abundance of rabbits in the Mediterranean scrubland was not spatially uniform, as density for 1994 and 1995 varied from 42–55/ha in the area close to the edge of the marsh (locally called the Vera) to 2–7/ha far from the Vera. Rabbit density was 3.5 times higher during spring than during autumn. A decline in rabbit density occurred in 1996 when numbers were 72–91% lower than the previous years.

We mapped warren density in Mediterranean scrubland and pastureland to determine intra-habitat differences in spatial distribution of rabbits. Warren density, entrance density, and mean number of entrances per warren declined significantly with distance from the Vera in the Mediterranean scrubland, following a negative exponential function (adj. r^2 ranging between 83 and 97%). However, none of these variables showed any trend in relation to the Vera in the pastureland.

The lynx population contained three stable pairs of adults plus young raised each year, some of which remained on the study area as subadults (older than one year). The seasonal number of different lynx in the study area ranged between 7 and 17. Average adult and young/subadult seasonal density was 0.77 (range = 0.72–0.88) and 0.46 individuals/km² (range = 0.07–1.12), respectively.

We estimated home range and daily movements of lynx to determine changes that might be due to sex, season, or changing prey density. On average, total lynx home range size was 7.3 km² for young, 9.5 km² for adult females, and 18.2 km² for adult males. Mean core areas (60% isopleth using the kernel approximation) were on average 15%, 10%, and 34% of total home ranges of young, adult females, and adult males, respectively. Significant differences were found for home range and core area sizes among sex-age classes, but neither season nor year affected home range size or core area size. Daily movements averaged 8.0 km. Daily distance traveled was not affected by sex-age class or season, but was different among years, with lynx traveling

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shorter distances in 1993 and 1996. Daily home range size averaged 1.46 km², and again only varied by year. Lynx daily movements were associated with permanent, artificial water sites.

Habitat use by lynx was remarkably constant, with no differences detected among sex-age classes, active or inactive locations, seasons, or years. The habitat most frequently used was Mediterranean scrubland (53% of locations), and both it and ash stands were the only habitats preferred by lynx; pine and eucalyptus plantations were avoided, and marsh, pastureland and lentiscus in plantations were neither preferred or avoided. When lynx were found in the non-preferred habitats, on most occasions (78%) animals were closer than 300 m from the edge of one of the two preferred habitats, whereas on only 4% of occasions were animals further than 1 km. This behavior was particularly accentuated when lynx moved through open habitats. Lynx appeared to respond to high human presence, as they were mainly located inside the National Park (82% of occasions), and when outside the Park they more frequently used the areas that were farther from a tourist village.

We used a Geographical Information System (GIS) to estimate average rabbit density and number of rabbits within lynx home ranges. On average, rabbit density within home ranges was 5.6/ha. The habitats that sustained more rabbits were Mediterranean scrubland (74.2% of total number of rabbits within home ranges) and ash stands (32.2% for 6 home ranges where these habitats were available). Rabbit densities within core areas were similar to those found in home ranges. Throughout the study period the lowest rabbit density estimated within home ranges was about 1/ha in autumn 1996. The number of rabbits per lynx ranged between 1,367 in spring 1994 and 73 in autumn 1996. Rabbit density within home ranges, core areas, and the trapping area were not correlated with range size (P 's > 0.2).

Lynx and rabbits preferred the least human-transformed scrubland habitats; therefore natural habitats must be favored over plantations and pastureland areas. The edges of the preferred habitats were also heavily used by rabbits and consequently by lynx. The vegetation structure of the preferred habitats was characterized by intermediate understory cover (25–35%), low tree cover, and large and frequent grasslands. The rabbit decline observed during the study did not affect lynx spatial behavior or reproduction. Therefore, rabbit densities as low as 1 and 4.6/ha for the times of the lowest and highest rabbit density (i.e., autumn and spring, respectively) were enough to sustain the lynx population. Other factors such as the presence of permanent water sites and relatively low human presence are important components of quality lynx habitat.

WILDLIFE MONOGRAPHS 148, 1–36

Key Words: daily movements, density, European rabbit, habitat use, home range size, human influence, Iberian lynx, line transect sampling, *Lynx pardinus*, *Oryctolagus cuniculus*, Spain.

CONTENTS

INTRODUCTION	3	<i>Seasonal Home Range Size</i>	20
<i>Acknowledgments</i>	4	Lynx Daily Movements	20
STUDY AREA	5	Lynx Movements and Water Sites	21
METHODS	5	Lynx Habitat Use	22
Rabbit Abundance and Distribution	7	<i>General Pattern</i>	22
<i>Rabbit Abundance</i>	7	<i>Seasonal and Annual Variations</i>	23
<i>Variations in Rabbit Abundance within</i>		<i>Penetration Distance within Non-preferred</i>	
<i>Habitats</i>	8	<i>Habitats</i>	23
Lynx Diet	9	Effects of Protection and Human Influence on	
Capture and Radiotelemetry	9	Lynx Space Use	24
Number of Lynx and Density	10	Number of Rabbits within Lynx Home Ranges	
Lynx Space Use	11	and Trapping Area	24
<i>Home Range</i>	11	DISCUSSION	25
<i>Daily Movements</i>	11	Rabbit Abundance and Distribution	25
<i>Movements in Relation to Water Sites</i>	11	Lynx Diet	27
<i>Habitat Use</i>	12	Lynx Density	27
<i>Protection and Human Influence</i>	13	Lynx Home Range and Daily Movements	27
Rabbit Density and Number of Rabbits within		Lynx Movements in Relation to Water Sites	28
Lynx Home Ranges	14	Lynx Habitat Use	28
General Remarks on Statistics	14	Effect of Protection and Human Influence on	
RESULTS	15	Lynx	28
Importance of Rabbits in Lynx Diet	15	Number of Rabbits within Lynx Home Ranges	29
Rabbit Abundance	15	MANAGEMENT IMPLICATIONS	30
Variations in Rabbit Abundance within Habitats		The European Rabbit	30
The Lynx Population	18	The Iberian Lynx	31
Lynx Home Range	19	LITERATURE CITED	32
<i>Total Home Range Size</i>	19	APPENDICES	35

INTRODUCTION

Information on the use of space is of prime importance for adequate management of wildlife species, as it is basic to conservation plans and habitat suitability analyses (e.g., Haslett 1990, Maehr and Cox 1995, Knick and Dyer 1997). The Iberian lynx (*Lynx pardinus*), the most threatened felid species in the world (Nowell and Jackson 1996), has a global population of only about 1,000 individuals in several isolated areas (Rodríguez and Delibes 1992). Vegetation removal and transformation, decline of its main prey, the European rabbit (*Oryctolagus cuniculus*), and human-caused mortality have been identified as the main factors responsible for the decline of lynx during the last few decades (Rodríguez and Delibes 1992). The conservation and management of Iberian lynx require an understanding of the factors that determine its use of space.

To study the use of space by lynx and the factors that affect it, we selected a population localized in the north of Doñana National Park, southwestern Spain. The total lynx population of Doñana area has been estimated at 40–50 individuals, which are subdivided in two spatially isolated stable sub-populations (Palomares et al. 1991). These sub-populations are connected through the dispersal of individuals living both within Doñana National Park and the surrounding area. The north sub-population has several characteristics that make it special for the conservation and management of lynx in the area and elsewhere. First, lynx numbers are low. Second, this subpopulation is adjacent to areas heavily used by humans where disturbance and mortality are likely high (Ferrerías et al. 1992). Third, this area is where Iberian lynx reach their highest density, one of the highest reported for any similar-sized cat species (e.g., Lembeck 1986). Therefore, this area can provide useful insights for optimal management of lynx populations in other areas, as well (Rodríguez and Delibes 1992). Finally, a preliminary study indicated that the area used by lynx seemed small and quite isolated by generally un-

suitable habitats (Palomares et al. 1996a), favoring relatively easy monitoring of the total population and hence an opportunity to determine the ecological factors regulating them.

From December 1992 through December 1996 we studied home range size, daily distance traveled, and habitat use of radio-marked lynx. Because Iberian lynx feed almost exclusively on rabbits, knowledge of rabbit abundance and distribution, and the factors that affect them, is basic to interpreting lynx use of space and for managing lynx populations. Furthermore, the recovery of declining rabbit populations (Rogers et al. 1994) is desirable because rabbits are also the basic prey for other endangered predators (Delibes and Hiraldo 1981) and an important species for hunters in southwestern Europe (Rogers et al. 1994). Thus, a specific objective of our study was to determine abundance and distribution of rabbits in relation to habitat types and other landscape features. Rabbit abundance and distribution were studied by direct surveys in the most representative habitats of the study area; this provided useful baseline information for management and also provided estimates of rabbit numbers within lynx home ranges.

No previous researchers have specifically studied the variation in European rabbit abundance among habitats. However, this was a major interest because we wanted to relate lynx habitat use to presence of adequate shelter (i.e., scrubland) and to the abundance of its prey base. Rabbits thrive in areas near moist grassland at the borders of land systems (Rogers and Myers 1979, Rogers 1981, Beltrán 1991, Palomares et al. 1996b) and in areas with natural scrubland vegetation and/or warrens (Myers and Parker 1965, Wheeler et al. 1981, Kolb 1991a, Palomares et al. 1996b, Palomares and Delibes 1997) that provide good intercalation of both shelter and food. Therefore, we expected to find higher rabbit densities in the habitats where feeding grounds (grasslands) and natural understory vegetation or warrens were more abundant than in habitats where

grass and/or protection availability was low, or in habitats which had been highly transformed by humans.

The climate during the first three years of study was characterized by a severe drought with precipitation 2–3 times below average, and by large flooding during the last year with twice the normal precipitation for the study area (see below). Myers and Parker (1974) found that rabbit abundance strongly declined during drought in Australia; hence, we expected rabbits to be less abundant during the first part of the study period. Because rabbit abundance did change during the study, the situation provided us with the opportunity to test the hypothesis of change in space use by lynx (especially home range size and daily movements) and to test numerical or functional responses of lynx to changes in abundance of their main prey (Bailey 1974, Ward and Krebs 1985, Knick 1990, Jedrzejewski et al. 1995).

Human influence also has been clearly identified as affecting movements and abundance of carnivores (McLellan and Shackleton 1988, Thurber et al. 1994). Based on higher mortality and lower number of tracks found outside than inside protected areas, lynx may be sensitive to high levels of human influence (Palomares et al. 1991, Ferreras et al. 1992, Travaini et al. 1997). Thus, we studied whether use of space by lynx was affected by human influence and legal protection within our study area. The study area was close to a tourist village and just inside the north edge of a national park where protection is much more intense than outside. We expected that lynx would use areas with high levels of human presence (outside the Park) less than areas with low human presence inside the National Park.

Finally, the study area has dry, hot summers, and during summer free water is only available at artificial sites. We also hypothesized that water is an important and limiting resource for lynx, particularly during summer, and therefore investigated possible associations between lynx movements and the location of points with water (hereafter water sites).

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STUDY AREA

The study was carried out in the north of Doñana National Park and its surroundings, in a 50-km² area called Coto del Rey (south-western Spain; 37°9'N, 6°26'W). Doñana National Park is a flat, sandy area containing three main biotopes: scrubland, dunes, and marsh (Valverde 1958). The climate is Mediterranean sub-humid with mild, wet winters and hot, dry summers. Annual rainfall is between 500 and 600 mm; however, during the study period the area suffered a drought with scarce precipitation in 1992/93 (374 mm), 1993/94 (414 mm), and 1994/95 (252 mm), and unusual flooding during 1995/96 (1,031 mm) and 1996/97 (590 mm up to December 1996).

Coto del Rey is characterized by a mixture of relatively well-conserved areas of Mediterranean scrubland and ash stands where *Pistacia lentiscus* shrubs predominate, plantations of mainly *Pinus pinea*, and cleared areas for cattle grazing with isolated trees (*Quercus suber* and *Olea europaea*); marsh extends to the south of the study area (Fig. 1). There are a few small patches of eucalyptus (*Eucalyptus* sp.) plantations that we considered similar to pine plantations because vegetation structure is similar; they represent 12% of the surface described as pine. Mediterranean vegetation is mainly composed of plants typical of the *Oleo-Quercetum suberis* and

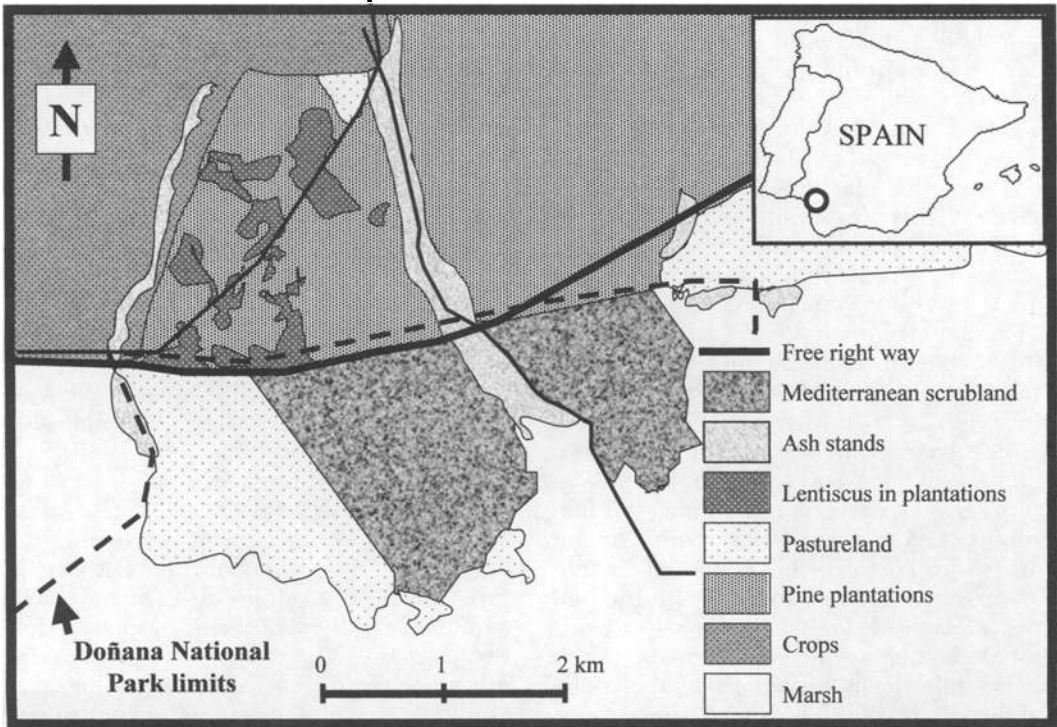


Fig. 1. Map of the study area (Coto del Rey) showing the main vegetation types, the boundary of Doñana National Park, and a free right-of-way that crosses the study area. There were two other free access car-tracks in the north of the study area that are represented as thin black lines. For simplicity, a few small patches of eucalyptus plantations are represented as pine plantations.

Ficario-Fraxinetum angustifoliae associations described in Rivas-Martínez et al. (1980). Pine plantations have a limited understory with plants typical of the *Halimio-Stauracanthetum genistoides* association. Interspersed between the pine plantations are small, poorly conserved patches of the *Oleo-Quercetum suberis* association. In Coto del Rey, there are good populations of red foxes (*Vulpes vulpes*), European badgers (*Meles meles*), Egyptian mongooses (*Herpestes ichneumon*), and European genets (*Genetta genetta*) (Palomares et al. 1996a).

In most of the National Park, human access is restricted to researchers and guards, and hunting is totally forbidden. Conversely, outside of the National Park, levels of human access depend on land owners and game hunting is frequent (although lynx are strictly protected everywhere). To the north of the Park there is

a free right-of-way used for religious pilgrimages, horseback riding, walking, and car travel mainly on weekends and holidays.

METHODS

Rabbit Abundance and Distribution

Rabbit abundance was estimated in 6 habitat/vegetation types: Mediterranean scrubland, ash stands (both inside and outside the National Park, here considered as two different habitats), pine plantations without *P. lentiscus*, patches of Mediterranean scrubland interspersed with pine plantations (hereafter lentiscus in plantations), and pastureland. Habitats were delineated using aerial photographs and ground truthing. The total area of these habitats within the study area ranged from < 100 ha for ash stands inside the National

Park to > 20,000 ha for the pine plantations (Fig. 1). The most common plant species in each habitat are listed in Table 1. Very small patches of rushes (*Juncus* sp.), and grassland, located mainly in the edge between the Mediterranean scrubland and the marsh, were considered as marsh in this study. Similarly, there were also very small patches (< 5 ha) of rushes and scrub within the pastureland habitat which were not considered separately.

Habitat structure was recorded for each area where rabbit abundance was sampled (Table 1). Seven variables were measured in each of 15 20-m-diameter plots for each habitat type. Variables were: tree cover, taller shrub layer cover, shorter shrub layer cover, grass/herb cover, percentage of bare ground, taller shrub layer modal height, and shorter shrub layer modal height. Cover was visually estimated with the help of patterns of known proportions. For modal heights, we measured one plant that we considered as representing the modal height in the site. The shrub species present in the study area form two clearly different layers according to their potential height (Table 1). *P. lentiscus* shrubs are 2.5–4 m tall, whereas the other species are rarely >1.5 m.

Rabbit Abundance.—Rabbit abundance was estimated by line transect sampling (Buckland et al. 1993) carried out in randomly selected areas within each of the habitat types. Transects ranged from 1,100 m to 2,040 m per habitat and were slowly (ca. 1.5–2.5 km/hr) surveyed at dusk (15–20 min before sunset to 25–30 min after sunset), which is the best time of the day to conduct surveys in Doñana (Villafuerte et al. 1993, Moller et al. 1996). For each rabbit observed, the perpendicular distance to the transect line was estimated. We grouped observation distances of rabbits in 10-m intervals and truncated distance at 50 m. Because rabbits could move prior to detection, grouping improved robustness of the estimator of density. The truncation distance and the grouping options were decided after three pilot samplings. Transects were always the same, did not follow any track or road in the

study area, followed straight lines, and were always walked by the same observer.

Rabbits were counted in October–November and June each year (*a priori* times of the lowest and highest rabbit density; Soriguer 1981) from autumn 1993 to autumn 1996 in each habitat. Additionally, for the Mediterranean scrubland and both ash stand habitats, transects were also walked at 2–3 month intervals between June 1994 and October 1996. Each transect was walked between 1 and 4 times per period (mean = 2.0, SE = 0.09) to count the numbers of individuals needed to narrow the confidence interval of the estimates (40, see Burnham et al. 1980).

Densities of rabbits were estimated using the program TRANSECT (Burnham et al. 1980). Analyses were performed using the default options of the TRANSECT program. The program also provides 95% confidence intervals of the estimated density, and these were used to test for significant differences between habitats and periods. On some occasions, results of part of the transects were not considered for the analysis due to people moving in the area during the sampling. On other occasions, the number of rabbits seemed to be very low, but we were not able to identify any possible disturbance. In these cases, results of the overall transects were not considered ($n = 21$) if numbers of rabbits were 30% lower than at any other sampled day during the same period for the same habitat. The figure of 30% was decided upon after exploratory data analysis proved density was severely underestimated when such transects were included. In total, there were 135 days of valid surveys, during which 210,270 m were walked and 8,675 rabbits were counted.

In a few samples and habitats (mainly during the autumn 1996 survey), the number of rabbits observed was too low (between 2 and 16) to confidently run the program TRANSECT. To obtain a rabbit density estimate in these cases, we tested for any correlation between number of rabbits observed 10 m from the sampling line per km walked and the estimated density for 69 samples where rabbit density

Table 1. Vegetational characteristics of the main habitats of the Iberian lynx study area in and near Doñana National Park, southwestern Spain. Percent cover sums to >100 because it was measured in multiple layers.

Habitats	Trees	Taller shrub	Shorter shrub	Grass/herb	Bare ground
Ash stand (inside the National Park)					
Mean cover (%)	7.5 ± 1.7	19.1 ± 4.0	4.5 ± 0.8	58.3 ± 5.5	18.1 ± 4.2
Mean height (m)	—	3.54 ± 0.13	1.33 ± 0.08		
Genus of main species ^a	<i>Fraxinus, Olea</i>	<i>Pistacia, Tamarix</i>	<i>Juncus, Chamaerops</i>		
Ash stand (outside the National Park)					
Mean cover (%)	4.5 ± 2.3	23.9 ± 4.8	0.4 ± 0.3	61.9 ± 5.8	13.7 ± 2.9
Mean height (m)	—	3.41 ± 0.24	0.90 ± 0.06		
Genus of main species	<i>Fraxinus, Olea</i>	<i>Pistacia, Tamarix</i>	<i>Chamaerops, Juncus</i>		
Mediterranean scrubland					
Mean cover (%)	3.0 ± 2.0	30.0 ± 4.6	6.3 ± 2.2	10.9 ± 3.8	52.8 ± 5.6
Mean height (m)	—	3.47 ± 0.23	0.66 ± 0.07		
Genus of main species	<i>Olea, Quercus</i>	<i>Pistacia</i>	<i>Halimium, Chamaerops, Ulex</i>		
Pastureland					
Mean cover (%)	1.1 ± 0.7	0.2 ± 0.2	3.9 ± 2.0	55.5 ± 5.6	41.3 ± 6.1
Mean height (m)	—	1.25	0.68 ± 0.15		
Genus of main species	<i>Quercus, Olea</i>	<i>Rubus</i>	<i>Juncus, Halimium, Ulex</i>		
Lentiscus in plantations					
Mean cover (%)	13.7 ± 6.0	46.3 ± 4.6	5.0 ± 1.7	31.5 ± 3.9	17.1 ± 3.7
Mean height (m)	—	2.49 ± 0.13	0.69 ± 0.05		
Genus of main species	<i>Pinus</i>	<i>Lentiscus</i>	<i>Cistus, Halimium</i>		
Pine plantations					
Mean cover (%)	37.0 ± 3.0	2.8 ± 0.9	18.1 ± 4.4	11.7 ± 2.1	68.5 ± 5.6
Mean height (m)	—	2.41 ± 0.19	1.01 ± 0.04		
Genus of main species	<i>Pinus</i>	<i>Pinus</i>	<i>Halimium, Ulex</i>		

^a A maximum of three species is listed.

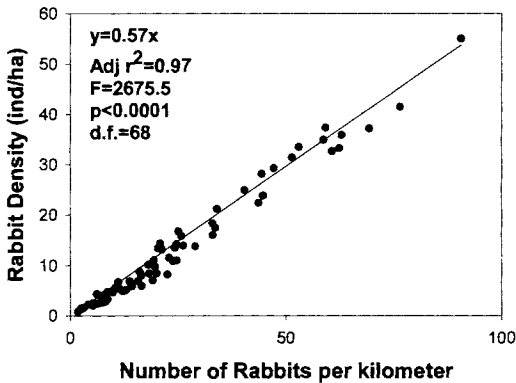


Fig. 2. Linear regression of absolute rabbit density (no./ha) and the number of rabbits observed within 10 m of each side of the transect line per km walked for 69 transects where density could be estimated in and near Doñana National Park, southwestern Spain.

could be estimated (Fig. 2). We truncated the distance to 10 m on each side of the sampling line to diminish the possible differences in visibility among habitats. A linear regression line with forced intercept to zero was fitted using the TableCurve 2D software package (Jandel Scientific Software 1996) to estimate the corresponding densities and their 95% confidence interval values. We considered that these density estimates were suitable since correlation between rabbit density and number of rabbits observed per km walked was very high.

Variations in Rabbit Abundance within Habitats.—Rabbits in Mediterranean habitats may be distributed in patches even within the same habitat types (Rogers and Myers 1979, Rogers 1981). Preliminary information for the study area (Palomares et al. 1996b, Palomares and Delibes 1997) indicated that rabbits might be patchily distributed in the Mediterranean scrubland and pastureland habitats in relation to the marsh border. To check for this possibility, two additional direct rabbit counts in the Mediterranean scrubland (the habitat most important for lynx in the study area) were carried out in June 1994 and June 1995. One count was undertaken in the north of the largest patch, and another in the center of the smallest patch; each crossed several border areas of the scrub-

land and the marsh and other areas far away from the marsh border, an area which is locally called the Vera.

Nevertheless, a direct count of rabbits is not a suitable method to determine rabbit distribution on a fine-grained scale (Burnham et al. 1980, Buckland et al. 1993). Therefore, we mapped rabbit warrens in 126 ha of the Mediterranean scrubland and 342 ha of pastureland between April and October of 1995 to check if warren distribution accurately reflected rabbit distribution within these habitats. Because previous information indicated that abundance of rabbits and warrens may vary in relation to distance to the border of the Vera (Palomares et al. 1996b, Palomares and Delibes 1997), the warren mapping was carried out covering areas from the Vera to 1600 m away (the available range of distances in the sampled habitats). Warren mapping consisted of recording the position of every warren within these areas in U.T.M. coordinates using a Global Positioning System (GPS; model Garmin 75). Coordinates were considered valid if the internal estimated error position (EPE) of the GPS was ≤ 30 m. Nevertheless, GPS error was also independently estimated to EPE by recording 20 times 20 points of known coordinates from 1:5,000 maps of the study area. On 72% of the occasions GPS error was below 50 m, and on 97% GPS error was below 100 m. The number of entrances was also counted in every warren mapped. A total of 1,301 warrens was mapped. For warren mapping, teams of 3–5 people slowly walked small sections of survey areas inspecting for warrens everywhere. We used fire breaks as limits for the area surveyed in the Mediterranean scrubland habitat. A total of 353 hours/person were dedicated to warren mapping.

For each habitat type, data on density of warrens, density of entrances, and mean number of entrances per warren were separately obtained for every 100-m-wide belt (starting from the Vera) using the IDRISI geographic information system software (Eastman 1995). The Vera was considered the border of Mediterranean scrubland habitat, and the potential flooding line of

the marsh in the pastureland was easily determined from 1:5,000 maps of Dirección General del Medio Ambiente. Using IDRISI, a distance surface was generated using the Vera line as a target feature. The distance from the Vera to every warren was measured. The area sampled for every 100-m interval (see Appendix 1) was also obtained with IDRISI using a 10×10 m grid.

The trend in density of warrens, density of entrances, and number of entrances per warren in relation to the distance to the Vera was analyzed using regression techniques and the TableCurve 2D software package (Jandel Scientific Software 1996). Trends were compared between the Mediterranean scrubland and pastureland habitats. Furthermore, differences in the number of entrances per warren between habitats were tested by a two-way analysis of variance with habitat and distance interval as fixed effects and number of entrances transformed as $\log(X)$.

Lynx Diet

Diet was determined by analyzing feces collected twice per month on the study area. Feces were oven-dried before their contents were separated and identified with the aid of reference collections. Frequencies of occurrence (number of feces with remains of a prey category/total number feces analyzed $\times 100$) were calculated for each prey category. The following prey categories were distinguished: rabbits, other small mammals, ungulates, birds, reptiles, and insects.

Lynx diet was determined for the full period of study, and for seasons based on rabbit densities and reproductive behavior: winter (January–March; mating), spring (April–June; nursing and weaning in females), summer (July–September; females accompanied by young), and autumn (October–December; independence of young). The average number of feces collected per season was 73.2 (SE = 13.2, range = 15–191, $n = 16$ seasons). Variation in food habits among family groups was examined by assigning feces to different lynx pairs or

family groups of individuals living in different parts of the study area by spatial location of each feces. To be sure of the identity of the feces, we plotted 80% isopleth kernel home ranges (Worton 1989) of all adult females living on the study area, and only feces collected within these non-overlapping home ranges of each female were considered for analysis.

Capture and Radiotelemetry

Lynx were captured with box-traps ($1.7 \times 0.5 \times 0.5$ m) and padded foothold traps (Victor softcatch no. 1.5 and 2, Woodstream Corporation, Lititz, Pennsylvania, USA; Delibes and Beltrán 1986), usually between November and February every year. During the last three years, lynx also were captured during short periods in April and May. All animals were immobilized with ketamine mixed with xylazine (Ferrerías et al. 1994) or with zoletil (Travaini and Delibes 1994). Lynx were then weighed, sexed, measured, tagged with subcutaneous transponders (Fagerstone and Johns 1987), and fitted with 150–151 MHz radio-collars (Wildlife Materials, Inc., Carbondale, Illinois) which contained tip switches to monitor activity.

Lynx were classified as young (<12 months old starting 1 April), subadult (12–24 months old), or adult (>24 months old) according to tooth eruption patterns and body size. Most young and subadult individuals were tagged with transponders when kittens (less than 1 month old); thus, their age was known when they were subsequently captured. Specific age in years was also estimated for most adults by tooth cementum annuli (Zapata et al. 1997).

Every radio-tagged lynx was located from the ground 4 times per week (2 times during the day and 2 times at night on different days) using two signal bearings, usually (78% of occasions) <0.8 km from the animal to decrease triangulation error. Triangulation error was estimated by locating test transmitters; 10 radio-collars were placed in the study area and 8 different observers independently located them without knowing the transmitter positions.

On 37% of occasions error was >200 m and, since errors of this size would be important for analyses of habitat use, we moved in close to radioed lynx close to the edges of vegetation types to exactly determine in which habitat they resided. During intensive, once-weekly 24-hr tracking periods selected lynx were located once every hour, beginning at 1200 hr of a given day and ending at 1200 hr of the next day. Some young and subadults dispersed from the study area or were expelled from their territories by other adults (see below). Only data previous to their leaving the study area were considered for these individuals.

Number of Lynx and Density

The minimum number of different lynx present on the study area was determined from 1) trapping and radio-monitoring, 2) intensive radio-tracking of the females during the breeding period, and 3) lynx sightings on the area. In this last case, the spatial position, the number of individuals observed, the age-class of the animals, and the presence or absence of a collar (when it was possible to determine) were recorded for each observation. Collars were of different colors to distinguish animals if the transmitters were not working. Lynx are quite easily observable in the study area, which when coupled with intense research activity, allowed us to accurately account for all lynx. Most observations (82%) were opportunistic except when we attempted to determine the number of young accompanying radio-collared females.

Density was estimated by season (as for diet), and an individual was considered present in a given season if it was on the study area for at least one day. In two cases of adult males involved in territory disputes, we did not know when the animals arrived on the study area. However, Ferreras et al. (1997) showed that males are in dispute of a territory for at least 4 months before the loser leaves. Thus, we assumed that the new male was present on the study area during the 4 months before

the former resident male left the study area.

Young were considered as new individuals as soon as they were seen travelling with females (summer), although they were already present on the study area as kittens in spring. During 1993 we knew the total number of kittens (8), but because our research activity then was not as intense as later, we could only verify that 3 of these kittens were present in the study area as young. Nevertheless, studies on reproduction in Doñana indicated that usually 2 young survived per female, and young were most likely to leave the area during winter (Ferreras 1994, authors unpubl.). Thus, we considered that another 3 young were present on the study area between summer 1993 and winter 1994.

Three basic factors must be considered to confidently estimate density of a given carnivore population: 1) decide the area where density will be estimated, 2) know how many animals are using the area, and 3) estimate the time spent by each animal within the area. We used the trapping area (McLellan 1989) as the area in which to estimate lynx density. This is the minimum convex polygon area that includes all locations where animals were trapped. The number of animals using the trapping area was equal to the number of individuals known to be present in the study area. Finally, the proportion of time spent for each individual within the trapping area was estimated as the proportion of independent locations within the trapping area.

Once the number of individuals and their use of the trapping area was known, we considered that each individual proportionally contributed to the density estimate according to its percentage of locations within the trapping area and time spent in it (e.g., an individual with 55% of locations within the trapping area and recorded on the study area only during 2 months for a given 3-month season contributed $(0.55 \times 60 \text{ days})/90 \text{ days} = 0.37$ individuals to the density estimate). For two adult males and seven young, we did not know what use they made of the trapping area because they were not radio-

tracked during the study period. In these cases we considered that the adults made use of the trapping area in a similar way to other adults radio-tracked in the same area. We considered young as having use similar to their mother's during summer (when young accompany the female; Aldama 1993), or as the average use of their siblings in other seasons.

Lynx Space Use

Home Range.—Home range size was estimated using the Ranges software package (Kenward and Hodder 1996) to calculate the 100% (MCP100), 95% (MCP95), and 90% (MCP90) minimum convex polygons of all available isolated locations. MCP100 and MCP95 were included because these are most often used in radio-tracking studies (Harris et al. 1990, White and Garrott 1990). MCP90 was also used because excluding 10% of the most external locations yielded a more reliable estimate of home range size for some individuals that were involved in temporal excursions that crossed large open areas. Size of core areas (Adams and Davis 1967, Worton 1989) also was calculated as the 60% isopleth using the kernel approximation (KM60) and the procedure proposed by Harris et al. (1990).

Home range and core area sizes were estimated for different periods: the full period of radio-tracking, and on a seasonal basis considering four seasons (as for diet) from 1993 to 1996. For most seasonal home ranges estimated as MCP100, size reached an asymptote after 30 fixes; home ranges estimated using <30 fixes were not included in analyses.

We performed an analysis of covariance (ANCOVA) to test for differences in home range and core area size among sex-age classes (adult females, adult males, and young-subadult individuals) for all radio-tracking periods. Because there was an unequal number of fixes for each sex-age class, mainly for young individuals (Appendix 2), the number of fixes was included in the analysis as covariate to test for any potential effect. Before performing the AN-

COVA, we tested for the assumption of parallelism of slopes of Y on X for all sex-age classes (Sokal and Rohlf 1995). In a second analysis, we tested for any difference in seasonal home range and core area size through a three-way analysis of variance of sex-age class (three levels), season (four levels) and year (four levels). We also tested for any first- and second-order interactions between independent variables. For simplicity, seasonal home range data are presented only for MCP90 and KM60 methods, although statistical analyses were performed for MCP100 and MCP95, as well. For all statistical tests, home range sizes were log-transformed for analysis and the individual was considered as the sampling unit, thus avoiding the inherent problems associated with pseudoreplication (Hurlbert 1984).

Daily Movements.—Daily distance traveled was considered as the sum of the straight-line distances between successive relocations in each of the 24-hr periods of intensive tracking. Daily home range was also estimated for every 24-hr period by the minimum convex polygon method using 100% of available locations. A total of 97 24-hr tracking periods was available (Appendix 2).

Differences in daily distance traveled and daily home range size were examined for sex-age classes, seasons, and years using a nested analysis of variance. The independent variables were sex-age class, season, year, or individual nested within the other three variables to account for the potential autocorrelation for data coming from the same individuals. We also tested for any first- and second-order interactions between independent variables. Daily distance traveled and daily home range size were log-transformed for analyses, and the individual was considered as the sampling unit.

Movements in Relation to Water Sites.—We tested whether lynx were attracted to water sites more than expected from random. For each of the 97 24-hr intensive radio-tracking periods we determined 1) the occurrence of animals near a water site, 2) the total distance that animals

moved around the water site, and 3) the number of times throughout the 24-hr period that animals visited the water site. Because our sampling interval during the intensive tracking periods (one hour) did not preclude an animal visiting a water site undetected, and because of potential radio-tracking error, we made a conservative decision that animals visited the water site if any straight line connecting two locations crossed through an imaginary 200-m-radius circle around the site. In this way it was possible to count the number of intensive periods that animals were in the circle at least once, the distance animals moved inside the circle, and the number of times during an intensive period that animals were in the circle.

The observed data were compared with the data obtained after 100 simulations of the same set of 24-hr intensive tracking periods but using randomly generated points as the water sites. Because one of the three actual water sites of the study area was inside each pair's home range, random water sites were generated within the females' home ranges. Female home ranges were chosen because the male of a pair could not be tracked. Additionally, two females were also tracked in the same area at different times, and in this case the composite home range from the two females was used. For the 100 simulations, the mean and its 95% confidence intervals were obtained for the number of periods animals were in the water site, the distance moved in the water site, and the number of different times animals visited the water site throughout a period. If the data for these three variables were below, within, or above the 95% confidence interval obtained from the simulated data, lynx were considered as avoiding, using at random, or showing a positive association to water sites.

Because water is not available during some periods of the year except as permanent, artificially provided water, we also tested for different behavior of lynx in relation to water sites depending on whether there was water in other places. Throughout the study, water was absent every-

where except in artificial water sites during the dry season of every year (from June to October), and in many other times during the winters 1993, 1994, and 1995 when there was a severe drought in the study area. Therefore, we considered every 24-hr radio-tracking period either as belonging to times with available water only in the artificially permanent water sites or to times when water was available in other places due to rain. We considered that water occurred only in the artificial water sites during the following times: 24-hr periods during the dry season when there was no rain (< 5 mm) during the sampling days or the day before, and 24-hr periods during the wet season of 1993 and 1994–1995 when there was no rain the previous month. The remaining periods were considered to have water available in other places. Under the circumstances mentioned above we were confident that water was or was not available in other places on the study area. Nevertheless, for five tracking periods undertaken when some rainfall occurred a few days previous to the tracking during the wet period of 1993/94 and 1994/95, we were not confident if water was or was not available in other places and they were excluded from analyses. For each subset of data, the same analyses as for the full data set were performed.

Additional information on the use of water sites was provided by opportunistic lynx sightings obtained throughout the study and by an 8-day period of systematic observations carried out during August 1995 by a team of wildlife film recorders (J. Cobo, pers. comm.).

Habitat Use.—Habitat use was studied using independent locations. One of 7 habitat types delineated in the study area (i.e., the 6 described earlier plus eucalyptus plantations) was assigned to each lynx location. We tested for significant differences in habitat use considering active or inactive locations separately (Palomares and Delibes 1992). Differences in habitat use were also tested for sex-age classes, and seasons and years (Schooley 1994), using multivariate analysis of variance (MANOVA) in which all dependent vari-

ables (habitat types) are included in a single analysis (Scheiner 1993). For ease of understanding, habitats were grouped in three categories to analyze seasonal and annual variations in habitat use by lynx. The three categories were scrubland (Mediterranean scrubland and ash stand habitats), plantations (pine and eucalyptus plantations and lentiscus in plantations), and open habitats (pastureland and marsh). To simplify the analysis, we first conducted a MANOVA where the activity and age-sex class were considered the independent variables, followed by another MANOVA to test for significant differences among seasons and years. Individuals were always considered the sampling unit, and the dependent variable was the percent of locations within each habitat type transformed by the square root of arcsine. The Pillai's trace was chosen as the MANOVA statistic (Scheiner 1993). For all analyses, only individuals with 20 independent locations were considered.

Preference for each habitat type was determined by the Jacobs index (Jacobs 1974), which varies from +1 (maximum preference) to -1 (maximum avoidance). Availability of each habitat type was the proportion of the total area contained within individual home ranges (delineated by the minimum convex polygon method using all available locations). Individuals were again considered as the sample unit, and each habitat type was preferred or avoided if the mean value of the Jacobs index was significantly different from zero (t-test). Value of the Jacobs index is not accurate when habitats are little represented within home ranges; thus, a given habitat was considered for analysis only if its availability was >5% within an individual's home range.

Penetration distances of lynx within non-preferred habitats according the Jacobs index (i.e., distance of a lynx location from the edge of a preferred habitat) were measured using IDRISI geographic information system software. A distance surface was first generated using the patches of preferred habitats by lynx as the target features. Then a distance was assigned to ev-

ery lynx location, and a frequency table was generated.

Protection and Human Influence.—We estimated the effect of protection and human presence on local use of space by lynx by counting the number of locations inside and outside of the National Park boundaries, under the assumption that human disturbance is less inside the National Park than outside it. This assumption was reinforced because just to the north of the National Park there is a free right-of-way (Fig. 1) that is used for religious pilgrimages almost every weekend and horse riding, walking, and car travel mainly on weekends, Easter holidays, and summer vacations.

Habitat availability in our study area was different inside and outside the National Park. Therefore, we also compared distances to El Rocio (a tourist village 1.5 km to the west of the study area) for individual lynx located outside of the National Park, because most of the people having access to the study area came from El Rocio through the free right-of-way. The western half of the area outside the National Park (i.e., closest to El Rocio) was open to people who used it for recreation. Moreover, there were two other roads surrounding the western area where people could move freely (Fig. 1). In the eastern half of the area outside the National Park, there was only the fenced free right-of-way, within which people cannot move, and human presence there was generally very reduced. According to levels of human access and the spatial situation of home ranges of lynx, three categories of distance to El Rocio were established: close, intermediate, and farthest. The close area included part of the western half of the study area; the intermediate included parts of the western and eastern parts of the study area; and the farthest included only part of the eastern half of the study area.

Because animals living at different distances from El Rocio also had different habitat availability outside the National Park (see Fig. 1), results could be a consequence of different habitat availability rather than level of human influence. To

test for this alternative hypothesis, two different approaches were used. First, we only considered locations outside the National Park in the pine plantations, eucalyptus plantations, and lentiscus in plantations habitats (all of them non-preferred habitats and situated to the north of the free right-of-way; see Fig. 1 and Results), and second we quantified how frequently lynx used the largest patch of ash stand habitat (running from north to south in the middle of the study area; see Fig. 1), which was divided in two by the border of the National Park (i.e., two parts of the same habitat but with different levels of protection and human influence).

Differences in the percent of locations outside the Park in any habitat, and outside the Park in non-preferred habitats, were tested for sex-age classes and the distance categories from El Rocio by analysis of variance with the percentage of locations arcsine-transformed. A distance category from El Rocio was assigned to each lynx depending on patterns of land use.

Rabbit Density and Number of Rabbits within Lynx Home ranges

A Geographical Information System (GIS) was used to help estimate rabbit density and number of rabbits within lynx home ranges and core areas, and to estimate the number of rabbits per lynx in the study area. All estimates were for the spring and autumn seasons between autumn 1993 and autumn 1996, when most of the habitats were sampled for rabbits.

To estimate rabbit density within ranges, value raster maps of 50-m grids of general rabbit densities were created for each season, on which the corresponding seasonal lynx home ranges were overlapped. Average rabbit densities for each range were then extracted. For the Mediterranean scrubland, rabbit density (y) decreased in relation to distance to the grassland areas of the Vera and the pastureland (x) following a negative exponential function ($y = a + be^{-x}$). Therefore, for this habitat, rabbit density was calculated for each grid according to this function and

the densities estimated in the areas closest and farthest to the Vera and the pastureland during the line transect samplings. For the rest of the habitats, the estimated rabbit density from the line transect surveys for each season and year was considered when creating the value raster maps. For some seasons and habitats (autumn 1995 and 1996 for lentiscus in plantations and pine plantations, and autumn of each year and spring 1996 for Mediterranean scrubland farthest from the Vera) actual rabbit density was not estimated. In these cases, rabbit density was considered equal to the previous autumn season for lentiscus in plantations and pine plantations. For Mediterranean scrubland farther from the Vera we considered that rabbits seasonally fluctuated similar to the Mediterranean scrubland habitat closest to the Vera.

Once rabbit density within lynx ranges was known, the total number of rabbits was calculated for the total home range and for each habitat within the home range. Rabbit density and number of rabbits in home ranges were calculated for the 90MCP home range and core areas (60% kernel isopleth) for a total of 22 lynx-seasons.

Number of rabbits within lynx ranges did not provide information on numbers of rabbits per lynx, since different lynx may have had overlapping home ranges (Ferreras et al. 1997). Therefore, we approximated the number of rabbits per lynx from the generated maps on rabbit densities in the study area and the estimated lynx density in the area. The number of rabbits was calculated for the trapping area where lynx densities were estimated; seasonal numbers of rabbits per lynx were then obtained by dividing the total number of rabbits within the trapping area by total number of lynx in the same area for each season. We calculated 95% confidence intervals for the number of rabbits per lynx from 95% confidence intervals of rabbit density estimates.

General Remarks on Statistics

Throughout the text and figures, mean values are presented with ± 1 standard er-

Table 2. Frequency of occurrence of different prey categories in Iberian lynx feces in and near Doñana National Park, southwestern Spain, 1993–1996.

Prey category	Overall (<i>n</i> = 1,171)	Family group		
		West (<i>n</i> = 220)	Central (<i>n</i> = 527)	East (<i>n</i> = 233)
Rabbits	99.3	97.7	99.4	100.0
Small mammals	2.5	3.6	1.7	2.2
Ungulates	0.9	1.4	1.1	0.4
Birds	2.0	3.2	1.9	2.6
Reptiles	0.1	0.0	0.2	0.0
Insects	0.9	1.4	1.0	0.4

ror (SE). Data were unbalanced in all tests; therefore ANOVA, ANCOVA and MANOVA were performed using the GLM procedure in SAS (SAS Institute Inc. 1990) and a Type III sums of squares. Non-parametric analysis of variance was performed using the procedure NPARIWAY in SAS (SAS Institute Inc. 1990). *P* < 0.05 was considered statistically significant.

RESULTS

Importance of Rabbits in Lynx Diet

Lynx ate rabbits almost exclusively. Rabbit remains were present in 99.3% (*n* = 1171) of feces analyzed, and no other prey category appeared in more than 2.5% of feces (Table 2). Seasonally, rabbits were also the basic prey with frequencies of occurrence of 100% for 10 seasons, between 98% and 99% for 5 seasons, and 92% for one season (autumn 1994). A similar pattern resulted when feces from each family group were analyzed separately, with rabbits appearing between 97.7% and 100% of the feces analyzed; no other single prey species appeared in more than 3.7% of the feces (Table 2).

Rabbit Abundance

Numbers of rabbits observed during the surveys ranged between 0.5/km for pine plantations and 81.6/km for Mediterranean scrubland. Rabbit density in the study area ranged between less than 1 rabbit/ha during autumn of every year and June 1996 in pine plantations, and 55.1

rabbits/ha during June 1994 in the Mediterranean scrubland (Table 3). Rabbit density had to be estimated (Fig. 2) during both autumn surveys and the June 1996 survey in the pine plantation habitat due to the extremely low number of rabbits recorded (13 rabbits seen on 11,5 km of survey). Similarly, density had to be also estimated for all habitats during the autumn 1996 survey when we did not count more than 5.7 rabbits/km walked in any habitat.

In most samplings, the Mediterranean scrubland contained the highest rabbit density. Nevertheless, in November 1993, June 1995, November 1995, and June 1996, rabbit densities in the Mediterranean scrubland were not significantly different from rabbit densities in ash stands inside and outside of the National Park. Rabbit densities did not differ statistically between the two ash stand habitats in June 1994, autumn 1994, and autumn 1995. Mediterranean scrubland and both ash stand habitats were followed in rabbit numbers by the pastureland and the lentiscus in plantations, both with approximately 78% fewer rabbits than the Mediterranean scrubland, and finally by the pine plantations with 93–95% fewer rabbits than the Mediterranean scrubland (Table 3). Rabbit density generally was higher (3.5 times on average) during June surveys than during those in autumn, except for the last year when differences between both periods were even larger (Table 3).

Rabbit density peaked in April/June of each year in the three habitats where rabbit abundance was estimated throughout

Table 3. Density (no./ha) of rabbits in different habitat as estimated from line transect surveys conducted between November 1993 and October 1996 in and near Doñana National Park, southwestern Spain. Within each habitat type, the mean total distance walked = 17.98 km (range = 11.93–23.09), mean total rabbits counted = 496 (range = 82–1,171), and mean total number of valid census days = 12.7 (range = 11–14).

Date	Ash stand (NNP) ^a			Ash stand (NP) ^a			Mediterranean scrubland			Pastureland			Lentiscus in plantations			Pine plantations		
	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI	Mean ± SE	95% CI
November 1993	5.0 ± 1.0	3.1–6.8	11.5 ± 1.4	8.8–14.2	18.3 ± 2.5	13.4 ± 23.2	2.5 ± 0.5	1.5–3.5	3.2 ± 0.8	1.7–4.8	0.2 ^b	0.2–0.2	3.2 ± 0.8	1.7–4.8	2.5 ± 0.4	1.7–3.3	2.5 ± 0.4	1.7–3.3
June 1994	31.4 ± 3.7	24.2–38.7	37.4 ± 4.2	29.1–45.6	55.1 ± 4.2	46.9–63.3	7.1 ± 0.9	5.3–8.8	14.3 ± 2.3	9.8–18.8	0.3 ^b	0.3–0.3	14.3 ± 2.3	9.8–18.8	2.0 ± 0.4	1.3–2.8	2.0 ± 0.4	1.3–2.8
October 1994	4.8 ± 0.7	3.3–6.2	6.9 ± 0.7	5.5–8.3	13.2 ± 1.6	10.1–16.3	5.5 ± 0.8	3.9–6.9	2.0 ± 0.4	1.3–2.8	0.3 ^b	0.3–0.3	2.0 ± 0.4	1.3–2.8	6.0 ± 0.8	4.4–7.6	6.0 ± 0.8	4.4–7.6
June 1995	8.2 ± 1.0	6.3–10.2	32.7 ± 3.3	26.2–39.1	41.5 ± 4.1	33.6–49.5	14.2 ± 2.0	10.2–18.1	14.2 ± 2.0	10.2–18.1	1.7 ± 0.3	1.0–2.3	14.2 ± 2.0	10.2–18.1	5.7 ± 1.1	3.4–7.9	5.7 ± 1.1	3.4–7.9
November 1995	8.8 ± 1.3	6.2–11.4	11.1 ± 1.4	8.3–13.9	7.0 ± 1.5	4.1–9.9	5.9 ± 0.8	4.3–7.5	7.0 ± 1.5	4.1–9.9	1.1 ^b	1.0–1.1	7.0 ± 1.5	4.1–9.9	1.1 ^b	1.0–1.1	1.1 ^b	1.0–1.1
June 1996	13.4 ± 2.3	8.9–17.9	4.9 ± 0.7	3.5–6.4	16.8 ± 2.1	12.7–20.9	1.4 ± 0.3	0.8–1.9	16.8 ± 2.1	12.7–20.9	1.1 ^b	1.0–1.1	1.4 ± 0.3	0.8–1.9	5.7 ± 1.1	3.4–7.9	5.7 ± 1.1	3.4–7.9
October 1996	1.2 ^b	1.2–1.2	1.0 ^b	0.9–1.0	2.0 ^b	2.0–2.1	1.1 ^b	1.1–1.2	2.0 ^b	2.0–2.1	1.1 ^b	1.0–1.1	1.1 ^b	1.1–1.2	1.1 ^b	1.0–1.1	1.1 ^b	1.0–1.1

^a NNP = not national park, NP = national park.

^b Density could not be estimated using the program TRANSECT because a very low number of rabbits (range = 2–16) were observed; density and 95% confidence intervals were estimated from the number of rabbits observed/km walked and using the regression equation in Fig. 2.

^c No survey was undertaken.

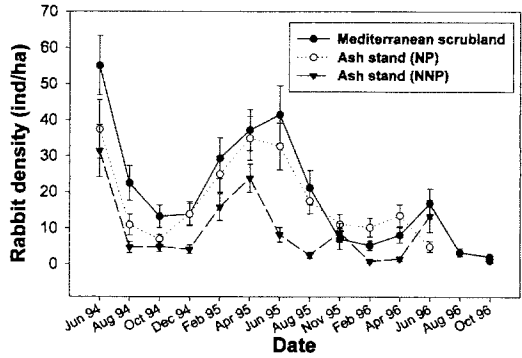


Fig. 3. Rabbit densities estimated by line transect sampling for three habitats throughout the study period in and near Doñana National Park, southwestern Spain. NP = inside National Park, NNP = outside National Park.

the year. The lowest rabbit densities occurred from August to February (Fig. 3). Rabbit density was on average 81% and 78% lower in 1996 than in 1994 and 1995 for Mediterranean scrubland; 82% and 77% lower in 1996 than in 1994 and 1995 for ash stand inside the National Park; and 72% and 91% times lower in 1996 than in 1994 and 1995 for ash stand outside the National Park (Fig. 3).

Variations in Rabbit Abundance within Habitats

Within Mediterranean scrubland, rabbit density was higher on the transect closest to the Vera (55.1 ± 8.2 and 41.5 ± 8.0 rabbits/ha in 1994 and 1995, respectively) and lower in the farthest one (6.8 ± 1.9 and 2.4 ± 0.6 rabbits/ha). The middle distance transect had intermediate values (33.5 ± 7.8 and 16.0 ± 3.8 rabbits/ha).

We mapped 829 warrens in Mediterranean scrubland and 472 in the pastureland. The number of entrances counted was 4,946 and 5,528, respectively. The overall mean number of entrances per warren was 6.0 ± 0.19 ($n = 829$, range = 1–54) for the Mediterranean scrubland and 11.7 ± 0.76 ($n = 472$, range = 1–218) for the pastureland.

Warren density, entrance density, and mean number of entrances per warren decreased with increasing distance to the

Vera in the Mediterranean scrubland (Fig. 4). The trend was significant and highly adjusted to the negative exponential function, with adjusted r^2 ranging between 83% and 97%. Warren density, entrance density, and mean number of entrances per warren quickly decreased from the Vera up to the distance interval between 201–300 m, after which all three variables remained constant (Fig. 4). As expected, warren density, entrance density, and number of entrances per warren were highly inter-correlated according to the distance to the Vera (all r 's ≥ 0.90 , all P 's < 0.0001 , $n = 16$; Pearson Product Moment Correlation).

Warren density, entrance density, and number of entrances per warren in the pastureland were not correlated to distance to Vera (Fig. 4). Although the three variables initially decreased until the distance interval between 201–300 m was reached, as in the Mediterranean scrubland, after that there was no clear trend. The highest values for the density of warrens and entrances were between 801 and 1,000 m from the Vera (Fig. 4d and 4e) and between 301–400 m from the Vera for the number of entrances (Fig. 4f). In pastureland, correlation between variables was only significant between density of warrens and entrances ($r = 0.86$, $P = 0.0002$, $n = 13$), not between number of entrances per warren and density of warrens ($r = 0.13$, $P = 0.6830$) or density of entrances ($r = 0.52$, $P = 0.0702$).

Differences in the mean number of entrances per warren were significant between habitats ($F = 48.49$, $df = 1$, $P < 0.0001$) and distance intervals to the Vera ($F = 13.58$, $df = 15$, $P < 0.0001$). There was no significant interaction between habitat and distance categories to the Vera ($F = 0.91$, $df = 11$, $P = 0.5269$).

The Lynx Population

Twenty-one different lynx (4 adult females, 3 adult males, 4 young or subadult females, and 10 young or subadult males) were captured and radio-collared during the study (Appendix 2). In addition, we

made 486 lynx observations, 250 of which were of collared individuals, 214 of uncollared ones, and 22 in which it was not possible to determine whether or not animals were collared. The adult lynx population on the study area was composed of three male-female pairs (Fig. 5), except during parts of 1994, 1995 and 1996 when at least one adult female (FA73) was in territorial conflict with another unmarked female (FA62), and three adult males were also present while in territorial conflict with former resident males (MA84 vs. MA75 and another unmarked individual vs. MA54), or meeting females during the mating period. All but two adults living in the study area (the adult male of one of the pairs during the full study period and another adult male during the second half of the last study year) were trapped and radio-collared for at least some part of the study. The number of adults that were collared ranged between 50% at the start of the study to 87% in 1996, averaging 69% for the full study period. No adult lynx died during the study.

The number of known young in the study area per year ranged between 1 to 10, with the highest numbers during the summer and lowest numbers usually during the winter (Fig. 6a). Numbers for the first half of 1993 are probably below the actual numbers, but after this date, and particularly after the second half of 1994, the exact number of young in the study area was known because all young born in 1994, 1995, and 1996 were trapped. Altogether there was a minimum of between 7 and 17 lynx on the study area, with the highest numbers present in 1994 (Fig. 6a). This time coincided with the period when two females that were in territorial conflict successfully produced a combined total of 7 young. Only two young lynx died during the study, both of unknown causes.

The trapping area was 5.38 km², and the mean percentage of times lynx were radio-located within it was 60 ± 4.8 ($n = 20$, range = 12–89). The average adult density was 0.77 ± 0.01 ind/km² ($n = 16$ seasons) ranging between 0.72 and 0.88, whereas density of young was 0.46 ± 0.07 and var-

Mediterranean Scrubland

Pastureland

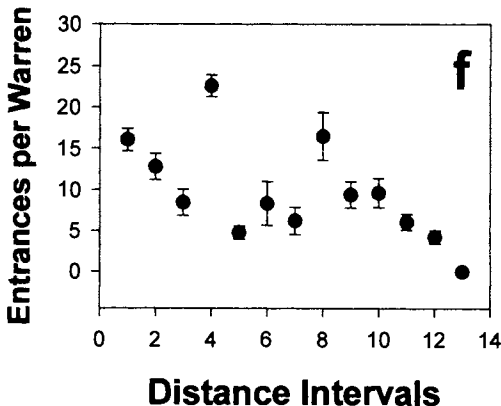
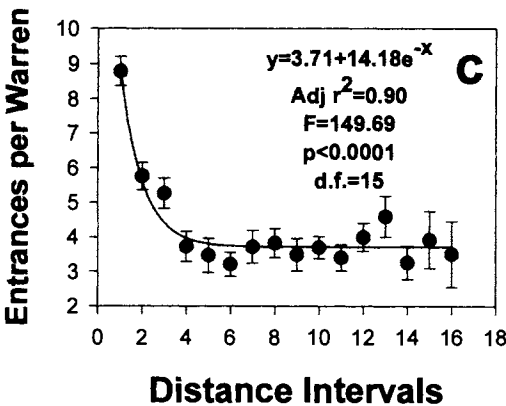
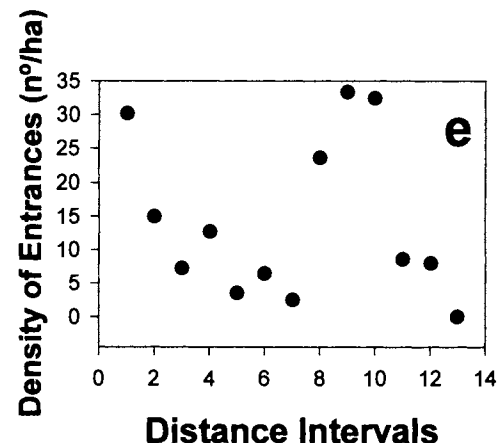
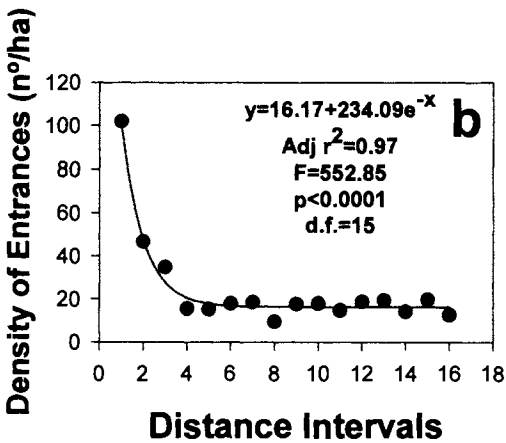
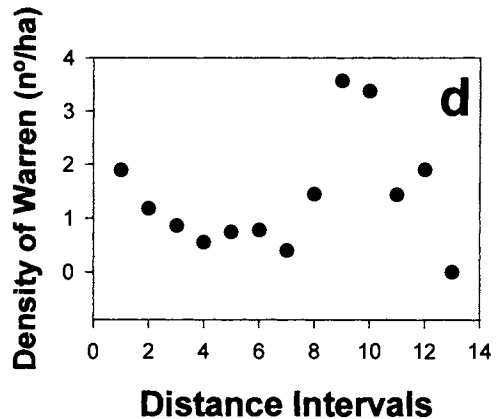
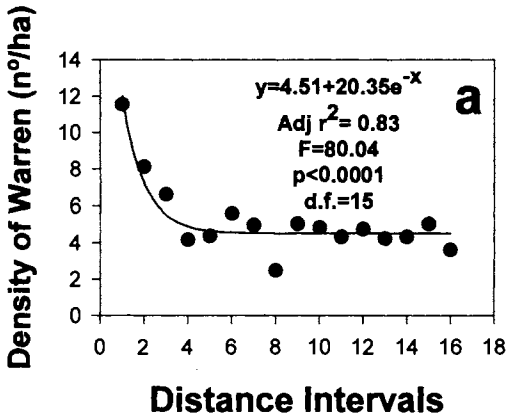


Fig. 4. Density of warrens, density of entrances, and mean (\pm SE) number of entrances per warren in Mediterranean scrubland and pastureland in relation to each 100-m distance interval to the Vera during 1995 in and near Doñana National Park, southwestern Spain. For the three variables in Mediterranean scrubland we also show the statistic and adjusted regression line following an exponential decay. Numbers in distance intervals represent the top limit of the 100-m distance intervals (i.e., 2 represents the distance interval 101–200 m).

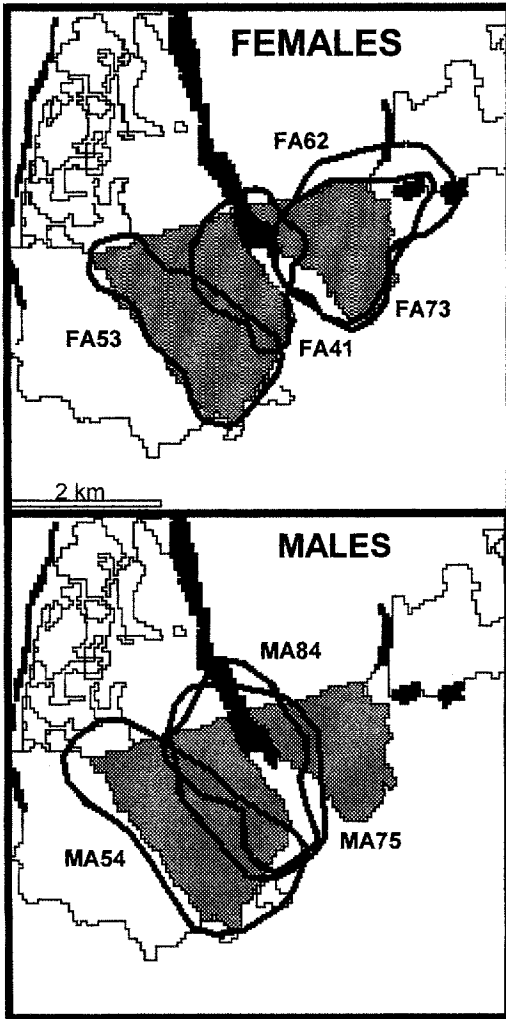


Fig. 5. Home ranges of adult lynx radio-tracked between 1993 and 1996 in and near Doñana National Park, southwestern Spain. Home ranges represent 80% kernel isopleth for each individual. The 80% kernel isopleth was chosen for representation because it reduced the overlap among individuals and delimited quite well the most likely exclusive territories of adults. Females FA62 and FA73, and males MA75 and MA84, were not simultaneously using the area except during a short period when they were disputing the territory. Mediterranean scrubland (gray) and ash stand (black) are also filled with different patterns.

ied more widely (between 0.07 and 1.12) than in adults (Fig. 6b). Seasonally, overall density fluctuated due to the variation in young produced; adult density was quite stable through the study period (Fig. 6b).

All lynx we trapped were radio-collared, but few locations were collected from a

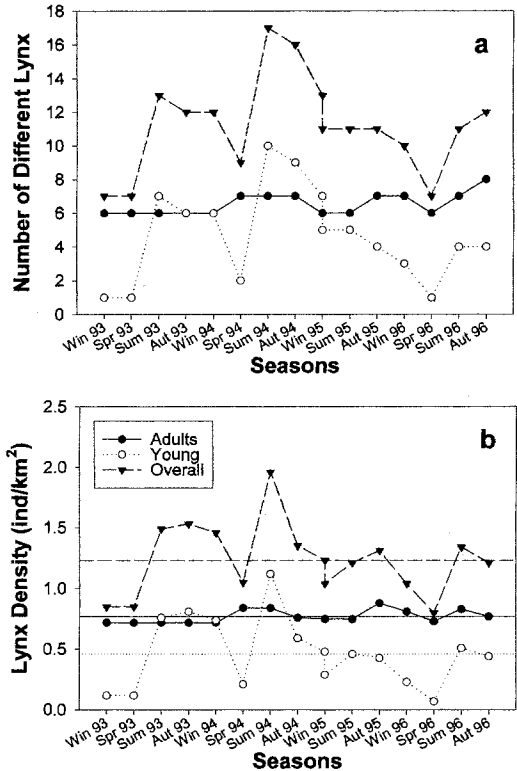


Fig. 6. Minimum number of individuals present (a) and minimum density (b) for adult, young and total (adult plus young) lynx by season in the study area between the start of 1993 and the end of 1996. Reference lines in (b) indicate mean seasonal densities for each age and all individuals.

young female prior to her death and from a young female and a subadult male that dispersed within 2 weeks of capture (Appendix 2). Another young male died one month after capture, and 8 young or subadult individuals dispersed.

Lynx Home Range

Total Home Range Size.—Mean home range size (MCP100) varied from 7.3 to 18.2 km² for marked lynx (Table 4). The size of home ranges greatly decreased when the most external 5 and 10% of locations were excluded, representing only 33–73% of the MCP100. Mean core area sizes varied from 1.4 km² in females to 2.5 km² for young individuals and were about 10% to 34% of the MCP100.

Male MCP90 home ranges were 1.5

Table 4. Minimum convex polygon home range sizes (km²) of Iberian lynx using 100% (MCP100), 95% (MCP95) and 90% (MCP90) of all available locations, and estimated core area size (KM60) using the 60% kernel isopleth in and near Doñana National Park, southwestern Spain, 1993–1996.

Age	Sex	n	Number of locations			MCP100			MCP95			MCP90			KM60		
			Mean ± SE	Range	Mean ± SE	Range	Mean pm SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range			
Adult	Female	4	438.8 ± 123.3	132–733	9.5 ± 1.5	6.4–12.9	5.3 ± 0.6	3.9–6.6	4.1 ± 0.4	3.0–4.9	1.4 ± 0.2	1.0–1.7					
	Male	3	308.3 ± 117.3	190–543	18.2 ± 8.2	6.6–34.0	10.3 ± 4.1	4.8–18.3	6.0 ± 1.5	3.7–8.9	1.8 ± 0.2	1.6–2.2					
Young	Both	7	73.0 ± 11.9	37–134	7.3 ± 1.0	3.6–11.1	5.3 ± 0.7	3.0–8.4	4.7 ± 0.7	3.1–8.1	2.5 ± 0.7	1.2–6.4					

times larger than female home ranges and 1.3 times larger than home ranges of young (Table 4). However, core areas of young were 1.8 and 1.4 times larger than in adult females and males (Table 4). In spite of these differences, there were no significant differences among sex-age class for any method of home range estimation ($F = 0.32$ – 2.02 , $df = 2$, all P 's > 0.1952). Number of locations did not affect home range sizes in any analysis ($F = 0.01$ – 2.01 , $df = 1$, all P 's > 0.1943).

Seasonal Home Range Size.—Sex-age classes in home range and core area size differed only when seasonal home ranges were estimated ($F = 4.35$ and 4.03 , $df = 2$, $P = 0.0263$ and 0.0331 for MCP90 and KM60, respectively). Neither season, year, nor interactions between any independent variable were significant (P always > 0.2405). Results for MCP100 and MCP95 were similar.

MCP90 seasonal home range size was very similar through seasons and years within each sex-age class (means ranging between 1.8 and 3.8 km²) except for males during summer (Fig. 7) and in 1995 (Fig. 8) when home ranges increased two-fold. Seasonal core area sizes were on average $47.0 \pm 1.61\%$ ($n = 56$) of the MCP90 home ranges and in some seasons and years did not reach 1 km² (winter and spring in females, Fig. 7; and years 1993 and 1994 in females and year 1994 in young, Fig. 8). Sizes of core areas were on average 31% ($n = 56$) of seasonal MCP100. The summer and 1995 increases in home range size for males was not so evident for core areas (Fig. 7 and 8).

Lynx Daily Movements

On average lynx traveled 8.0 km each day ($SE = 0.53$, range = 5.3–13.4, $n = 16$ individuals; range was 2.5–17.0 for the 97 days of continuous tracking). Neither sex-age classes nor season significantly affected daily distance traveled ($F = 1.42$ and 0.72 , $df = 2$ and 3 ; $P = 0.2473$ and 0.4898 , respectively; Fig. 9a and 9b). However, daily distance traveled was different among years ($F = 5.27$, $df = 3$, $P = 0.0032$) with

higher values for 1994 and 1995 than for 1993 and 1996 (Fig. 9c). No interaction between any main factor was significant (P always >0.1140).

Daily home range size (minimum convex polygon for all daily re-locations) averaged 1.46 km^2 ($SE = 0.16$ range = $0.40\text{--}2.75$, $n = 16$ individuals; range was $0.22\text{--}6.92 \text{ km}^2$ for the 97 days of continuous tracking). Only year significantly affected daily home range size ($F = 3.81$, $df = 3$, $P = 0.0158$), with the highest values in 1995, followed by 1994, 1996 and 1993 (Fig. 10).

Lynx Movements and Water sites

Thirty-two observations were made of lynx drinking water at the 3 water sites present, and only 1 in a temporal small pool after a rain. During August 1995, when observations were carried out during eight consecutive nights, lynx were seen at a water site 14 times in 7 nights. All but 1 of the 32 observations of lynx drinking were during the dry season. Additionally, lynx were also seen at water sites but not drinking on at least 19 other occasions (animals were probably disturbed by the arrival of the observer).

On 60% of 24-hr intensive tracking periods lynx were close (i.e., within the 200-m radius circle around them) to actual water sites (Table 5). The mean distance traveled within the 200-m-radius circle was 0.36 km, and the animals were inside the circle throughout the 24 hours a mean number of 3.0 times (Table 5). Lynx were more often near water sites than expected when compared to random locations; results were similar in dry and wet seasons (Table 5).

Lynx Habitat Use

General Pattern.—The habitats present within the home ranges of every lynx we monitored were Mediterranean scrubland (on average, 40% of lynx MCP100 home ranges), marsh (19%), pine plantations (20%), and pastureland (9%). Mediterranean scrubland also was the habitat most

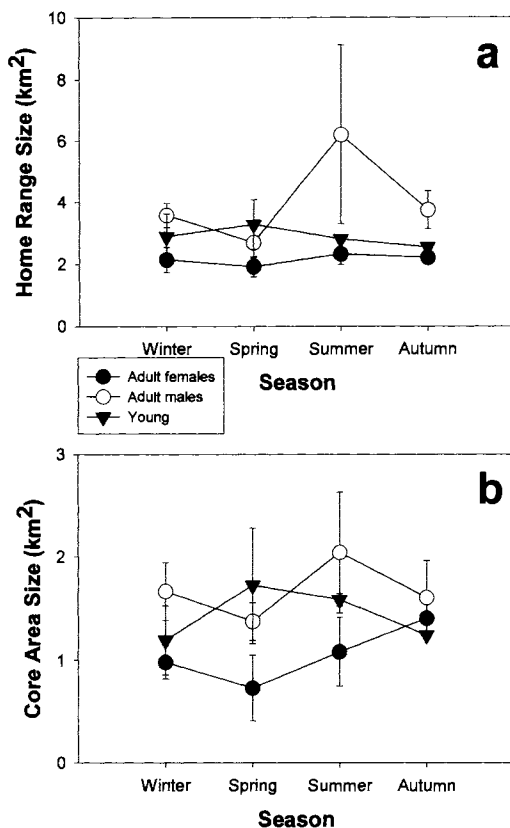


Fig. 7. Mean ($\pm SE$) seasonal home range size (MCP90; a) and core areas (KM60; b) of adult females, adult males and young individuals for Iberian lynx in and near Doñana National Park, southwestern Spain. Sample sizes from winter to autumn were 8, 8, 9, and 6 for adult females, 3, 2, 2, and 1 for young, and 3, 5, 5, and 4 for adult males. There were no significant differences among years; therefore data were pooled by seasons for representation.

often used by lynx (on average, 53% of occasions), followed by marsh (18%); the other habitats were little used, especially the eucalyptus plantations and lentiscus in plantations.

Ash stands and Mediterranean scrubland were significantly preferred, whereas eucalyptus and pine plantations were significantly avoided (Fig. 11). The rest of the habitats were used according to their availability.

Habitat use did not differ among sex-age classes ($F = 1.27$; $df = 14,122$; $P = 0.2351$), or when only active or inactive locations were used in the analysis ($F = 0.23$; $df = 7,60$; $P = 0.9773$). No interac-

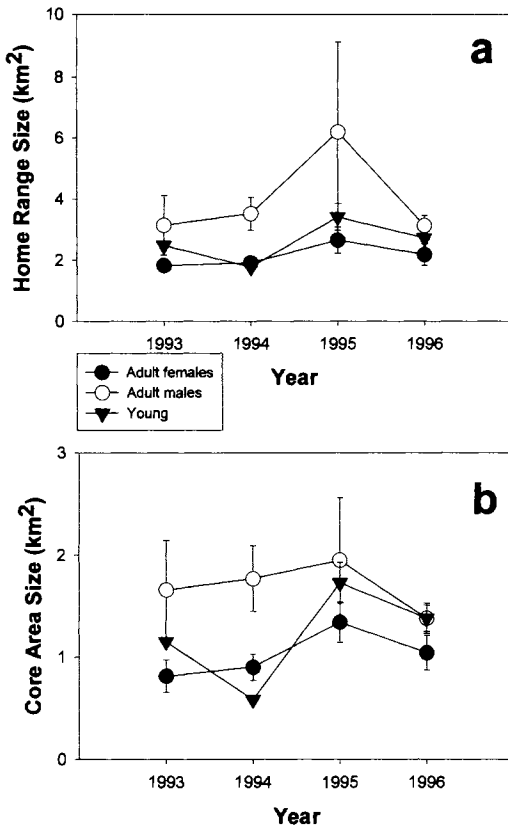


Fig. 8. Mean (\pm SE) seasonal home range size (MCP90; a) and core area size (KM60; b) of adult females, adult males and young Iberian lynx for each study year. Sample sizes from 1993 to 1996 were 8, 7, 8, and 8 for adult females, 1, 1, 4, and 2 for young, and 2, 4, 5, and 6 for adult males. There were no significant differences among seasons; therefore data were pooled by years for representation.

tion was found between activity and sex-age class ($F = 0.10$; $df = 14,122$; $P = 1.0$). Therefore, activity or sex-age class was ignored in looking for differences among seasons and years.

Seasonal and Annual Variations.—Pooled habitat use was not significantly different among years ($F = 1.27$, $df = 9,366$, $P = 0.2496$) or seasons ($F = 0.53$, $df = 9,366$, $P = 0.8501$). The interaction between season and year also was not significant ($F = 0.56$, $df = 27,366$, $P = 0.9635$). Scrubland was always used most by lynx, with percentages of use that ranged on average between 59% and 76%. Other habitats were always little used, with the mean use ranging from 10–25%.

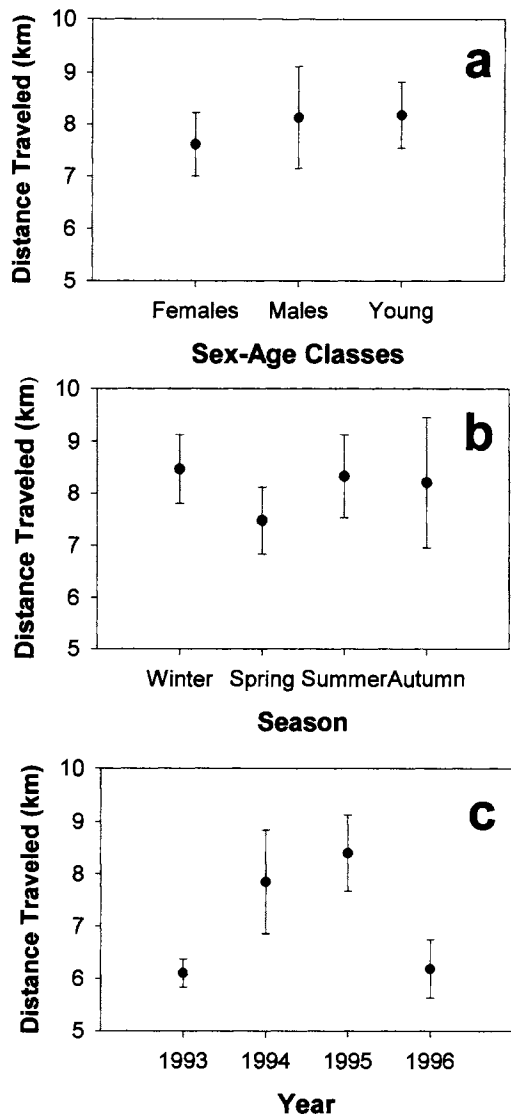


Fig. 9. Mean (\pm SE) distance traveled for each sex-age class (a), season (b) and year (c) for Iberian lynx in and near Doñana National Park, southwestern Spain. According to order in X axis, sample sizes were 4(57), 9(13), and 3(27) in (a); 10(23), 10(36), 8(18) and 7(20) in (b); and 2(11), 5(25), 11(46) and 6(16) in (c) (numbers represent individuals and 24-hr periods in brackets).

Penetration Distance within Non-preferred Habitats.—Because no difference was detected in habitat use, penetration distance within non-preferred habitats was analyzed for pooled habitats. The maximum distance where any lynx was located from any patch of the preferred habitats

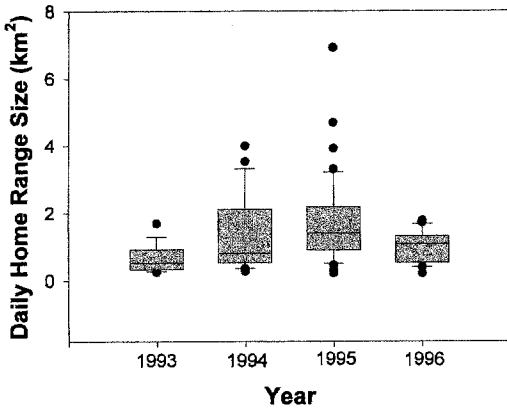


Fig. 10. Annual variation in daily home range size (estimated by the minimum convex polygon using 100% of fixes) of Iberian lynx in and near Doñana National Park, southwestern Spain. Boxes indicate the 25–75th percentile range and contain the median and mean (dots) lines, whereas capped bars represent the 10th and 90th percentile values; closed dots represent points outside these values. Sample sizes from 1993 to 1996 are as in (c) of Fig. 9.

(Mediterranean scrubland and ash stand) was 7,250 m. However, for most locations (78%, $n = 1,063$ locations), lynx were 300 m from the border of preferred habitats, and very few (4%) were > 1 km. When lynx were located outside the preferred habitats there was a clear difference depending on whether they moved through open (marsh and pastureland) or closed (pine plantations, eucalyptus plantations, and lentiscus in plantations) habitats (Fig. 12). In 72% of occasions lynx were 200 m to the preferred habitats when they were in open habitats ($n = 670$), whereas this figure was only 36% in closed habitats ($n = 393$). Therefore, lynx tended to stay closer to the preferred habitats when they

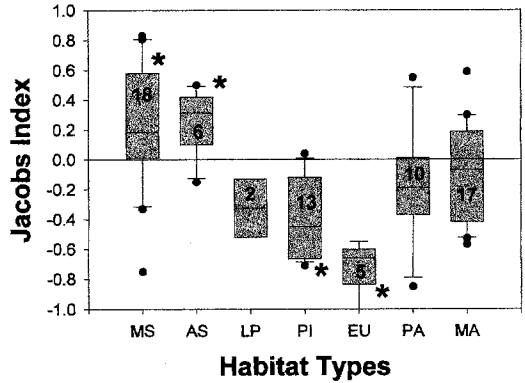


Fig. 11. Jacobs index for each habitat used by 18 lynx in and near Doñana National Park, south-western Spain (1993–1996), considering all available independent locations. Positive and negative values indicate preference and avoidance, respectively. Boxes indicate the 25–75th percentile range and contain the median line, whereas capped bars represent the 10th and 90th percentile values; closed dots represent points outside these values. Asterisks represent means significantly different from zero. Numbers indicate sample sizes (i.e., number of individuals where availability of that habitat type was higher than 5% within MCP100 home range). MS = Mediterranean scrubland, AS = ash stand, LP = lentiscus in plantations, PI = pine plantations, EU = eucalyptus plantations, PA = pastureland, MA = marsh.

moved through open than when they moved through close habitats.

Effects of Protection and Human Influence on Lynx Space Use

Lynx were mainly located inside the National Park (mean = 82%, SE = 4.17, range = 32–100, $n = 18$). Only two individuals (both young) were more frequently located outside (68% and 53% for 84 and 51 locations, respectively) than inside. Sex-age class did not affect the percentage of

Table 5. Observed and simulated values for percent of 24-h intensive tracking periods when lynx were inside a 200-m-radius circle around permanent water sites, distance traveled (km) within the circle, and number of different times animals moved through the circle during the same 24-h period in and near Doñana National Park, southwestern Spain, 1993–1996.

	n	Percent of 24-h periods lynx near water site		Distance traveled		Number of times lynx moved through site	
		Mean ± SE	95% CI	Mean ± SE	Range	Mean ± SE	Range
Overall	97	59.8		0.36 ± 0.04	0.00–1.69	3.02 ± 0.42	0–21
Dry season	63	58.7		0.35 ± 0.05	0.00–1.69	2.89 ± 0.53	0–21
Wet season	29	62.1		0.42 ± 0.08	0.00–1.40	3.55 ± 0.81	0–18
Simulations	100	25.9 ± 1.2 ^a	7.5–45.5	0.16 ± 0.41	0.04–0.34 ^b	1.27 ± 0.08	0.26–2.67 ^b

^a Mean + standard error.
^b 95% confidence intervals.

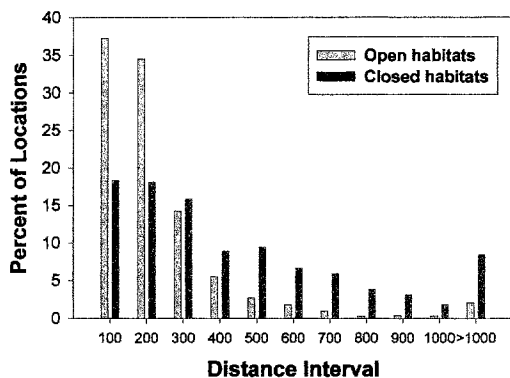


Fig. 12. Distance distribution of lynx locations within non-preferred habitats for open (marsh and pastureland, $n = 670$ locations) and closed (pine and eucalyptus plantations, and lentiscus in plantations, $n = 393$) habitats in and near Doñana National Park, southwestern Spain, during 1993–1996.

occasions that lynx were located outside of the National Park ($F = 0.06$, $df = 2$, $P = 0.9374$). However, distance from El Rocio did affect the percentage ($F = 5.62$, $df = 2$, $P = 0.0151$).

Sex-age class did not affect the percent of locations outside the National Park ($F = 0.21$, $df = 2$, $P = 0.8113$), but category of distance to El Rocio may have ($F = 3.13$, $df = 2$, $P = 0.0731$; Table 6). Percent use of ash stand outside the National Park by five lynx (two adult males, one adult female, one subadult male and one young male) averaged $23.0 \pm 9.4\%$, whereas according to its availability within home ranges percentage of use should have averaged $57.5 \pm 6.1\%$. Differences were statistically significant (paired t-test; $t = 2.826$, $df = 4$, $P = 0.048$).

Number of Rabbits within Lynx Home Ranges and Trapping Area

Rabbit density estimated within lynx MCP90 home ranges ($5.57 \pm 1.01/\text{ha}$, range = 0.78–18.21), and core areas ($5.61 \pm 1.03 \text{ ind}/\text{ha}$, range = 0.86–16.28) were similar ($n = 22$ home ranges of 9 different lynx and 7 seasons). Mediterranean scrubland contributed with the highest number of rabbits within MCP90 home ranges ($74.2\% \pm 5.0$); the rest of the habitats were much less important ($<15\%$). Nevertheless, for individual lynx ($n = 6$) inside the National Park that had ash stands available, this habitat contributed on average $32.2 \pm 5.0\%$ (range = 12.3–50.2) of the rabbits in spite of its low availability. Percentages of number of rabbits for each habitat were very similar for MCP90 home ranges and core areas, suggesting that lynx core areas were not places richer in rabbits.

Throughout the study period, the density of rabbits within home ranges and core areas followed parallel variations, with the highest figures during spring 1994 and 1995 and the lowest ones during autumn 1996 (Fig. 13). Rabbit density within the trapping area ranged between 14.35 and 0.88/ha for spring 1994 and autumn 1996, respectively. Therefore the number of rabbits per lynx ranged between 1,367 in spring 1994 and 73 in autumn 1996 (Fig. 14).

We regressed the figures obtained on rabbit density within MCP90 home ranges and core areas against range and area size for the 22 cases in which both types of

Table 6. Mean percent of locations of Iberian lynx outside Doñana National Park, southwestern Spain, considering all available locations for each individual, and only considering locations in the three plantation habitats (pine, eucalyptus, and lentiscus) for three categories of distance to El Rocio.

Relative distance to El Rocio	No. of individuals	All locations outside the park		Only locations within the 3 plantation habitats	
		Mean \pm SE	Range	Mean \pm SE	Range
Closest	7	5.7 \pm 1.38	0.0–10.0	4.9 \pm 1.43	0.0–8.8
Intermediate	5	22.4 \pm 2.24	15.4–28.6	17.5 \pm 2.17	13.3–25.0
Farthest	6	29.2 \pm 10.4	4.0–67.9	17.7 \pm 7.63	0.0–52.4

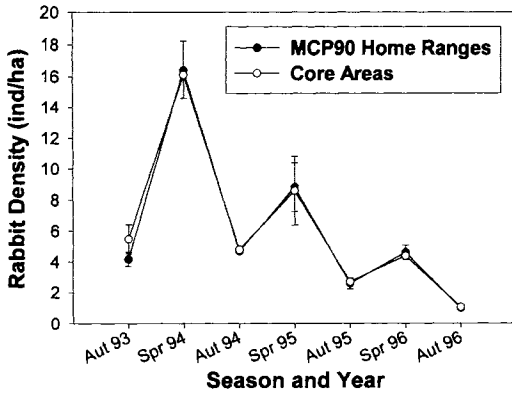


Fig. 13. Density (mean \pm SE) of rabbits within MCP90 home ranges and core areas for seven seasons in and near Doñana National Park, southwestern Spain.

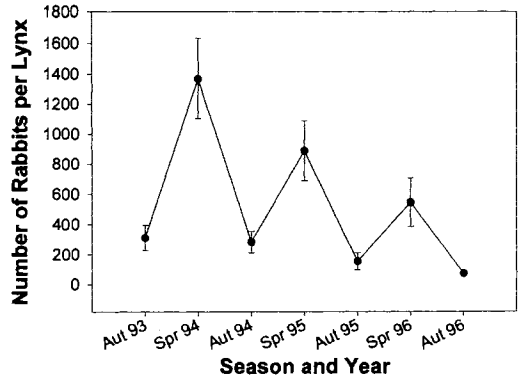


Fig. 14. Number (mean and 95% confidence intervals) of rabbits per lynx within the trapping area in and near Doñana National Park, southwestern Spain.

data were available (Fig. 15). Neither MCP90 home range size nor core area size were significantly correlated with rabbit density ($F = 0.25$ and 0.71 , $df = 21$, $P = 0.6210$ and 0.4082 , respectively). The same result was obtained when we considered the number of locations used to estimate range sizes as another independent variable in the regression model ($F = 0.12$ and 0.51 , $df = 21$, $P = 0.8874$ and 0.6064 , respectively). Two further analyses were performed that considered rabbit density within the trapping area instead of within ranges. This allowed us to use a more general and independent rabbit density estimation for the study area. Results were again identical; the size of both MCP90 and core areas were not affected by rabbit density in the trapping area (all F 's < 1.57 , all P 's < 0.2245).

DISCUSSION

Rabbit Abundance and Distribution

In this study, rabbits were more abundant in Mediterranean scrubland and ash stands than in pine plantation or other habitats. Rabbits were patchily distributed in pastureland, with high abundance in very localized parts of the habitat, whereas in other parts they were totally absent. Similarly, rabbits were not evenly distributed in Mediterranean scrubland. Rabbits were much more abundant close to the

Vera (edge with marsh), with a diminishing abundance for approximately 300 m, and then remaining at quite constant, relatively low densities farther away. Because rabbits

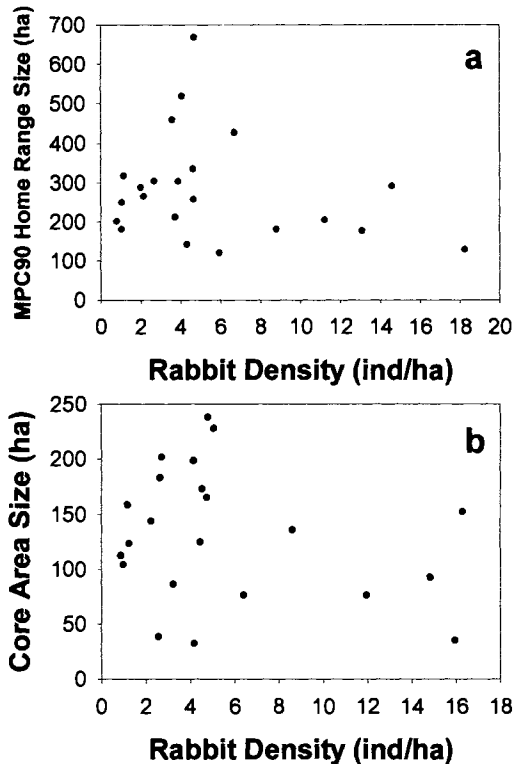


Fig. 15. Relationship between the size of MCP90 home ranges (a) and core areas (b) of lynx, and rabbit density as estimated within these ranges in and near Doñana National Park, south-western Spain, 1993–1996.

mainly feed on grasses in Doñana (Soriguer 1988), and large grasslands were found in the Vera, we suggest that large feeding grounds are important for rabbits to attain high densities. Ash stands, which are characterized by large open grassy areas, also had high rabbit abundance. The importance for rabbits of large feeding grounds and the edges between land systems has been previously pointed out (Rogers and Myers 1979, Rogers 1981, Soriguer and Rogers 1981, Beltrán 1991, Palomares et al. 1996*b*).

Rabbits were more abundant in the best-conserved natural scrubland habitats of the study area. Although Mediterranean scrubland and ash stands have historically been managed for cattle grazing, they also have suffered less transformation and therefore have the best natural vegetation (Rivas-Martínez et al. 1980). Mediterranean scrubland and pastureland were identical until 1970 when shrub vegetation of the latter was totally removed and the ground ploughed and sowed with different grasses and herbs for improving cattle grazing (Palomares et al. 1996*b*). Due to habitat transformation, the pastureland held many fewer rabbits than the Mediterranean scrubland, in spite of more abundant grass.

Special mention also must be given to the results obtained for ash stands inside and outside of the National Park. Although differences sometimes were not significant between these two habitats, overall rabbit densities in ash stands inside the National Park were higher than in ash stands outside the National Park. In addition to higher protection from hunting within the National Park, different predator composition and abundance might be responsible for this difference (Palomares et al. 1995).

Seasonally, rabbits were much more abundant during spring than the rest of the year. The lowest densities were attained between September and November of every year after several months without breeding (Delibes and Calderón 1979, Soriguer 1981), and after myxomatosis has its higher incidence (Soriguer 1981, Rogers et al. 1994). After November, rabbits may start to

breed again, coinciding with the availability of fresh grass after the autumn rains (Soriguer 1981, Wallage-Drees 1983). The highest levels of breeding are attained during the spring (Delibes and Calderón 1979, Soriguer 1981, Rogers et al. 1994). This pattern of seasonal variation has been regularly reported for rabbits both in European Mediterranean habitats, where rabbits are native (Rogers 1981, Soriguer 1981, Soriguer and Rogers 1981), and elsewhere (e.g. Myers and Poole 1961, Myers 1971).

Rabbit populations typically fluctuate (Myers 1971, Myers and Parker 1975, Rogers et al. 1994). In addition to the effect of human-induced diseases such as myxomatosis and the new viral haemorrhagic disease (Soriguer 1981, Rogers et al. 1994, Villafuerte et al. 1994), severe droughts also have been considered responsible for declines in rabbit numbers (Myers and Parker 1975). We believe that none of these factors caused the decline in rabbit abundance during this study. Droughts were not the cause because rabbits were more abundant during the drought period. Conversely, rabbits declined when heavy rains start to fall on the study area. A survey carried out during February 1996 in the pastureland and Mediterranean scrubland showed that most warrens were under water, had been blocked by sand, or had collapsed after the heavy rains. For approximately 350 ha sampled in the pastureland habitat, only about 50 ha were free of the effect of heavy rain. Thus, heavy rain might provoke rabbit declines by acting on warrens and hence on survival and reproduction.

Distance to the Vera was highly correlated to density of warrens and entrances; the size of warrens similarly correlated for Mediterranean scrubland. For our estimates of rabbit density within the Mediterranean scrubland, we considered that rabbit abundance varied in direct proportion to warren abundance. The exact relationship between rabbit abundance and warren density remains unexamined. However, we found with another independent method that rabbit densities were clearly much lower far from Vera, as also

happened for warren and entrance density and size of the warrens. Warren counts (and especially use of the warrens) are good predictors of rabbit density (Parker et al. 1976, Parer 1986, Parer and Wood 1986). Even though rabbits rarely use warrens outside the breeding period in scrubland habitats (Wheeler et al. 1981, Kolb 1991b, Gibb 1993, Palomares 2001), they use them heavily during the breeding period (Parker et al. 1976, Rogers 1981, Kolb 1991b, authors unpubl.). In addition, there is no reason to think that rabbits leave warren surroundings when they are not using the warrens. Therefore, at least for the breeding period, the relationship between warren density and rabbit density may be correct.

In contrast to the Mediterranean scrubland, warren density, entrance density, and size of warrens were not related to distance to Vera in the pastureland. The historical management of this habitat for cattle grazing may be responsible for the observed pattern. When the ground was plowed after the removal of shrubs in 1970, a few areas were left unplowed to conserve rabbit warrens (A. Ram, pers. comm.). Therefore, the actual pattern of warren dispersion in this habitat may reflect this transformation.

Lynx Diet

Rabbits were almost the exclusive prey of lynx in the study area. Their importance in lynx diet did not fluctuate among seasons or years despite the large variations in rabbit abundance, and all three lynx groups studied showed the same diet. Our results contrast with other lynx species where the main prey may greatly diminish in the diet during times of low abundance (Brand and Keith 1979). In other areas supporting generally lower rabbit densities, Iberian lynx also take alternative prey more frequently than in our study area (Delibes 1980, Beltrán and Delibes 1991, Gil et al. 1997).

Lynx Density

Although the total number of individuals trapped and radio-tracked might seem

low, most of the adults present in the study area were studied. All young produced between 1994 and 1996 also were trapped and radio-tracked. Therefore, the number of individuals studied was very close to the actual number of lynx present in the study area.

The most remarkable aspect of this lynx population was its high density throughout the study. Although similar densities have been reported elsewhere for a similar-sized cat (the bobcat, *Lynx rufus*, e.g., Lembeck 1986), densities $>10/100 \text{ km}^2$ are rarely reported for other *Lynx* species (Knick 1990, Koehler 1990, Breitenmoser et al. 1993a, Poole 1994). Our high density must correspond with an exceptional situation for the Iberian lynx; according to estimates reported by Rodríguez and Delibes (1992) for the entire distribution of Iberian lynx, "areas of high density" are considered to be between 13 and 21/100 km^2 .

Density fluctuations were explained by the variations in the number of young/sub-adult individuals. Adult density remained stable through the study period, except when adults of the same sex were involved in territory disputes, or during the mating period when a male was searching for resident females. Nevertheless, this increase in the number of adults on the study area had little effect on adult density, as the interactions lasted only a few weeks.

Lynx Home Range and Daily Movements

Both total and seasonal home ranges and core areas were much smaller than those reported for other similar-sized felids (Fuller et al. 1985, Ward and Krebs 1985, Litvaitis et al. 1986, Knick 1990, Koehler and Hornocker 1989, Koehler 1990, Breitenmoser et al. 1993a, Poole 1994). Seasonal home ranges were also smaller than those reported for a nearby area (10.3 and 8.7 km^2 for males and females, respectively; Ferreras et al. 1997). The only variable that affected home range size was sex-age classes, with adult males having larger home ranges and core areas than

adult females and young/subadults. Home range size did not change in response to varying rabbit abundance either seasonal or annually.

In contrast to home ranges, daily movements did not show any variation with sex-age classes, but lynx traveled longer distances in 1995 and 1994 than in 1993 and 1996. This variation in daily movements was not be related to variations in rabbit abundance as both patterns of annual variation did not coincide. Because few animals were radio-tracked, results might be due to subtle individual variations that could not be detected.

Lynx Movements in Relation to Water Sites

Lynx showed a clear positive association to water sites and were frequently seen drinking during summer, which suggests that water was an important resource for lynx in the study area. This result was expected because the study area is characterized by a very long dry season when rain rarely occurs and water is available only in the artificial water sites. However, lynx were also attracted to water sites during times of the year when there was available water from rains in other parts of the home ranges. If water sites are a limiting resource during a great part of the year, lynx might visit water sites in these times to mark the area and the resource that later will be necessary to defend from other conspecifics. In 5 cases when lynx were observed at water sites, animals were seen spraying urine or defecating, and at one water site a mark was left on a small wall by lynx urine after repetitive and frequent marking. Tracks were also frequently seen going to and coming from this small wall next to the water site.

Lynx Habitat Use

Habitat use was almost identical among sex-age classes, activity periods, seasons, and years, highlighting the importance of the best conserved natural habitats (i.e., the Mediterranean scrubland and ash

stands) for lynx. These habitats had the highest rabbit densities and acceptable understory vegetative cover needed for successfully stalking prey and breeding in most felid species (Kleiman and Eisenberg 1973, Bothma and le Riche 1989, Koehler 1990). Other habitats on the study area that were little used had either low understory cover and low protection (pastureland), low rabbit abundance (pine and eucalyptus plantations), or both (marsh). Lynx did not use lentiscus in plantations, despite the presence of good understory cover and, occasionally, relatively good rabbit densities.

Lynx made relatively high use of the marsh (it was the second most-used habitat), although marsh is a habitat that does not have rabbits and shrubs. Nevertheless, some other factors must be considered. First, most locations were very close to the edge of Mediterranean scrubland or ash stand habitats, which typically have large grasslands and small patches of rushes. Grasslands at the edge of scrubland are heavily used by rabbits for feeding during the night (Cowan et al. 1989, Gibb 1993, Moreno et al. 1996), and small patch of rushes may be used by lynx as temporary resting places or for stalking rabbits. Second, despite being concerned with checking which habitats animals actually were using when we suspected they were close to an edge, the radio-tracking error might have situated a lynx in an open habitat when it was actually in the border of the scrubland, especially when the patch of scrubland was small in size.

Effect of Protection and Human Influence on Lynx

Lynx were primarily located within the limits of the National Park where human access was restricted throughout the year. Only two young individuals were frequently located outside the National Park, behavior that probably corresponded with pre-dispersal movements. Although this distribution of lynx might be due to avoidance of human presence, more likely it simply reflects habitat selection because

habitat composition inside and outside the National Park was different. If lynx were sensitive to high levels of human presence, animals likely would respond differently to the three categories of human presence in relation to distance to El Rocio (a tourist village close to the study area) and to fencing of the areas outside the National Park. Individuals living farther from El Rocio were more frequently located outside the National Park than individuals living closer to El Rocio. Furthermore, there was a habitat that extended beyond the limits of the National Park (the largest ash stand; see Fig. 1). Therefore, we could expect that each part of the stand (i.e., inside and outside the National Park) was not used by lynx according to its availability within the home ranges. The ash stand outside the National Park was used less than expected by those lynx that included the patch within their home ranges.

Individual lynx used the areas outside the National Park less than expected if they were living closest to El Rocio. Habitats outside the National Park closest to El Rocio were slightly better for lynx (there was more *lentiscus* in plantations) than habitats outside the National Park farther from El Rocio, which were dominated by pine plantations. *Lentiscus* in plantations held higher rabbit densities and had a more adequate understory cover than the pine plantations.

According to the home range sizes in this study and the patterns of home range overlap between and within sexes in lynx (Ferrerías et al. 1997), there was space outside the National Park for at least two pairs of lynx with home ranges of 4.5 km². However, no lynx consistently lived outside the National Park during the study. Two factors could impede lynx use of this area: 1) high human disturbance, and 2) a very low availability of prey. The first factor is difficult to prove, and only the data presented above for the restricted use that resident lynx living within the National Park made of the area suggest that this might be the reason. Nevertheless, the hypothesis of high human disturbance outside the National Park would gain support if the area

outside the National Park contained enough rabbits to sustain a pair of resident lynx.

To test this hypothesis, we used GIS to estimate the number of rabbits within home ranges of the two hypothetical extra pairs of lynx to the north of the National Park. GIS calculations indicated that the number of rabbits within one hypothetical home area would have ranged between 322 during the time of lowest rabbit density (autumn 1996) and 3,505 during the time of highest rabbit density (spring 1994), and for the other hypothetical home range between 161 and 1,513 rabbits, respectively. Comparing these results with those obtained for the studied lynx (Fig. 14), at least part of the area outside the National Park could have supported an additional lynx pair throughout the full study period. Given the probable number of rabbits within the hypothetical home ranges outside the National Park, high human presence may indeed have been impeding lynx use in that area. In addition to the behavioral avoidance that human presence can cause in lynx, a higher rate of human-caused mortality might also impede the permanent presence of lynx outside the National Park (Ferrerías et al. 1992).

Number of Rabbits within Lynx Home Ranges

Lynx home ranges should have average densities of 5.6 rabbits/ha. Nevertheless, during the season when rabbit densities were the lowest on the study area (autumn 1996), lynx home ranges averaged as few rabbits as 1/ha. Lynx did not change their spatial behavior and decrease density during the low phase of the rabbit decline. These results suggest that minimum average densities of at least one rabbit per hectare must be available to support a stable lynx population.

Core areas were much smaller than home ranges and thus held fewer total numbers of rabbits. However, seasonal mean rabbit densities were always almost identical for MCP90 home ranges and

core areas. This suggests that rabbit density was not the factor determining habitat selection when lynx situated their core areas. In fact, habitat inside home ranges and core areas contributed in a similar way to the total number of rabbits for both type of ranges, with Mediterranean scrubland and ash stands always being the most important.

The size of MCP90 home ranges or core areas for our lynx was not correlated with the density of rabbits. In contrast, individual home ranges of bobcats were correlated with an indirect measure of the most important prey for bobcats (Litvaitis et al. 1986). However, our results were expected because range size did not change even across seasons when there were fluctuations in rabbit abundance. Iberian lynx relying on seasonally fluctuating rabbit populations (Soriguer 1981, Beltrán 1991; Fig. 3) might well have evolved to adopt home range sizes that accommodate enough prey during the times of lowest rabbit abundance, as proposed for altricial vertebrates (von Schantz 1984), or Canada lynx (*Lynx Canadensis*; Breitenmoser et al. 1993b). Nevertheless, lynx in different areas have adopted different home range sizes as a function of available rabbits. In fact, for the southern lynx population of the Doñana National Park, where rabbits are less abundant than in our study area (Rau 1988, Villafuerte 1994), average home ranges were slightly larger (Ferrerias et al. 1997).

MANAGEMENT IMPLICATIONS

The European Rabbit

Highly transformed habitats had fewer rabbits than less transformed ones (except for the marsh); therefore, managers must favor natural habitats and reduced the amount of plantations and pastureland areas. The best habitats for rabbits in the study area were the Mediterranean scrubland close to the Vera (i.e., the border with the marsh) and the ash stands around small streams on clay grounds. These habitats were characterized by intermediate

understory cover (between 25–35%), low tree cover (which could favor grass growth), and large and frequent grasslands that are used as feeding grounds for rabbits. Therefore, if habitats are to hold a high number of rabbits, they must fulfill all these characteristics. Habitats with denser understory vegetation must be cleared to the level mentioned, favoring grasslands. Cleared areas would not need to be >40 m from the edge from the scrubland (Moreno and Villafuerte 1995).

In addition to feeding grounds, rabbits need cover against predators and places for breeding to successfully thrive (Rogers 1981, Wheeler et al. 1981, Kolb 1991a, Gibb 1993, Palomares and Delibes 1997). The understory vegetation structure of the habitats where rabbits were most abundant appeared to be optimal, as rabbits are even able to elude >2 domestic ferrets (*Mustela furo*) when they were inside lentiscus shrubs (authors, pers. observ.). The structure of the dominant shrub species (lentiscus) within these habitats, with dense foliage close to the ground, enables rabbits to escape easily from predators. Lentiscus plants also are important for rabbits as most of the warrens were below them, suggesting that warren building is easy and safe in these locations.

In other areas where understory vegetation cover is absent rabbits also may thrive (Myers 1971, Kolb 1991a; the pastureland area in this study), even in higher densities than in scrubland areas (Myers and Parker 1965). In these cases the existence of warrens is important (Rogers 1981, Kolb 1991a, Palomares and Delibes 1997), as they provide both refuges and breeding sites. Rabbit populations in open areas can therefore be improved by providing them with adequate warrens. Nevertheless, even though other predator species that hunt in open habitats could benefit from the increased rabbit populations, lynx cannot make great use of these areas due to a lack of understory cover. Only areas close to scrubland edge (to a maximum of approximately 200 m) might be used by hunting lynx. The best long-term strategy to recover these areas for lynx and rabbits

favors growing and establishing scattered patches of natural shrubs similar in structure to lentiscus plants.

The Iberian Lynx

Our lynx population probably lives in one of the best areas for lynx throughout its entire distribution, as suggested by the high density of lynx in the study area. Therefore, the general habitat characteristics of the area should be maintained over time. Management plans for the species recovery in other areas of Doñana and elsewhere must also take into account the general habitat characteristics found in the study area.

Lynx selected habitats having very high rabbit densities, medium understory cover, and edges between these and other open grassy habitats. Lynx rarely moved into open habitats far from scrubland edges. Preferred habitats were less altered where natural vegetation had persisted, with mean understory cover ranging between 25% and 35%, and shrub plant species that provided refuge and safety for lynx and rabbits. These habitats were always close to wet areas such as the marsh and small streams, as both were used by rabbits for feeding grounds. For the whole Doñana area, lynx sign was also found more frequently near moist areas than elsewhere (Palomares et al. 1991). Therefore, moist areas must be preserved.

Since total home ranges of lynx were 4–6 km², patches provided as lynx habitat should be at least of this size, or preferably larger as to completely enclose 3–5 lynx territories (Knick 1990, Gaona et al. 1998). At least 50–60% of the area should be similar to the Mediterranean scrubland or ash stand habitats, and 20% should be grassland/scrubland edge habitats.

Accurate minimum rabbit densities at which lynx cannot thrive cannot be properly addressed with this study. Nevertheless, several results can help give insights into this important aspect of lynx management. First, rabbit densities of 1.0–4.6/ha during the season of lowest and highest density (i.e., autumn and spring, respec-

tively) are able to support lynx reproduction in a given area. Rabbit densities of 1/ha at any time of the year should support lynx in a given area, although the lynx may not breed. Second, a minimum of 1 rabbit/ha might be adequate for lynx, because lynx did not change space use at that rabbit density. Third, areas with low rabbit densities (0.2–0.3 to 2.5/ha for seasons of low and high density, respectively), such as those found in pine plantations during this study, cannot maintain a stable lynx population. They could, however, support lynx temporarily during the seasons of high rabbit density. At densities <1 hare/ha, Canada lynx changed their spatial behavior and moved larger daily distances. Below <0.5 hares/ha, Canada lynx abandoned their home ranges and became nomadic (Ward and Krebs 1985).

We also could not determine the effect of rabbit density on the number of females breeding in the population, litter size, or cub survival. All these aspects are known to vary with prey density in other similar sized cats (Brand and Keith 1979, Parker et al. 1983, Koehler 1990, Poole 1994) and are of extreme importance for modeling the long-term viability of a population (Brand and Keith 1979, Knick 1990, Gaona et al. 1998).

Other factors not related directly to habitat characteristics were important for lynx, such as water sites and human presence. For hot, dry summers such as those found over most of the distribution of Iberian lynx, water availability might be of extreme importance during the dry period. In Doñana, where soils are sandy and most of the small streams and winter lagoons dry out during summer, the artificial maintenance of water sites is a necessary management activity. Because underground water is close to the surface in Doñana, water sites may be easily established. Maintenance of existing water sites or the creation of new ones would favor lynx, as well as other wildlife that use water sites extensively (J. Cobo, pers. comm.). Based on lynx home range sizes determined in this study and elsewhere (Ferrerías et al. 1997), water sites should be spaced 1–2

km from each other. Also, water quality should be monitored by managers at these sites.

Accurate levels of human presence outside the National Park could not be measured during this study. Nevertheless, it should not be difficult for managers to compare levels of human presence inside and outside the National Park. In general, fencing free right-of-ways to prevent people from moving outside them might be the first step to recover areas for lynx, especially if these right-of-ways are very close to a village. Of course, lynx would successfully colonize the area only if the other habitat requirements also were adequate.

Because rabbits are the staple prey for lynx in the areas where diet has been studied (Delibes 1980, Beltrán and Delibes 1991, Gil et al. 1997, this study), any conservation plan for the predator cannot be implemented without parallel plans for the management of rabbit populations. Rabbit populations must be maintained in areas where rabbits are already important, and actions leading to higher rabbit populations must start in areas where they are scarce. The high lynx density found in our study area was undoubtedly attained due to the high rabbit densities supported there.

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Appendix 1. Extent (ha) of the areas surveyed for rabbit warren mapping in pastureland and Mediterranean scrubland in relation to distance to Vera in both habitats during April and July–October 1995 in and near Doñana National Park, southwestern Spain.

Distance to Vera (m)	Pastureland	Mediterranean scrubland
0–100	59.7	26.0
101–200	47.8	15.2
201–300	36.1	9.5
301–400	32.0	5.3
401–500	29.9	4.4
501–600	27.0	5.9
601–700	24.9	5.0
701–800	23.1	4.9
801–901	22.4	7.0
901–1000	16.6	10.4
1001–1100	12.0	10.4
1101–1200	8.5	8.4
1201–1300	1.6	5.9
1301–1400	0	4.4
1401–1500	0	2.4
1501–1600	0	1.1
Total	341.6	126.2

Appendix 2. Sex, age, radio-tracking period, number of single locations, 24-h radio-tracking periods and fate for 21 lynx radio-tracked in and near Doñana National Park, southwestern Spain, 1993–1996.

ID ^a	Radio-tracking period	No. of single locations	No. of 24-h radio-tracking periods	Fate
FA53	5-12-92/14-11-94 ^b 13-5-95/31-12-96	733	21	Radio-collar still working
FA41	12-1-93/30-11-94 28-02-95/9-8-95	415	17	Radio-collar failed
FA62	23-11-93/11-10-94	132	7	Moved away by HA73
FA73	6-12-94/31-12-96	475	12	Radio-collar still working
MA54	1-3-93/2-2-95 14-5-95/6-8-96	543	14	Radio-collar failed
MA75	29-1-95/21-2-96	190	9	Moved away by MA84
MA84	11-2-96/31-12-96	192	4	Radio-collar still working
FY64	2-2-94/24-02-94	9	0	Died
FY71	1-12-94/25-6-95	84	1	Dispersed
FY69	18-1-95/2-2-95	5	1	Dispersed
FS77	27-6-96/31-12-96	134	1	Radio-collar still working
MY55	11-3-93/22-7-93	65	0	Dispersed
MY61	15-11-93/18-5-94	80	0	Dispersed
MS57	6-7-94/10-7-94	0	0	Dispersed
MY72	4-12-94/2-5-95	60	3	Dispersed
MY74	8-12-94/15-3-95	37	2	Dispersed
MY68	31-1-95/22-2-95 24-11-95/4-1-96	28	1	Dispersed
MS82	19-5-95/10-9-95	51	2	Dispersed
MS83	13-11-95/26-12-95	25	1	Dispersed
MY76	24-2-96/27-03-96	23	1	Died
MY88	26-11-96/31-12-96	22	0	Radio-collar still working
Total		3,303	97	

^a F = female, M = male, A = adult, S = subadult, and Y = young.

^b Day-Month-Year.