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# Iberian Lynx in a Fragmented Landscape: Predispersal, Dispersal, and Postdispersal Habitats

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**Abstract:** *Applied conservation biology must provide solutions for the conservation of species in modern landscapes, where prime habitats are being continuously fragmented and altered and animals are restricted to small, nonviable populations. We studied habitat selection in a fragmented population of endangered Iberian lynx (*Lynx pardinus*) by examining 14 years of radiotracking data obtained from lynx trapped in two different source areas. Habitat selection was studied independently for predispersal lynx in the source areas, for dispersing individuals through the region, and for postdispersing animals, most of which settled far from their point of origin. A multivariate analysis of variance showed that habitat use differed significantly among these phases and between area of origin, but not between sexes. The habitat type most used, and best represented within home ranges, was the mediterranean scrubland. Pine plantations were also important during and after dispersal. The rest of the habitats were either avoided (open habitats) or used according to availability (pine and eucalyptus plantations) by dispersing lynx. Differences due to lynx origin were detected only during predispersal and dispersal and were observed because animals from each area had different habitat availability. Lynx with established territories did not use areas at random. They occupied patches of mediterranean scrubland more often than would be expected from scrubland availability during predispersal; the rest of the habitats were included within home ranges less than would be expected from their availability in the landscape. Results indicate that dispersing animals may use habitats of lower quality than habitats used by resident individuals, which suggests that conservation strategies applied across regions might be a viable objective.*

El Lince Ibérico en un Paisaje Fragmentado: Hábitats Seleccionados Antes, Durante y Después de la Dispersión

**Resumen:** *La biología de la conservación aplicada debe proporcionar soluciones para la conservación de las especies en los paisajes actuales donde los hábitats primitivos están siendo continuamente fragmentados y alterados y los animales presentan poblaciones pequeñas, con frecuencia inviábiles. Estudiamos la selección del hábitat en una población fragmentada del amenazado lince ibérico (*Lynx pardinus*) usando datos de radio-monitoreo obtenidos durante 14 años en animales capturados en dos áreas fuente. La selección del hábitat fue estudiada independientemente en las áreas fuente antes del inicio de la dispersión, en lincees en dispersión en toda la región, y en lincees establecidos después de la dispersión, la mayor parte de los cuales se asentaron lejos de sus lugares de origen. Un análisis multivariante de la varianza mostró que el uso del hábitat varió significativamente entre fases y entre el área de origen, pero no entre sexos. El tipo de hábitat más usado y mejor representado dentro de las áreas de campeo fue el matorral mediterráneo. Las plantaciones de pinos fueron también importantes durante la dispersión y postdispersión. El resto de los hábitats fueron rechazados (hábitats abiertos) o usados según su disponibilidad (plantaciones de pinos y eucaliptos) por los lincees en dispersión. Las diferencias debidas al origen del lince fueron solo detectadas durante la predispersión y dispersión, y se debieron a que los animales de cada área tuvieron diferente disponibilidad de hábitats. Los lincees que se establecieron en territorios no usaron las áreas al azar. Ocuparon manchas de matorral mediterráneo más a menudo que lo esperado según la disponibilidad de matorrales durante la predispersión; el*

resto de los hábitats fueron incluidos en las áreas de campeo menos de lo esperado según su disponibilidad en la región. Los resultados indican que los individuos en dispersión pueden usar hábitats de menor calidad que los hábitats usados por individuos residentes, lo cual sugiere que las estrategias de conservación que se apliquen a nivel de regiones podrían ser un objetivo viable.

## Introduction

Human activities have profoundly affected landscapes, decreasing the quantity and quality of habitats available to many species. These activities have extirpated or endangered many species, especially those with large habitat requirements such as mammalian carnivores (Myers 1994; Noss & Csuti 1994). A current challenge for conservation biology is to preserve species in fragmented landscapes where, as a rule, small, nonviable populations remain (e.g., Beier 1993; LaHaye et al. 1994; Hanski et al. 1996; Gaona et al. 1998). Conservation planning for these populations must be carried out at broader spatial and temporal scales than has been attempted previously (e.g., entire landscapes), and connectivity among local populations must be considered (Fahrig & Merriam 1994; Noss et al. 1996; Hanski & Simberloff 1997).

Landscapes planning should include strictly protected areas (i.e., core areas) connected through discrete habitat corridors or through matrix lands that permit safe movement among reserves. Core areas should be composed of high-quality habitats in which the target species can find enough food, protection, and possibilities for reproduction. Matrix lands should be suitable for compatible human use, although no test of this idea has been evaluated empirically (Noss et al. 1996). Conservation planners, however, often lack information on the general patterns that govern habitat selection by animals, found mainly at the scale of ecological landscapes where a standard of plausibility must inevitably be applied (Lima & Zollner 1996). It is largely unknown whether habitat selection is similar for resident and dispersing individuals or if it is similar at local and landscape scales (Soulé 1991; Harrison 1992; Maehr & Cox 1995; Lima & Zollner 1996; Noss et al. 1996). To address these questions, we studied the endangered Iberian lynx (*Lynx pardinus*).

Habitat destruction and fragmentation are among the main factors responsible for the decline of the Iberian lynx (Rodríguez & Delibes 1992). At present, lynx survive in a highly fragmented landscape in which dispersal between subpopulations is necessary for survival across the region (Gaona et al. 1998). We tested the hypotheses that habitat selection differs in resident and dispersing lynx and that lynx are more restricted in habitat selection at a local scale than at a landscape scale.

## Methods

### Study Area

The study was carried out in the Doñana region (approximately 2500 km<sup>2</sup> in southwestern Spain). The study area is bordered to the south and west by the Atlantic Ocean, to the east by the Guadalquivir River, and to the north by the foothills of the Sierra Morena. The region is flat, with marsh on the east and sandy soils of aeolian deposits of marine origin in the remaining areas. The landscape is highly fragmented and has a diversity of vegetation types; 49% of the area is cropland. Vegetation in the remainder is a mixture of mediterranean shrub dominated by species such as *Halimium* spp., *Cistus* spp., and *Pistacia lentiscus*; plantations of pines (*Pinus pinea*) and eucalyptus (*Eucalyptus* sp.); and areas of pastureland. The southeastern part of the study area is protected by the Doñana National Park, which occupies 550 km<sup>2</sup>. Inside the national park, a dune system borders the Atlantic Ocean.

The climate is mediterranean subhumid, with mild, rainy winters and hot, dry summers. More information on the Doñana region, the Doñana National Park, and the areas where lynx were trapped has been provided by Palomares et al. (1991, 1996a) and Ferreras et al. (1997).

### Radio Telemetry

Habitat use by lynx was studied by means of radio-tracking information. Lynx were captured with box traps and padded foothold traps, usually between November and February. Trapping occurred between 1983 and 1991 in the Doñana lynx subpopulation of the Reserva Biológica and between 1991 and 1997 in the Doñana lynx subpopulation of Coto del Rey (for details on the spatial structure of the lynx population of Doñana see Palomares et al. [1991] Gaona et al. [1998]). Lynx were weighed, sexed, measured, and fitted with radiocollars working at 150–151 MHz. In the Reserva Biológica, lynx were classified according to tooth-eruption patterns and body weight as young (<12 months old starting 1 April), subadult (12–24 months old), and adults (>24 months old). In the Coto del Rey, almost all cubs (<1 month old) born since 1993 were tagged with transponders. Thus, age was known when they were later recaptured for fit-

ting a radiocollar. Three other lynx were opportunistically trapped in other points of the Doñana area and also were radiotagged and tracked.

Every radiotagged individual was usually located between 2 and 10 times per week from two signal bearings, normally <1 km from the animal to decrease triangulation error. Most locations (>75%) were taken during daylight. During the last three years, animals were frequently located by homing to the actual position with a global positioning system (GPS; model Garmin 75). The GPS error was estimated: on 72% of the occasions error was below 50 m, and on 97% of occasions error was below 100 m. To avoid statistical dependence of data, no location was separated by <12 hours from any other (Swihart & Slade 1985). Triangulation error was determined by locating test transmitters. In 95% of cases, error was <207 m.

### Habitat Map and Classification

We recognized eight vegetation types for the study: (1) mediterranean scrubland, areas dominated by variable density of shrubs between 1 and 3 m tall and with low tree cover (<25%); (2) pine plantations, areas dominated by *Pinus pinea* with a tree canopy cover >25% and scattered and variable understory cover; (3) eucalyptus plantations, same as pine plantations but with trees of *Eucalyptus* spp.; (4) riparian vegetation, or dense (usually >80%), relatively well-conserved natural vegetation associated with some small streams; (5) pasturelands, grassland areas with or without variable tree canopy cover of native species (*Quercus* spp., *Olea* spp.); (6) dunes, areas of bare sand of the dune system in the Doñana National Park; (7) marshes, flat areas potentially flooded during the rainy period; and (8) cropland, any cultivated land.

We obtained a raster-based habitat map of the study area with 50-m resolution from the Sistema de Información Ambiental de Andalucía (SINAMBA; Moreira & Fernández-Palacios 1995). The habitat map was constructed through satellite imagery (Landsat) information and aerial photographs obtained in 1991 (Moreira & Fernández-Palacios 1995). To test the suitability of the habitat map for our study, we ground-truthed 314 points (231 where lynx were located and 83 at random) using a GPS to locate them. In 73.6% of the points, we correctly identified the habitat using the habitat map of the SINAMBA. For 51 points (16.2%), the habitat was incorrectly identified, but the locations were <50 m from the edge of the correct habitat type. Because the GPS error and the map resolution were close to 50 m, these points were not considered incorrectly classified. Finally, only 10.2% of the points were obviously incorrectly classified (i.e., >50 m from the edge of the correct habitat). Thus, we considered the SINAMBA map reliable.

### Data Analysis

#### DETERMINATION OF PREDISPERSAL, DISPERSAL, AND POSTDISPERSAL PHASES

We consider dispersal as beginning when a lynx has left its subpopulation of birth for at least 1 week. Lynx of the Doñana area are distributed in spatially separated subpopulations (Palomares et al. 1991; Gaona et al. 1998), and spatial limits of the subpopulations were determined by a polygon including the 90% minimum convex polygon home ranges of every adult lynx radiotracked in that subpopulation. The two source subpopulations have been studied without interruption from 1983 through 1992 (Reserva Biológica) and from 1991 through 1998 (Coto del Rey), and the spatial arrangements of the adult populations are well known (Palomares et al. 1996a; Ferreras et al. 1997; Gaona et al. 1998).

The end of the dispersal was determined by measuring site fidelity over short time intervals through computer simulations and through a graphical representation of the distances between the centers of the successive home ranges established. We split the data set of the observed radiolocations into small sequential blocks, estimated the home-range size for each of these blocks, measured the distance between the centers of these consecutive home ranges, and calculated the average distance from the locations in each block to the trapping point. Then we used random-movement paths for each individual to obtain 100 groups with the same number of locations as in the previous observed blocks. If the observed home-range size and the observed mean distance from locations in each block were smaller than the lower 95% confidence interval of the 100 random estimates, then the lynx was considered to be moving with site fidelity (i.e., temporally established in a given area). Distance between centers of the consecutive home ranges should be constant during the phases of site fidelity but not during dispersal (e.g., Fig. 1).

#### HABITAT USE AND COMPOSITION WITHIN HOME RANGES

To study habitat use within areas traversed by animals, we used the Idrisi geographical information system (GIS; Eastman 1995) to assign one of the eight habitat types to each lynx location. Habitat composition within areas traversed by lynx (hereafter, home ranges, although by definition a true home range cannot be considered for dispersing animals) was also calculated with the GIS. We used the minimum convex polygon method (Hayne 1949) to delineate home ranges during each phase.

We tested for the effects of sex, origin (i.e., the subpopulation), and phase (predispersal, dispersal, and postdispersal) in habitat use and habitat composition

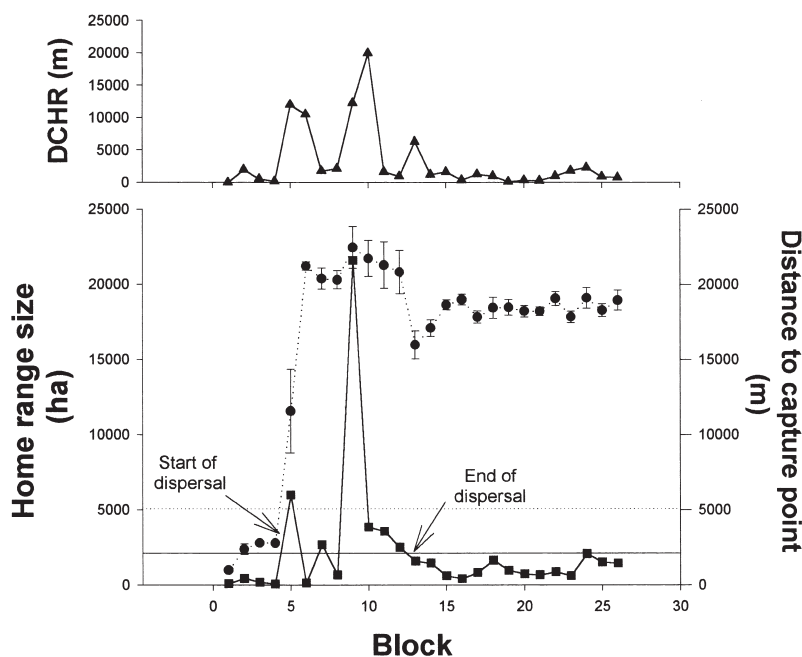


Figure 1. Analytical determination of pre-dispersal, dispersal, and postdispersal phases in a male lynx radiotracked between December 1994 and June 1997. The block refers to sequential groups of eight locations from the beginning to the end of the radiotracking period. Home-range size (squares), average distance ( $\pm$ SE) to the capture point (circles), and distance between center of sequential home ranges (DCHR) for each block are represented in ordinates. Reference lines indicate the lower limit of the 95% confidence interval for home-range size and average distance to capture point. Below these lines animals are moving with site fidelity and above at random. The reference line for average distance to capture point is useful only for determining the start of dispersal, whereas that for home-range size allows both the start and the end of the dispersal process to be determined. The distance between sequential home ranges mirrors the pattern inferred from home range size and distance to the trapping point.

within home ranges by multivariate analysis of variance (MANOVA) in which all dependent variables (habitat types or habitat composition) were included in a single analysis (Scheiner 1993). Using MANOVA reduces Type I error, a common potential problem in univariate multiple tests. We considered individuals as the sampling unit, and the dependent variable was the percentage of locations within each habitat type or the percentage of each habitat type within home ranges. To normalize data, both were transformed with the arcsine of the square root.

We chose Pillai's trace as the MANOVA statistic (Scheiner 1993). For all phases of analysis only individuals with 20 or more independent locations were considered. Origin was known for the animals from the Coto del Rey because they were tagged with transponders when they were cubs. We assumed that lynx came from the Reserva Biológica if they were captured inside the limits of this subpopulation. Moreover, most individuals were captured as young and were observed with known resident adults on many occasions.

#### HABITAT SELECTION WITHIN HOME RANGES AND LANDSCAPES

To study habitat selection within home ranges, we used the Jacobs index (Jacobs 1974), which varies from +1 for maximum preference to -1 for maximum avoid-

ance. Availability of each habitat type was the proportion of the total area contained within home ranges (i.e., habitat composition). Individuals were again considered the sample unit, and each habitat type was considered to be significantly preferred or avoided if its mean value on the Jacobs index was significantly different from zero. This was accomplished by constructing 95% confidence intervals and testing whether zero was inside or outside the interval. Because habitats not well represented within home ranges may have very high or very low Jacobs indices, and probably do not represent the true use that animals make of them, only individuals in which a given habitat made up >5% of its home range were considered for analysis.

To test whether lynx randomly established home ranges at the landscape scale, the habitat composition of lynx home ranges was compared to availability in a study area. Calculating availability in the study area is often a problematic and subjective question (Aebischer et al. 1993). We used the minimum convex polygon encompassing all available lynx locations considered. We measured selection by the Jacobs index, using the individual as the sampling unit, similarly to the way we tested for habitat selection within home ranges. All statistical analyses were performed with the SAS software package (SAS Institute 1990) and differences were considered significant if  $p < 0.05$ .

**Table 1.** Results of a multivariate analysis of variance of the effects of phase, origin, and sex on habitat composition of lynx home ranges and habitat use within home ranges.

	<i>Habitat use</i>			<i>Habitat composition</i>		
	F	df	p	F	df	p
Phase	12.96	16,160	<0.0001	14.63	16,158	<0.0001
Origin	6.43	16,160	<0.0001	4.41	16,158	<0.0001
Sex	0.91	8,79	0.5137	1.80	8,78	0.0901
Phase × origin	4.01	32,328	<0.0001	3.29	32,324	<0.0001
Phase × sex	1.20	16,160	0.2763	1.17	16,158	0.2961
Origin × sex	2.20	8,79	0.0361	1.68	8,78	0.1158
Phase × origin × sex	1.64	16,160	0.0642	1.01	16,158	0.4562

## Results

### Radiotracked Individuals

We used data from 42 different lynx (23 males and 19 females). When first captured, 29 lynx were young, 11 were subadults, and 2 were adults. Out of those 42 lynx, 32, 13, and 10 were radiotracked during the predispersal, dispersal, and postdispersal phases, respectively. Eight individuals were radiotracked in all three phases. All except two individuals radiotracked during the postdispersal phase had reached adulthood (i.e., >2 years), whereas animals monitored during the other two phases were mainly young and subadults or adults <4 years old. The average number of locations per radiotracked animal in each phase was 155 (range = 26–843), 96 (range = 23–343), and 123 (range = 27–415), for predispersal, dispersal, and postdispersal phases, respectively. For all lynx except three, it was possible to decide which subpopulation they came from: 21 from the Reserva Biológica and 18 from Coto del Rey.

### Habitat Use and Composition within Home Ranges

Habitat used by lynx was significantly affected by phase and origin, but not by sex (Table 1). Significant interac-

tions were found between phase and origin, between origin and sex, but not between phase and sex or among phase, origin, and sex (Table 1).

Lynx used mediterranean scrubland more often than other habitats in any phase. Its use, however, was higher during the predispersal phase (75% of locations) than during the postdispersal (52%) or the dispersal phase (50%; Table 2). During predispersal, the remaining habitats were rarely used (on average none above 9.4%), but during both dispersal and postdispersal, pine plantations were frequently used (25–30%; Table 2).

Lynx were infrequently located in open habitats (pastureland, crops, marsh, and dunes) in any phase. Furthermore, the use of open habitats was overestimated because of the sampling error, as ascertained when we approached animals on 34 occasions. On only five of these occasions (14.7%) were lynx actually within open habitats. On the remaining occasions, lynx were in the edge of adjacent scrubland or forested habitats. Furthermore, locations in open habitats were closer than 200 m to the edge in scrubland or forested habitats on 64.3% ( $n = 177$ ), 54.8% ( $n = 700$ ), and 81.6% ( $n = 76$ ) of occasions for predispersal, dispersal, and postdispersal phases, respectively.

The significant interaction between phase and origin detected by MANOVA suggested that origin did not af-

**Table 2.** Habitat composition (mean ± SE) of lynx home ranges and percentages of locations (mean ± SE) within each habitat type for lynx during the predispersal, dispersal, and postdispersal phases in Doñana area.\*

<i>Vegetation types</i>	<i>Phase</i>					
	<i>predispersal</i> ( $n = 32$ )		<i>dispersal</i> ( $n = 13$ )		<i>postdispersal</i> ( $n = 10$ )	
	<i>habitat composition</i>	<i>use</i>	<i>habitat composition</i>	<i>use</i>	<i>habitat composition</i>	<i>use</i>
Riparian vegetation	0.1 ± 0.1	0.2 ± 0.18	1.2 ± 0.97	1.1 ± 1.00	1.4 ± 1.4	4.8 ± 4.77
Crops	0.3 ± 0.27	0.1 ± 0.04	20.8 ± 5.61	8.7 ± 3.21	4.8 ± 3.36	3.2 ± 2.93
Pastureland	9.4 ± 2.18	9.4 ± 2.36	4.2 ± 1.33	2.7 ± 0.74	7.7 ± 4.96	8.6 ± 2.72
Dunes	0.61 ± 0.36	0.3 ± 0.14	5.0 ± 2.34	1.0 ± 0.55	0.2 ± 0.23	0.4 ± 0.37
Eucalyptus plantations	2.2 ± 0.94	1.3 ± 0.38	7.8 ± 2.43	8.8 ± 2.17	3.9 ± 2.26	2.7 ± 1.04
Marsh	8.5 ± 1.89	7.2 ± 1.25	5.8 ± 2.93	2.0 ± 1.49	0.4 ± 0.35	0.3 ± 0.31
Mediterranean scrubland	62.8 ± 4.19	75.0 ± 3.52	31.8 ± 6.73	50.4 ± 6.49	38.8 ± 8.78	51.6 ± 11.39
Pine plantations	14.6 ± 3.03	6.7 ± 2.22	21.7 ± 2.29	25.3 ± 5.46	39.2 ± 9.27	28.5 ± 10.10

\*Only animals located 20 or more times are included.

fect habitat use similarly for each phase. Therefore, we ran another MANOVA to test for differences in habitat use between both sex and origin for each phase separately. Because of the subsequent subdivision of data, the analysis could not be performed using eight habitat types. Thus, we grouped habitats into three categories according to vegetation structure: open habitat, plantations, and scrubland). As a rule, these habitats would correspond with the habitats avoided (crops, dunes, pastureland, and marsh), those sometimes used but generally avoided except during dispersal (pine and eucalyptus plantations), and always preferred (mediterranean scrubland and riparian vegetation), respectively.

The second MANOVA detected significant differences due to origin only for predispersal ( $F = 7.75$ ,  $p < 0.0007$ ) and dispersal ( $F = 14.43$ ,  $p < 0.0001$ ) but not for postdispersal ( $F = 0.31$ ,  $p = 0.8206$ ). These results reflect the fact that lynx from the Coto del Rey used the plantations more and the scrubland less during predispersal (Fig. 2), and used open habitats and plantations more during dispersal (Fig. 3) than did lynx from the Reserva Biológica.

Again, a significant interaction between sex and origin was detected during the predispersal phase ( $F = 4.63$ ,  $p = 0.0101$ ). Two females from Coto del Rey frequently used the pine plantations that surrounded their natal ranges before leaving the area. This produced a pattern indicating that females used the plantations more and the scrubland less than males (Fig. 2). This was not the case, however, for either sex in the Reserva Biológica. Sex did not affect habitat use during the postdispersal

phase ( $F = 1.99$ ,  $p = 0.2937$ ). The observed variations in the use of the habitats by lynx in the two subpopulations were caused by a different habitat composition in the two areas (Figs. 3 & 4).

The MANOVA showed that composition of habitat within lynx home ranges was significantly different among phases. Composition also differed by origin but not by sex (Table 1). The interaction between phase and origin was also significant (Table 1). The habitat most included within home ranges was the mediterranean scrubland for all phases except postdispersal, during which inclusion of pine plantations was slightly higher. Pine plantations were the second most included habitat for the predispersal and dispersal phases, although the percentage was low for the predispersal phase (Table 2). The quantity of mediterranean scrubland in home ranges was 63% and 32% for predispersal and dispersal phases, respectively (Table 2).

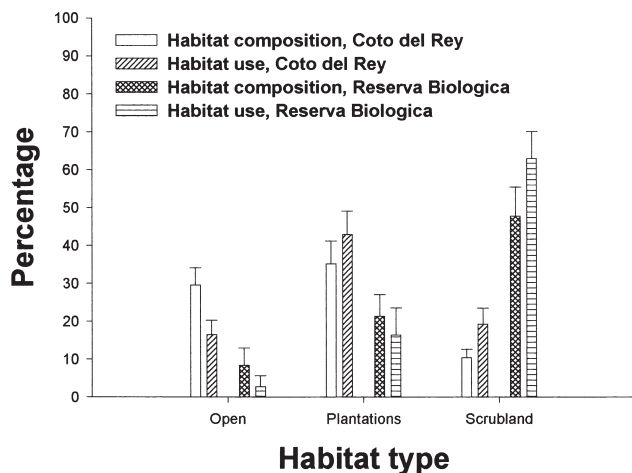


Figure 2. Mean ( $\pm$ SE) percentage of locations taken within each general habitat type and average ( $\pm$ SE) habitat composition within minimum convex polygon home ranges during the predispersal phase for 14 lynx (10 males and 4 females) from the Coto del Rey and for 18 lynx (7 males and 11 females) from the Reserva Biológica.

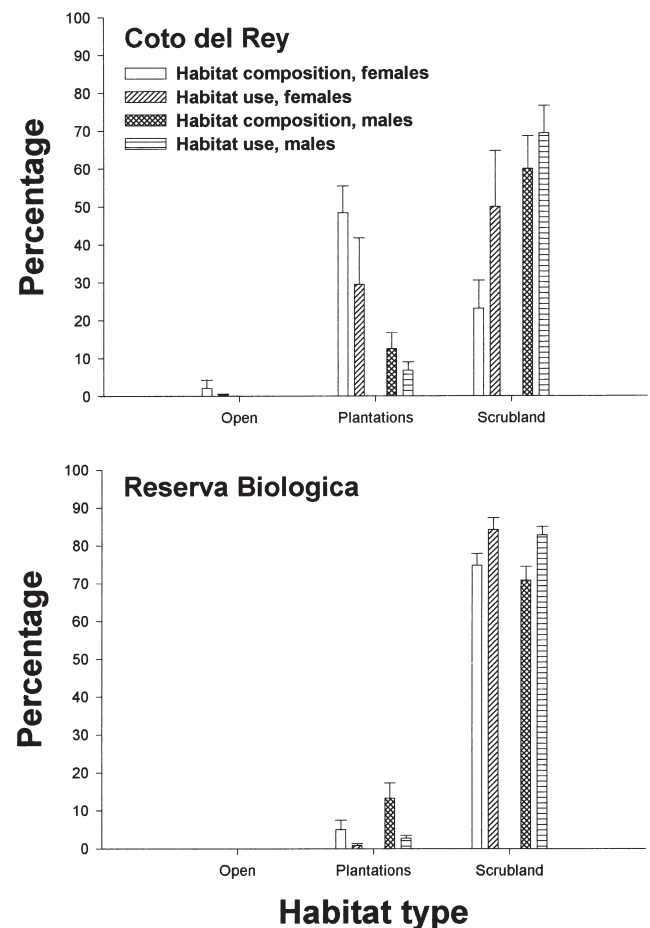


Figure 3. Mean ( $\pm$ SE) percentage of locations within each general habitat type and average ( $\pm$ SE) habitat composition within minimum convex polygon home ranges during the dispersal phase for 13 lynx from the Coto del Rey and for 10 lynx from the Reserva Biológica.

### Habitat Selection within Home Ranges and Landscapes

Analyses of habitat selection revealed more interesting differences among phases once we controlled for habitat availability. Predispersal and postdispersal phases showed that the only habitat preferred by lynx was the mediterranean scrubland and that pine plantations were avoided (Fig. 4). Lynx significantly avoided marsh and dunes during predispersal and eucalyptus plantations during postdispersal (Fig. 4). During dispersal, lynx significantly avoided all open habitats, whereas the forested habitats (pine and eucalyptus plantations and mediterranean scrubland) either were used according to their availability or were preferred (Fig. 4).

Crops were by far the best represented habitat type within the study area, and dunes and riparian vegetation were the least represented. Other habitat types had intermediate or low representation (Table 3). The Jacobs index indicated that during the predispersal phase the only habitat type significantly included in home ranges was mediterranean scrubland. The remaining habitat types, except for pastureland, were included significantly in home ranges but were used proportionately less than their availability in the landscape (Table 3). During the dispersal phase, mediterranean scrubland and pine plantations were traversed according to their availability, whereas the remaining habitats were traversed less than their availability in the landscape (Table 3). Finally, during postdispersal, lynx home ranges included mediterranean scrubland and pine plantations according to availability, and all other habitats were used proportionately less than their availability (Table 3).

## Discussion

### Habitat Selection

Habitat selection at a local scale was similar in pre- and postdispersal phases, whereas on a landscape scale habitat selection was more similar between dispersal and postdispersal phases. Therefore, habitat selection at a local scale was more restricted than habitat selection at a landscape scale. This indicates that dispersing lynx tend to settle in areas where habitat quality is inferior to that found in the predispersal source, suggesting that over a regional scale the best areas may be saturated with lynx.

Rabbits, the main prey of lynx (Delibes 1980), thrive best in mediterranean scrubland (Palomares et al. 1996b; Palomares & Delibes 1997). In this type of habitat, grassy areas are interspersed with shrubs, which is a necessary condition to support large rabbit populations (Rogers & Myers 1979; Rogers 1981; Soriguer & Rogers 1981; Moreno & Villafuerte 1995). Furthermore, most felid species need understory vegetation to provide cover for stalking prey and breeding (Kleiman & Eisenberg 1973; Bothma & le

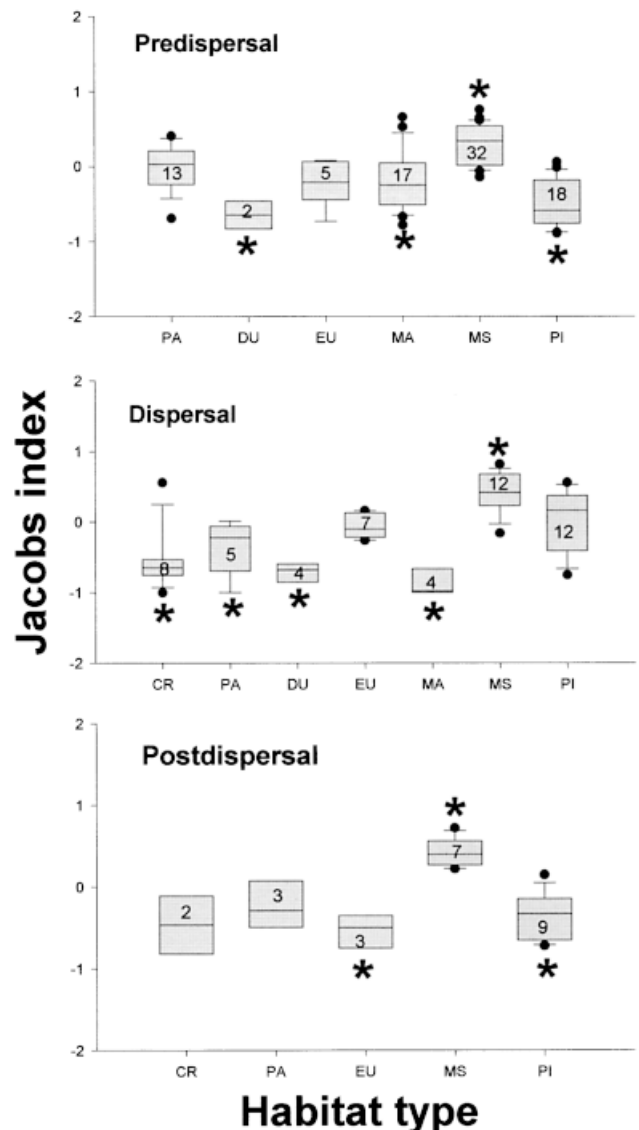


Figure 4. Jacobs index for each habitat used by 32, 13, and 10 lynx in the Doñana region between 1983 and 1997, considering all available independent locations and the predispersal, dispersal, and postdispersal phases, respectively. Positive and negative values indicate preference and avoidance, respectively. Boxes indicate the 25–75th percentile range and contain the median line. Whisker caps represent the 10th and 90th percentile values. Circles represent points outside these values. Asterisks indicate that the mean is significantly different from zero. Numbers indicate sample sizes, the number of individuals for which availability of that habitat type was higher than 5% within MCP100 home range (CR, crops; PA, pastureland; DU, dunes; EU, eucalyptus plantations; MA, marsh; MS, mediterranean scrubland; PI, pine plantations).

**Table 3.** Jacobs index (mean  $\pm$  SE) for habitat composition within home ranges<sup>a</sup> or areas traversed by lynx versus that for the overall study area for the predispersal, dispersal, and postdispersal phases in Doñana area.

Vegetation types <sup>b</sup>	Study area (2433 km <sup>2</sup> )	Predispersal (n = 32)	Dispersal (n = 13)	Postdispersal (n = 10)
Riparian vegetation	0.5	-0.98 $\pm$ 0.01 <sup>c</sup>	-0.32 $\pm$ 0.19	-0.81 $\pm$ 0.19 <sup>c</sup>
Crops	42.4	-0.99 $\pm$ 0.01 <sup>c</sup>	0.49 $\pm$ 0.12 <sup>c</sup>	-0.86 $\pm$ 0.09 <sup>c</sup>
Pastureland	4.5	-0.19 $\pm$ 0.13	-0.27 $\pm$ 0.14	-0.31 $\pm$ 0.21
Dunes	1.9	-0.85 $\pm$ 0.11 <sup>c</sup>	0.38 $\pm$ 0.23	-0.89 $\pm$ 0.11 <sup>c</sup>
Eucalyptus plantations	10.4	-0.79 $\pm$ 0.06 <sup>c</sup>	-0.34 $\pm$ 0.14 <sup>c</sup>	-0.67 $\pm$ 0.16 <sup>c</sup>
Marsh	11.6	-0.39 $\pm$ 0.09 <sup>c</sup>	-0.61 $\pm$ 0.15 <sup>c</sup>	-0.96 $\pm$ 0.05 <sup>c</sup>
Mediterranean scrubland	15.0	0.62 $\pm$ 0.05 <sup>c</sup>	0.19 $\pm$ 0.13	0.22 $\pm$ 0.21
Pine plantations	13.7	-0.27 $\pm$ 0.11 <sup>c</sup>	0.18 $\pm$ 0.09	0.33 $\pm$ 0.17

<sup>a</sup>Only home ranges from animals located 20 or more times were considered.

<sup>b</sup>Availability of the different vegetation types for the overall study area was obtained within the polygon encompassing all available lynx radio-locations.

<sup>c</sup>Different from zero, with  $p < 0.05$ .

Riche 1989; Koehler 1990). Therefore, it is not surprising that this habitat was the most used and preferred by lynx at both the local and landscape scales of analysis. The other habitats have either low understory cover (i.e., low protection; pastureland), low rabbit abundance (pine and eucalyptus plantations), or both (marsh, dunes, and crops) (F. P. et al., unpublished data). Pine and eucalyptus plantations show scarce understory vegetation in most places because of silvicultural activities.

Habitats used by a resident species must supply resources to satisfy all life-history requirements. Habitats used during dispersal, however, need only provide those ecological services and resources required when individuals are moving between source patches (Soulé 1991). Consistent with this idea, dispersing lynx were less selective and used forested habitats other than mediterranean scrubland. No lynx, however, settled exclusively within plantations. Therefore, plantation habitats apparently lack enough rabbits and/or scrubland for maintaining lynx over long periods.

The few studies of habitat selection by predators have produced contradictory results. For instance, Spotted Owls (*Strix occidentalis*) do not show strong habitat selection during dispersal (Miller et al. 1997), whereas dispersing coyotes (*Canis latrans*) select the same habitats as resident individuals (Roy & Dorrance 1985; but also see Person & Hirth 1991). Cougars (*Felis concolor*) and tigers (*Panthera tigris*) have been reported to use marginal or suboptimal habitats during dispersal (Smith 1993; Beier 1995; but see Maehr & Cox 1995), but detailed information is lacking for these and most species.

It was interesting that postdispersal lynx established home ranges in areas that had similar habitat characteristics on average as the areas used by dispersing lynx. Habitat selection differed, however, because the former avoided pine plantations and the latter did not. This suggests that lynx need to find suitable scrubland patches in which to settle, which as a rule occur in between plantations. Plantations were the habitat type that dominated

the closed areas of the Doñana region outside the national park, where most lynx settled after dispersal. These results also show the importance of considering both different spatial scales of analysis and different life-history phases of a species. Lynx selected different habitat types at local and landscape scales and for each phase studied.

Lynx of different origin used different habitat types during the predispersal and dispersal phases but not during the postdispersal phase. This probably occurred because sources had different habitats surrounding the basic mediterranean scrubland habitat, and because lynx from each subpopulation usually took different routes during dispersal. Because some lynx from different subpopulations settled in the same areas (Ferrerias 1994; F. P. et al., unpublished data), source of origin produced no difference in habitat use and availability during the postdispersal phase.

### Implications for Conservation

Our results can be used to maintain stable, resident lynx populations and to facilitate dispersal between established populations. The findings of general interest are mainly (1) the importance of selecting different habitats at different stages of life, (2) the possible selection of habitats compatible with human use while lynx are dispersing, and (3) variation in habitat selection over different spatial scales.

Mediterranean scrubland was the main habitat type in home ranges and the only preferred habitat for resident lynx; therefore, this habitat must be conserved. The proportion of mediterranean scrubland in areas adequate for stable lynx populations should be as close to 60% as possible. Even lower percentages (about 35–40%) may also hold resident lynx if this habitat is interspersed with pine plantations or pastureland containing scattered *Quercus* spp. trees. Because average lynx home ranges



are about 7–10 km<sup>2</sup> (Ferrerás et al. 1997), a minimum of 3.5 km<sup>2</sup>, preferably 5 km<sup>2</sup>, of mediterranean scrubland habitat would be required within each home range. Other vegetation types that support high rabbit densities and have well-developed undergrowth vegetation may replace the mediterranean scrubland habitat.

Conversely, all forested habitats allowed dispersal, including the mediterranean scrubland and pine and eucalyptus plantations. Therefore, patches with resident lynx populations could be connected by a matrix of these lower-quality habitats. Nevertheless, the matrix of unsuitable habitats for resident lynx should not exceed the capabilities of lynx to reach suitable patches.

Because lynx may use plantations for dispersal, the matrix land connecting areas of reproduction may be compatible with sustainable natural resources such as forestry or pine-seed harvesting. In the case of our study area, for example, it has been estimated that pine and eucalyptus plantations would yield an annual rent of more than 156 and 217 euros per hectare, respectively (Campos-Palacín & López-Linaje 1998). Thus, for the protected areas of Doñana, the exploitation of these habitat types would mean an important income source for people because it would total more than 4.1 million euros per year (Campos-Palacín & López-Linaje 1998).

The effect of adequate corridors, or matrix lands, on the probability of successful dispersal by lynx, or on the distance traveled, is unknown. It would be useful to have spatially explicit models integrating detailed information on lynx movements through different habitat types with specific landscape data (Fahrig & Merriam 1994; Gustafson & Gardner 1996).

We do not have much empirical information on buffer characteristics or matrix lands that allow movement of animals among suitable patches (Noss 1991; Franklin 1993; Noss et al. 1996). This information is important for conservation planners because dispersal may play a prime role in the demography and viability of natural populations (e.g., Gaona et al. 1998; Beier 1993). The information is also necessary to propose species-specific management recommendations that account for the explicit spatial patterning of environments (i.e., the characteristics of the landscape and the factors affecting it). Landscape ecology is a promising discipline that must be incorporated into conservation biology (Fahrig & Merriam 1994; Gustafson & Gardner 1996; Lima & Zollner 1996; Wiens 1997). Without information on how animal movements are affected by matrix lands, however, it will not be possible to bring metapopulation dynamics and landscape ecology together (Lima & Zollner 1996; Wiens 1997).

Studies on habitat selection in Iberian lynx provide a clear result that may affect large-scale management recommendations for wide-ranging species: dispersing animals may use habitats of lower quality than those used by resident individuals, and these habitats may be suit-

able for compatible human use. Thus, conservation strategies applied across regions might be a viable objective. Nevertheless, conservation strategies should not only contemplate the different habitat affinities of dispersing and resident individuals but also the spatial patterning of the different matrix lands connecting core areas (Fahrig & Merriam 1994; Gustafson & Gardner 1996).

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## Literature Cited

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio tracking data. *Ecology* 74:1313–1325.
- Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7:94–108.
- Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitats. *Journal of Wildlife Management* 59:228–237.
- Bothma, J. d. P., and E. A. N. le Riche. 1989. Evidence of a flexible hunting technique in Kalahari leopards. *South Africa Journal of Wildlife Researches* 19:57–60.
- Campos-Palacín, P., and J. López-Linaje. 1998. Renta y naturaleza en Doñana. A la búsqueda de la conservación con uso. Icaria Press, Barcelona.
- Delibes, M. 1980. El lince ibérico: ecología y comportamiento alimenticios en el coto de Doñana, Huelva. *Doñana Acta Vertebrata* 7:1–128.
- Eastman, J. R. 1995. Idrisi for windows. User's guide. Clark Labs for Cartographic Technology and Geographic Analysis, Clark University, Worcester, Massachusetts.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- Ferrerás, P. 1994. Patrones de dispersión del Lince ibérico (*Lynx pardina*) en Doñana e implicaciones para su conservación. Ph.D. thesis. Universidad Autónoma de Madrid, Madrid.
- Ferrerás, P., J. F. Beltrán, J. J. Aldama, and M. Delibes. 1997. Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*, Temminck, 1824). *Journal of Zoology* 243:163–189.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* 3:202–205.
- Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs* 68:349–370.
- Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77:94–107.
- Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology* 10:578–590.

- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego.
- Harrison, R. L. 1992. Toward a theory of inter-refuge corridor design. *Conservation Biology* 6:293–295.
- Hayne, D. W. 1949. Calculation of size of home range. *Journal of Mammalogy* 30:1–18.
- Jacobs, J. 1974. Quantitative measurements of food selection. A modification of the forage ratio and Ivlev's Electivity Index. *Oecologia* 14: 413–417.
- Kleiman, D. G., and J. F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour* 21:637–659.
- Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68:845–851.
- LaHaye, W. S., R. J. Gutierrez, and H. R. Akçakaya. 1994. Spotted Owl metapopulation dynamics in Southern California. *Journal of Animal Ecology* 63:775–785.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. *TREE* 11:131–135.
- Maehr, D. S., and J. A. Cox. 1995. Landscape features and panthers in Florida. *Conservation Biology* 9:1008–1019.
- Miller, G. S., R. J. Small, and E. C. Meslow. 1997. Habitat selection by Spotted Owls during natal dispersal in western Oregon. *Journal of Wildlife Management* 61:140–150.
- Moreira, J. M., and A. Fernández-Palacios. 1995. Usos y coberturas vegetales del suelo en Andalucía. Seguimiento a través de imágenes de satélite. Junta de Andalucía, Consejería de Medio Ambiente, Sevilla.
- Moreno, S., and R. Villafuerte. 1995. Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biological Conservation* 72:1–5.
- Myers, N. 1994. Global biodiversity II: losses. Pages 110–140 in G. K. Meffe and C. R. Carroll, editors. *Principles of conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Noss, R. F. 1991. Landscape connectivity: different function at different scales. Pages 27–39 in W. E. Hudson, editor. *Landscape linkages and biodiversity*. Island Press, Washington.
- Noss, R. F., and B. Csuti. 1994. Habitat fragmentation. Pages 237–264 in G. K. Meffe and C. R. Carroll, editors. *Principles of conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949–963.
- Palomares, F., and M. Delibes. 1997. Predation upon European rabbits and their use of open and closed patches in Mediterranean habitats. *Oikos* 80:407–410.
- Palomares, F., A. Rodríguez, R. Laffitte, and M. Delibes. 1991. The status and distribution of the Iberian lynx *Felis pardina* (Temminck) in Coto Doñana area, SW Spain. *Biological Conservation* 57:159–169.
- Palomares, F., P. Ferreras, J. M. Fedriani, and M. Delibes. 1996a. Spatial relationships between Iberian lynx and other carnivores in an area of southwestern Spain. *Journal of Applied Ecology* 33:5–13.
- Palomares, F., J. Calzada, and E. Revilla. 1996b. El manejo del hábitat y la abundancia de conejos: diferencias entre dos áreas potencialmente idénticas. *Revista Florestal* 9:201–210.
- Person, D. K., and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. *Journal of Wildlife Management* 55:433–441.
- Rodríguez, A., and M. Delibes. 1992. Current range and status of the Iberian lynx *Felis pardina* Temminck, 1824 in Spain. *Biological Conservation* 61:189–196.
- Rogers, P. M. 1981. Ecology of the European wild rabbit *Oryctolagus cuniculus* (L.) in Mediterranean habitats. II. Distribution in the landscape of the Camargue, S. France. *Journal of Applied Ecology* 18:355–371.
- Rogers, P. M., and K. Myers. 1979. Ecology of the European wild rabbit, *Oryctolagus cuniculus* (L.), in Mediterranean habitats. I. Distribution in the landscape of the Coto Doñana, S. Spain. *Journal of Applied Ecology* 16:691–703.
- Roy, L. D., and M. J. Dorrance. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. *Journal of Wildlife Management* 49:307–313.
- SAS Institute. 1990. SAS/STAT user's guide. Volume 1. Cary, North Carolina.
- Scheiner S. M. 1993. MANOVA: multiple response variables and multi-species interactions. Pages 94–112 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman & Hall, New York.
- Smith, J. L. D. 1993. The role of dispersal in structuring the Chitwan tiger population. *Behaviour* 124:165–195.
- Soriguer, R. C., and P. M. Rogers. 1981. The European wild rabbit in Mediterranean Spain. Pages 600–603 in K. Myers and C. D. MacInnes, editors. *Proceeding of the World Lagomorph Conference*. University of Guelph, Ontario.
- Soulé, M. E. 1991. Theory and strategy. Pages 91–104 in W. E. Hudson, editor. *Landscape linkages and biodiversity*. Island Press, Washington, D.C.
- Swihart, R. K., and N. Slade. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management* 49: 1019–1025.
- Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43–62 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego.

