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Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx

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Abstract

Among the factors threatening the Iberian lynx, (*Lynx pardinus*) (the most endangered species of all the Felidae), loss and fragmentation of its habitats are probably the most important. Connectivity between the remaining populations in the predominantly fragmented landscapes is a key factor in the dynamics and persistence of metapopulations. Based on the data collected during a long-term study on the ecology of this species in a small and fragmented population in SW Spain, I analyse the factors affecting connectivity between the two main sources and the rest of local populations. Connectivity was estimated as the proportion of dispersers from a source that reached a given subpopulation. Among the explanatory variables considered, only distance (both straight and effective distance, which takes into account habitat quality between local populations) and location of the source were clearly related to connectivity. Some other variables describing landscape features separating sources and target subpopulations (proportion of unsuitable habitats, patch cohesion, size of targets, overall size of subpopulations closer than the target) were not related to connectivity. Differences in the landscape surrounding sources help to explain the different connectivity from the two sources. An asymmetrical connectivity between the two sources and populations surrounding them (north and south) is likely explained by the configuration of habitats encountered by dispersers, which force those from one source to behave as crossers of unsuitable habitats. These results have consequences for the conservation of Iberian lynx populations and for ecologically similar species. Distance, the factor most affecting connectivity, is difficult to manage, although at least size and configuration of usable patches can be modified. Connectivity could also be improved through recovery of habitats with cover, suitable for dispersing. Reduction of mortality risks would also enhance connectivity indirectly, by allowing longer times and larger areas covered during dispersal. In the case of the study population, it is urgent to promote connectivity with other Iberian lynx populations due to genetic consequences of small population size and effective isolation. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Habitat loss and fragmentation are widely regarded as major threats to the viability of wildlife populations (Wilcove et al., 1986; Rolstad, 1991; Fahrig and Merriam, 1994; Wiens, 1995). Habitat loss reduces area of suitable habitat, and may also lead to fragmentation of the habitat into small, isolated remnants (Fahrig, 1997). The ecological consequences of habitat fragmentation include the indirect effects of reduced inter-patch dispersal (Schumaker, 1996). Populations become fragmented, resulting in smaller, more isolated, and "hard-edged"

patches surrounded by a more or less hostile matrix. In such situations, dispersal is a key process in determining the survival of the resulting metapopulations, sets of local populations connected by inter-patch dispersal (Davis and Howe, 1992; Fahrig and Merriam, 1994; Hanski et al., 1994).

To quantify the hindrance of dispersal caused by habitat fragmentation, landscape ecologists introduced the notion of habitat or landscape connectivity (Fahrig and Merriam, 1985; van Apeldoorn et al., 1992; Schumaker, 1996). Landscape connectivity is the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993). It depends not only on the landscape characteristics, but also on the species' movement ability, being, therefore, not only landscape-specific but also species-specific. It can be measured for a given organism using the probability of movement between all points or resource patches in a

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landscape (Taylor et al., 1993; Anderson and Danielson, 1997). In order to design conservation strategies for endangered species, it is crucial to obtain insights into the relation between dispersal and landscape characteristics. The importance of landscape connectivity for long-term population viability has been demonstrated for such species as the cougar (*Felis concolor*; Beier, 1993), the white-footed mouse (*Peromyscus leucopus*; Fahrig and Merriam, 1985), and the acorn woodpecker (*Melanerpes formicivorus*; Stacey and Taper, 1992).

The Iberian lynx (9–15 kg, Beltrán and Delibes, 1993), considered to be the most endangered species of all the Felidae (Nowell and Jackson, 1996), is restricted to the Iberian Peninsula (Rodríguez and Delibes, 1992). Similar to other medium and large size carnivores, its populations are threatened mainly by habitat loss and fragmentation. I investigated the factors influencing the connectivity between patches of a fragmented population of Iberian lynx living in southwest Spain (Palomares et al., 1991). Several factors are postulated as affecting connectivity: geographical location of the source patches, distance between patches, size of destination patch, and the landscape composition and structure between patches. Landscape determinants of animal movements during dispersal are explored to explain the connectivity between populations. Results could be useful for predicting connectivity within other metapopulations of Iberian lynx or metapopulations of other species with similar landscape requirements and for prioritising the establishment of corridors between patches with reduced connectivity to improve viability of the metapopulations.

2. Methods

2.1. Study area

The study was carried out in the Doñana region (southwest Spain), where field data on the species were collected between 1983 and 1998. The climate is Mediterranean subhumid, with rainy, mild winters and hot, dry summers. The region comprises ca. 2500 km^2, and is delimited by the Atlantic Ocean to the south and west, the Guadalquivir river to the east, and the foothills of Sierra Morena mountains to the north. The area is flat, and includes marshes to the east and sandy soils of aeolian deposits of marine origin in the remaining areas. The region was originally occupied by Mediterranean woodlands and scrublands, but it is currently highly modified by humans. The resulting landscape is highly fragmented, with about half of the area occupied by a cropland matrix. The remaining land is occupied by patches of Mediterranean shrub, dominated by species such as *Halimium* sp., *Cistus* sp., *Pistacia lentiscus* and interspersed cork oak (*Quercus suber*) stems, plantations of pines (*Pinus pinea*) and eucalyptus (*Eucalyptus* sp.),

and areas of pastureland. However, these habitats are not uniformly distributed along the study area. The southern half is dominated by plantations, scrubland and marshes, whereas the northern half is dominated by human agricultural activities, including croplands (Fig. 1). The most naturally preserved area in the south is protected by a 550 km^2 National Park, including mainly marshes, Mediterranean shrub, and a dune system bordering the Atlantic Ocean (for a detailed description of the area see Fernández-Delgado, 1997).

2.2. The Doñana lynx population

About 40–50 individuals constitute this small lynx population (Palomares et al., 1991). Only a small proportion of the study area (<10%) contains suitable habitat for reproduction, and breeding opportunities are currently limited to some 12–16 females and males (Palomares et al., 1991; Gaona et al., 1998; Delibes et al., pers. commun.). Due to loss and fragmentation of suitable habitat, several distinct subpopulations or local populations can be recognised (Palomares et al., 1991). Three of them (Vera, Marismillas, and Coto del Rey) are included within the National Park (Fig. 1), the most protected area in the whole Iberian lynx range. These subpopulations act as sources for the rest in the study area, according to demographic models recently developed (Gaona et al., 1998). Field studies concentrated on the two largest subpopulations: Vera and Coto del Rey. Up to five local populations (Acebuche, Moguer, Hato-Ratón, Torrecuadros and Puebla) can be identified outside the National Park, representing a minor contribution both in area and the number of individuals to the total Doñana population (Palomares et al., 1991; Table 1). These subpopulations have a negative average demographic balance and are considered sinks (Gaona et al., 1998). The peripheral and smaller local populations are subjected to a dynamic process of extinction-recolonisation, based on evidence gathered during two regional track surveys in 1986 and 1992 (Palomares et al., 1991; Delibes et al., pers. commun.) and on radio-tracking data (Gaona et al., 1998).

2.3. Habitat map and habitat use by lynx

I used a raster-based habitat map of the study area with 50 m resolution from the Environmental Information System of Andalucía (SINAMBA). This map is based on satellite imagery (Landsat) information and aerial photographs obtained in 1991 (Moreira and Fernández-Palacios, 1995). I simplified the original habitat classification of 151 categories to eight habitat classes, using as criteria merging the variants of habitats with common physiognomic features and level of human modification. The resultant habitat classes were: (1) Mediterranean scrubland; (2) pine plantations; (3) eucalyptus

Table 1
Lynx populations: characteristics and number of individuals marked and radio-tracked in Doñana between 1983 and 1998

Local population	Breeding territories	Area (km²)	No. lynx marked	No. resident lynx[a]	No. migrant lynx[b]
Vera	4	73	33	14	13
Coto del Rey	3	14	28	7	13
Marismillas	2	8	0	2	0
Acebuche	2	27	2	3	0
Moguer	1	9	0	2	0
Hato Ratón	1	3	0	1	0
Torrecuadros	1	3	1	2	0
Puebla	1[c]	5	0	0	0

[a] Resident individuals radio-tracked along the study. Although no lynx were tagged in Marismillas, Moguer and Hato Ratón, some dispersers tagged in the first two populations settled as residents there.
[b] Radio-tracked lynx which went out of their source when dispersing
[c] No recent evidences of the occurrence of breeding in this population, although habitat features could allow the settlement of a lynx pair.

plantations; (4) riparian vegetation; (5) pasturelands, either with or without variable tree canopy cover or native trees (*Quercus* sp., *Olea* sp.); (6) dunes; (7) marshes; and (8) croplands (for a detailed description see Palomares et al., 2000).

These habitats were used differently by the lynx in different stages of its life cycle (Palomares et al., 2000). Mediterranean scrubland is the habitat type most used and preferred by lynx throughout its vital stages. Lynx with established territories occupy patches of Mediterranean scrubland, and they generally avoid the rest of the habitats. Dispersing lynx also prefer this habitat, and use pine and eucalyptus plantations according to their availability. However, open habitats such as croplands, marshes, and dunes are avoided, even by dispersing lynx (Palomares et al., 2000). From the point of view of habitat use by lynx, the landscape of the study area can be regarded as a matrix of unsuitable habitat (mainly croplands and marshes; white in Fig. 1), with
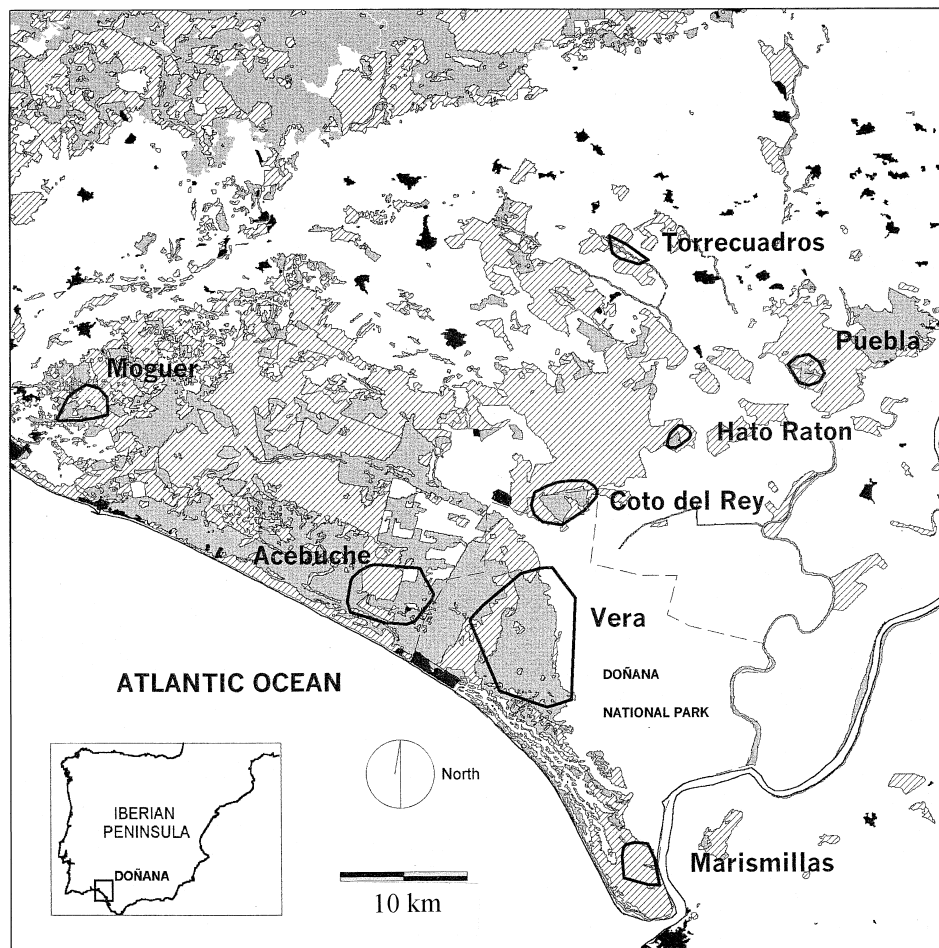

Fig. 1. Map of the study area, showing classes of habitats grouped according to their use by dispersing lynx, and location of lynx subpopulations. Grey areas represents Mediterranean scrubland, hatched areas are pine and eucalyptus forests, and white areas correspond to open habitats (mainly croplands and marshes). Black spots indicate human populations. Dashed line represents the limits of the Doñana National Park. Thick line polygons indicate location of lynx subpopulations, constituting the metapopulation of Doñana.

patches of habitat suitable for lynx establishment and breeding (mainly Mediterranean scrubland; grey in Fig. 1) and patches of suboptimal habitat (mainly pine and eucalyptus plantations; hatched in Fig. 1), unsuitable for the establishment and subsequent breeding but usable by dispersers.

A remarkable habitat feature for patch connectivity in Doñana is the existence of a potential barrier between Vera and Coto del Rey. These subpopulations are separated by a marshland strip about 1 km wide, which runs in an approximate west to east direction and continues to the west by the village of El Rocío and croplands surrounding it (Fig. 1). I postulate that this marshland strip affects connectivity between the subpopulations located to the south and west and those located to the northeast of the barrier, although they may still function as a single metapopulation.

2.4. Radio-tracking and movement data

A total of 65 individual lynx were fitted with radio-collars and radiotracked between 1983 and 1998 for ca. 31,000 radiodays, following standard radiotracking methods (Ferreras et al., 1997; Palomares et al., 2000). Most of the tracked lynx were initially radiotagged in the two largest subpopulations (Vera and Coto del Rey) although some dispersers, originally tagged there, established in the peripheral subpopulations (Table 1). For the purpose of this study, boundaries of subpopulations were defined with the help of radio-tracking and sightings as continuous areas occupied (either permanently or temporally) by adult, breeding lynx. The minimum convex polygon including 90% of all radio-fixes per each breeding lynx in each population was used as a measure of subpopulation area (Table 1). Although no lynx were tagged in Marismillas, Moguer and Hato Ratón, some dispersers initially tagged in the two largest subpopulations (Vera and Coto del Rey) settled as residents there, allowing estimation of subpopulation area. No resident lynx were observed in the Puebla subpopulation, but results from a regional track survey (Palomares et al., 1991) and suitable habitat and prey conditions, suggest at least occasional breeding lynx. The area of this potential subpopulation was indirectly estimated based on optimal habitat extent.

Lynx were considered as dispersers when they left their natal home range and did not return for at least two months (Ferreras, 1994). Dispersers that left their natal subpopulation were considered as migrants (following terminology usual in metapopulation theory, Stacey et al., 1997), and those reaching any subpopulation as successful migrants. Most male and female Iberian lynx leave their natal area and start the dispersal process when they are between 1- and 2-years-old (Ferreras, 1994). Duration of dispersal is highly variable, averaging 149±25 days ($n = 30$), which includes cases of

individuals which settled as a result of dispersal, others which died when dispersing and those whose fates were unknown because of radio-contact loss. Once dispersers leave their natal subpopulation, they can reach other subpopulations. However, they do not always settle in the first subpopulation reached, probably because of lack of vacancies or poor habitat quality. Therefore, each disperser can reach several subpopulations while dispersing.

I considered three variables related to space use by dispersers. Maximum dispersal extent was the distance between furthest locations during dispersal. Total distance travelled during dispersal was estimated as the sum of distances between daily sequential locations during dispersal. Total area covered during dispersal was estimated as the minimum convex polygon including all the fixes recorded during the process. Total area covered by each disperser was used as a summary of maximum extent and total distance travelled, since they are all highly correlated (area vs. maximum extent: $r = 0.779$, $P = 0.0001$, $n = 30$; area vs. total distance $r = 0.874$, $P = 0.0001$, $n = 30$). As a variable describing the landscape traversed during dispersal, I used the proportion of open-cover habitats within the total area covered by dispersers. Time dispersing was used as a covariate when comparing these spatial variables between sources.

2.5. Connectivity measurement and explanatory variables

Landscape connectivity can be measured for a given organism using the probability of movement between points or resource patches in a landscape (Taylor et al., 1993). According to this definition, I used, as a measure of the "inter-patch connectivity" or connectivity between subpopulations, the proportion of the dispersing animals going out from a given subpopulation ("source") that reach a given subpopulation ("target"). I evaluated the connectivity between the larger subpopulations acting as sources (Vera and Coto del Rey), where most lynx were radio-tagged, and the remaining subpopulations. First, I tested for differences between the two studied sources in the emigration rate (probability of a disperser going out from its subpopulation of origin), and for the probability of successful migration (reaching any other subpopulation). The "inter-patch connectivity" between a source and a target was estimated to be the fraction of individuals starting in the source that arrived in a certain target, either directly or after passing through other subpopulation(s) (Schippers et al., 1996). Maximum connectivity (one) would mean that all the dispersers going from a source reached a given target. Since some migrants do not reach any subpopulation (because of death or radio-contact loss) and some others reach several subpopulations, sum of the connectivities across all patches that receive animals from one of the given source populations do not necessarily add to exactly one.

I tested for relationships between inter-patch connectivity and some landscape-related variables. Connectivity was expected to be negatively affected by distance between source and target subpopulations, as generally assumed (Trewhella et al., 1988; Miller and Carrol, 1989; Porter and Dooley, 1993; Hanski, 1994; Whitcomb et al., 1996; Moilanen and Hanski, 1998). Two estimates of distance between local populations were used: straight-line distance, and "effective distance". Straight-line distance was measured as the length of the shortest straight line joining two subpopulations. However, in a landscape mosaic, interpatch distances are not Euclidean but rather a complex function of relative habitat viscosities to moving organisms (Wiens et al., 1993). According to this, "effective distance" was estimated with the help of the IDRISI Geographical Information System (GIS; Eastman, 1995). For this measure, an index of habitat friction was assigned to each grid cell in the GIS, inversely related to the score of the selection index specific to the habitat in each cell. Palomares et al. (2000) described habitat selection by dispersing lynx, using Jacobs' index (Jacobs, 1974) with radio-tracking data. This index compares the use (r) and the availability (p) of a resource through the formula:

$$\text{Jacobs' Selection Index} = \frac{r - p}{r + p - 2rp}$$

This formula provides values of the index ranging between -1 (maximum avoidance) and $+1$ (maximum preference). In our case, the use is estimated as the proportion of point locations of one animal in a given habitat, and the availability as the proportion of the area of movements occupied by that habitat. The scrubland was the habitat preferred by dispersing lynx (Jacobs' index = 0.36), and the marsh the most avoided habitat (Jacobs' index = −0.97), other habitats having intermediate values (Palomares et al., 2000).

In order to estimate effective distance between two patches, I assumed that the lower the habitat quality to be crossed, the higher the "cost" of movements by dispersing lynx. In order to compare the cost of alternative paths with different habitats, "friction" is defined as a value specific to each habitat and inversely related to its selection index. This measure must not be confused with the speed when travelling along a given habitat. It is rather the relative reluctance of a lynx to travel along a habitat related to others, equivalent to the "habitat resistance" defined by Knaapen et al. (1992). An arbitrary scale of friction from 1 to 10 was chosen, where the lowest value (1) is assigned to the preferred habitat (Mediterranean scrubland), and the highest value (10) is assigned to the most avoided habitat (marshland, Fig. 2). The GIS generates a distance/proximity surface (also referred to as a "cost surface") around a given

source, where distance is measured as the least effort in moving over the friction surface. The unit of measurement is "grid cell equivalents" (gce). A gce of 1 indicates the cost of moving through a grid cell when the friction equals 1. A cost of 10 gces might arise from a movement through 10 cells with a friction of 1 (scrubland), or 1 cell with a friction of 10 (marshland, for instance). Therefore, a route along 9 km of scrubland would be less "costly" (and therefore, preferred) than an alternative route of 1 km of marshland. With the help of the GIS, I determined the least cost route between the two subpopulations considered, and the corresponding gce is converted to its equivalent distance (km). This distance is defined as the "effective distance", being similar to the "minimal cumulative resistance" defined by Knaapen et al. (1992).

As another possible variable related with connectivity, I considered the area occupied by the target population. Larger lynx populations are expected to be met easier by dispersers in their movements (Root, 1973; Jones, 1977; Pokki, 1981).

Because dispersing lynx avoid open habitats, I expected the proportion of such habitats in the area separating the populations to be inversely related to their connectivity. To calculate this variable, I first defined the area separating two subpopulations as the zone of overlap of buffer strips around each local population as wide as the distance separating them (Fig. 3). Then, I calculated the proportion of croplands, marshes, and sand dunes within this zone of overlap for each subpopulation.

The connectivity between a source and a given destination is expected to be reduced by the existence of other, closer populations. Therefore, I considered, as another possible explanatory variable, the sum of the areas occupied by closer populations.

More indirect indices of habitat fragmentation and landscape pattern have been used to explain ecological
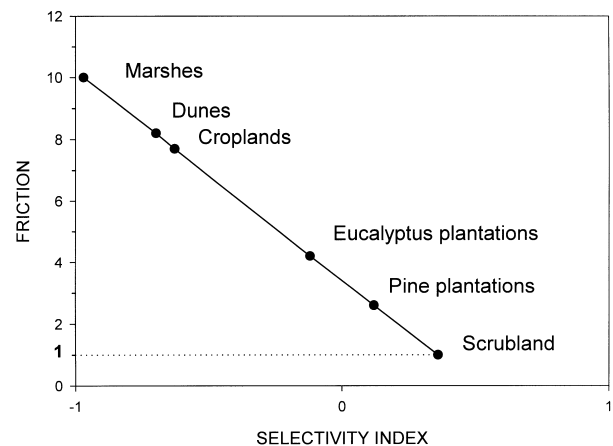

Fig. 2. Function linking habitat selectivity index (Jacobs, 1974) during dispersal and proposed values of friction to movement employed to calculate the "effective distance" between subpopulations. Dashed line indicates the minimum value arbitrarily assigned to the friction scale.

functions, and some of them have been evaluated as predictors of habitat connectivity (Schumaker, 1996). A recently developed pattern index, called "patch cohesion" has proved better correlated to a general dispersal model than commonly cited indices of habitat pattern, such as perimeter-area ratio, shape index and fractal dimension (Schumaker, 1996). I used patch cohesion as another possible explanatory variable of connectivity. Patch cohesion is proportional to perimeter-area ratio divided by shape index. It is numerically computed as:

$$PC = \left[1 - \frac{\Sigma p}{\Sigma(p\sqrt{a})} \right] \left[1 - \frac{1}{\sqrt{N}} \right]^{-1}$$

where: a and p are the area and the perimeter of a patch in pixels and pixels edges, respectively (they are dimensionless) and N is the total number of pixels in a landscape. PC is a dimensionless quantity ranging between zero and one. Using the IDRISI Geographical Information System (Eastman, 1995) this variable was computed for each source-target pair within the overlapping area between a buffer strip around each local population as wide as the distance separating them (Fig. 3).

Because the considered sources have different attributes and are located in different landscapes (Fig. 1), I tested also for the effect of the source (Vera/Coto del Rey) on connectivity.

I tested for univariate relationships between connectivity and candidate explanatory variables, using parametric regression when possible. Then I looked for the combination of variables that best explained the variation in connectivity between patches, by using generalised linear models (McCullagh and Nelder, 1983).
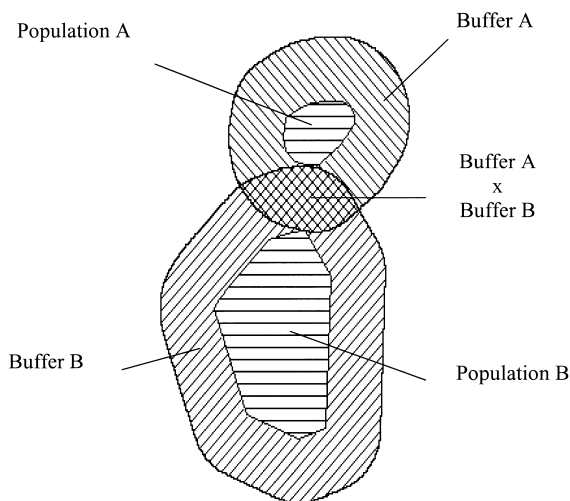

Fig. 3. Graphic representation of the method for defining the area between subpopulations. Horizontal lines represent subpopulations and diagonal lines buffers around each subpopulation as wide as the distance separating them. The proportion of open habitats and the patch cohesion index were calculated within the area of overlap between both buffers.

3. Results

3.1. Radio-tracked lynx

A total of 31 out of 65 radio-tagged lynx (16 from Vera and 15 from Coto del Rey) dispersed (left their home range) during the study (34 of them did not disperse). Twenty-six of these dispersers (13 from each subpopulation) were "migrants" (Table 1), and 21 out of these "migrants" reached at least a different population ("successful migrants"). Dispersers were not sex-biased (sex ratio: 0.63 females/male, $n = 31$, compared to non-dispersers (sex ratio: 0.89 females/male, $n = 34$; $P = 0.617$, Fisher-Exact test). The proportion of "migrants" from the total dispersers, was similar for both populations ($P = 1.00$, Fisher-Exact test). No differences were found between sources in the proportion of successful migrants (10 and 11 from Vera and Coto del Rey, respectively; $P = 0.704$, Fisher-Exact test).

3.2. Variables explaining connectivity

Univariate analyses indicated that inter-patch connectivity (square-root arc-sin transformed) was significantly related to straight-line distance ($r^2 = 0.333$, $F_{1,12} = 5.99$, $P = 0.031$) and, especially, to effective distance ($r^2 = 0.459$, $F_{1,12} = 10.192$, $P = 0.008$, Fig. 4), but not to the remaining potential explanatory variables (all Ps > 0.161), including patch cohesion. Higher connectivity was expected between closer populations (Fig. 4). The two measures of distance were correlated ($r = 0.641$, $P = 0.0136$, $n = 14$), as were straight-line distance and total size of closer subpopulations ($r = 0.660$, $P = 0.0102$, $n = 14$). Therefore, only effective distance was included in the multivariate analyses (see below). Considering each source separately, connectivity of Vera was significantly related to the size of the destination subpopulation ($r^2 = 0.787$, $F_{1,5} = 18.479$, $P = 0.008$), and to the total size of patches closer to the source than the target ($r^2 = 0.642$, $F_{1,5} = 8.956$, $P = 0.030$, Fig. 5), which were, in turn, negatively correlated ($r = -0.897$, $P = 0.0062$, $n = 7$). The regressions indicated that the connectivity of Vera is higher with larger local populations (Table 2). However, connectivity of Coto del Rey alone cannot be predicted by any of the variables considered. Despite the result that connectivity of Vera alone was not significantly related to distance, it is only connected with the three closest subpopulations, two of them located in the southwest half of the study area, where Vera itself is located (Fig. 1). On the other hand, I recorded contacts between Coto del Rey and all the remaining subpopulations (Table 2), even those located to the other side of the postulated marshland barrier.

Using multivariate statistics (generalised linear models, McCullagh and Nelder, 1983) for the whole sample (including connectivity from both sources) only effective

distance ($F_{1,11} = 12.313$, $P = 0.005$) and source ($F_{1,11} = 4.880$, $P = 0.049$) were included in the best model of connectivity ($F_{2,11} = 9.183$, $P = 0.005$). No improvement of the model was obtained with the inclusion of any of the remaining variables, even patch cohesion.

To explain the differences in connectivity of the two sources, I tested for differences between dispersers from both sources in their spatial behaviour. The variation in area covered is effectively explained ($F_{3,23} = 11.09$, $P = 0.0001$) by a model including as significant terms: source (but not sex) and time as a covariate ($F_{1,23} = 9.48$, $P = 0.0053$; $F_{1,23} = 17.47$, $P = 0.0004$, respectively; Fig. 6). According to this, dispersers from Coto del Rey cover larger areas than those from Vera, once the duration of dispersal was controlled (difference in slopes of regression lines: $t_{24} = 7.945$, $P < 0.0005$; see Fig. 6). This can be explained by the differences in the landscape surrounding each of the sources, where lynx mainly move while dispersing. Dispersers from Vera encounter a lower proportion of open habitats ($F_{1,23} = 6.741$, $P = 0.016$, once time effect is controlled, see Fig. 7), and they explore the large and nearly continuous area suitable for dispersal, where the source itself and other populations are included (Acebuche, Marismillas and Moguer). Dispersers from Coto del Rey soon finish exploring the northern Doñana area, due to its limitation of suitable areas for settlement and dispersal, and find their way into the southern area of Doñana.

Lynx movements also explain the different connectivity between the subpopulations located to both sides of the hypothesised barrier separating Vera and Coto del Rey (Figs. 1 and 4). Only one lynx (out of 13 migrants) was recorded to migrate from Vera to the subpopulations located northeast to the barrier (Table 2). However, this barrier seems less effective for lynx dispersing from Coto del Rey, that are able to reach any of the populations located southeast to their origin (five out of 13 migrants reached any of them).
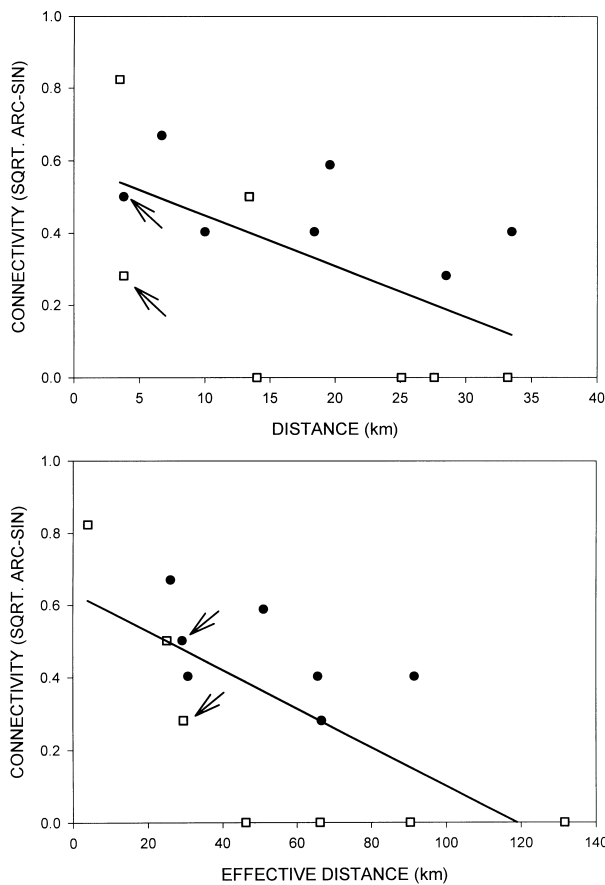

Fig. 4. Relationships between connectivity (square-root arc-sin transformed) and straight-line distance (top) and effective distance (bottom), a measure of distance and quality of habitat between populations. Blank squares indicate connectivity from Vera and black dots values from Coto del Rey. The regression lines for the whole sample (SQ. ROOT ARC-SIN (CONNECTIVITY) = 0.59 −0.024 × DISTANCE, $R^2 = 0.333$; and SQ. ROOT ARC-SIN (CONNECTIVITY) = 0.634 −0.0053 × EFFECTIVE DISTANCE, $R^2 = 0.459$) are also shown. Arrows indicate how the connectivity between the sources is asymmetric, being higher from Vera to Coto del Rey (upper arrows in each graph) than the other way round (lower arrows).
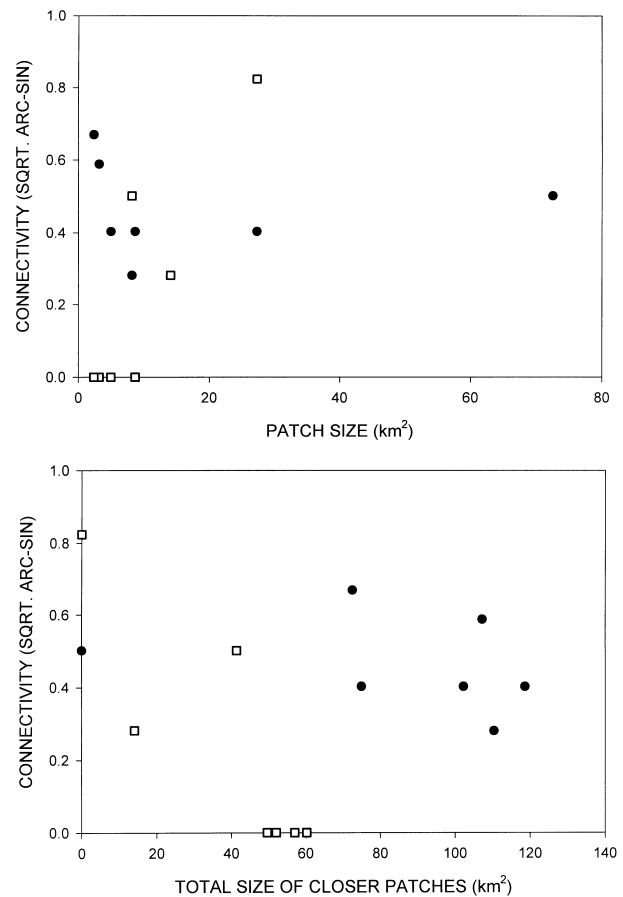

Fig. 5. Relationships between connectivity (square-root arc-sin transformed) and patch size of destination (top) and sum of size of populations closer to the source than the destination (bottom). Values corresponding to each source are marked with blank squares (Vera) and black dots (Coto del Rey).

Table 2
Values of connectivity between the sources studied and the remaining populations in the area, and variables used to explain its variability

|	Destination	Successful migrants	Connectivity	Straight-line distance (km)	Effective distance (km)	Patch size (km²)	Open habitats	Total size of closer patches (km²)	Patch cohesion
From Vera									
	Acebuche	7	0.538	3.5	4.0	27.3	0.02	0	0.9999
	Marismillas	3	0.231	13.4	25.1	8.2	0.81	41.4	0.9757
	Moguer	0	0	33.2	46.2	8.7	0.32	60.2	0.9987
	Coto del Rey	1	0.077	3.8	29.5	14.1	0.75	14.1	0.9889
	Hato Ratón	0	0	14.0	66.2	2.4	0.68	49.6	0.9925
	Puebla	0	0	25.1	131.6	5.0	0.72	52.0	0.9947
	Torrecuadros	0	0	27.6	90.4	3.2	0.59	57.0	0.9960
From Coto del Rey									
	Acebuche	2	0.154	10.0	30.8	27.3	0.35	74.9	0.9985
	Marismillas	1	0.077	28.5	66.6	8.2	0.75	110.4	0.9914
	Moguer	2	0.154	33.5	65.6	8.7	0.39	118.6	0.9984
	Vera	3	0.231	3.8	29.2	72.5	0.75	0	0.9889
	Hato Ratón	5	0.385	6.7	26.1	2.4	0.43	72.5	0.9958
	Puebla	2	0.154	18.4	91.5	5.0	0.67	102.2	0.9952
	Torrecuadros	4	0.308	19.6	51.1	3.2	0.56	107.2	0.9959
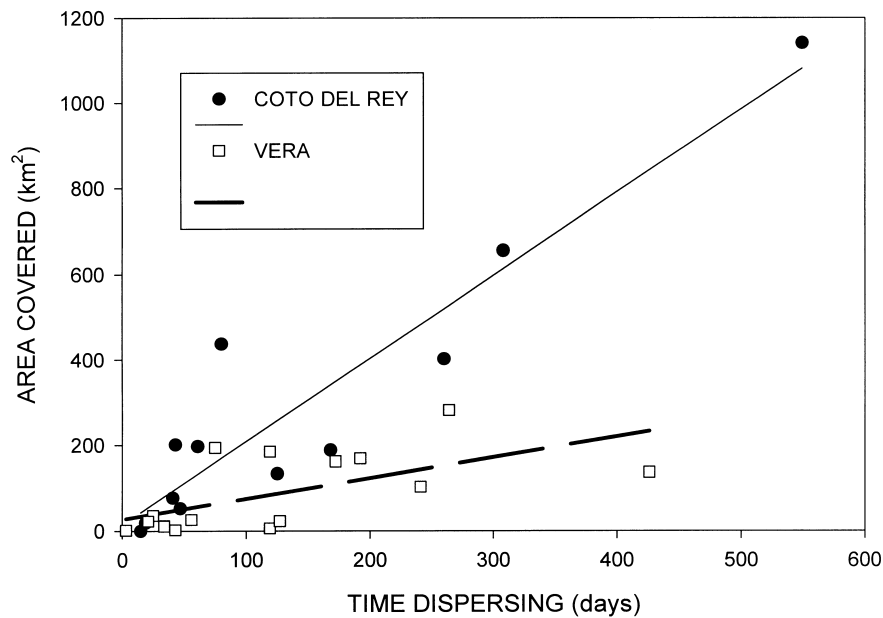
Fig. 6. Relationship between time dispersing and area covered during dispersal (as minimum convex polygon containing all the locations) for lynxes starting in Vera (blank squares and dashed line) and in Coto del Rey (black dots and continuous line). Regression lines are AREA $= 27.5 + 0.48 \times$ TIME, $R^2 = 0.376$, for Vera; and AREA $= 14.3 + 1.94 \times$ TIME, $R^2 = 0.875$; for Coto del Rey.

Therefore, a different directional permeability exists in the landscape between northwest (Coto del Rey and more northerly ones) and southeast populations (Vera and southerly ones). This asymmetry is clear when connectivity between Coto del Rey and Vera is compared in the two directions (see arrows in Fig. 4).

4. Discussion

According to these results, lynx populations in Doñana are connected through dispersal (Table 2). The

whole population can be considered, therefore, a metapopulation (Gaona et al., 1998), in the sense of "a group of interconnected populations that function as a unit" (Arnold et al., 1993; Hanski and Simberloff, 1997). The smallest and more peripheral populations are, however, only weakly connected with the main sources (Table 2). As a result, they are subjected to dynamic processes of extinction and recolonisation. This is supported by two regional surveys on presence of the species carried out in 1986 and 1992. In the first survey, no lynx were detected in populations of Torrecuadros, Moguer, and Hato Ratón. However, presence in Torrecuadros was detected
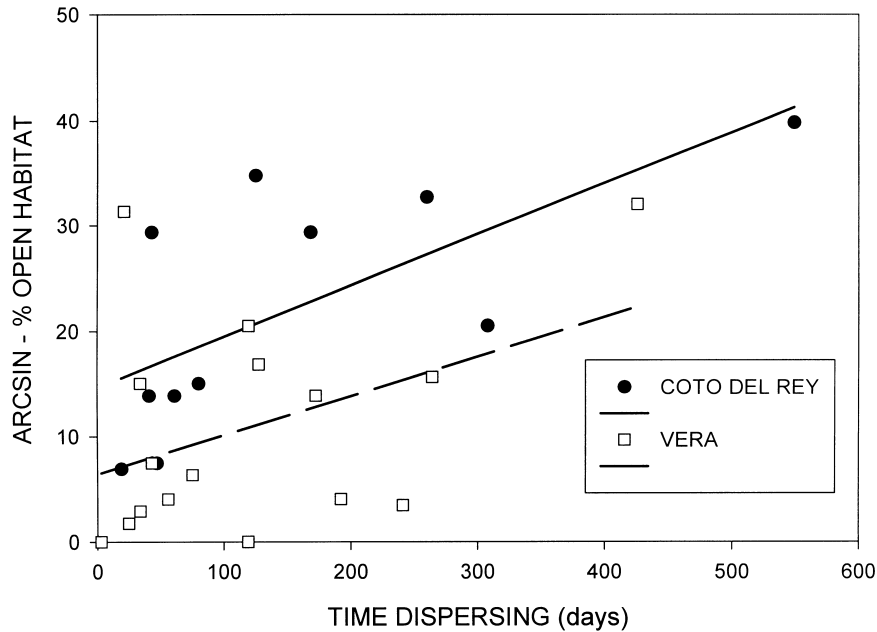
Fig. 7. Relationship between time dispersing and percentage of open habitat in the area covered during dispersal for lynxes starting in Vera (blank squares and dashed line) and in Coto del Rey (black dots and continuous line). Regression lines are SQ. ROOT ARC-SIN(OPEN-HABITAT) $= 0.287 + 0.0009 \times$ TIME, $R^2 = 0.162$, for Vera; and SQ. ROOT ARC-SIN(OPEN-HABITAT) $= 0.516 + 0.0008 \times$ TIME, $R^2 = 0.441$, for Coto del Rey.

in 1992, but no signs were found in Puebla, Moguer and Hato Ratón. Further radio-tracking detected breeding lynx in Torrecuadros, Moguer, and Hato Ratón. Therefore, the Doñana lynx population also fits the definition of metapopulation as "a set of populations that can recolonize vacant patches of suitable habitat" (Levins, 1969).

According to Fahrig and Merriam (1994) the probability of recolonisation depends on (1) the spatial relationships among landscape elements used by the population, including habitat patches for breeding and elements of inter-patch matrix through which dispersers move, (2) dispersal characteristics of the organism of interest, and (3) temporal changes in landscape structure. The results of this work validate points (1) and (2), but it was not designed to detect temporal changes in landscape structure (point 3). Similar conclusions are reached by Gustafson and Gardner (1996), analysing the effect of habitat heterogeneity between patches through simulation of animal movements.

Distance is a major factor of connectivity between lynx populations in Doñana (Fig. 4), further populations having lower connectivity, as described for other large mammals (Arnold et al., 1993). Although this relationship with distance is not significant when connectivity is considered for each source separately, this could be the result of reduced sample size ($n = 7$) in the split data. Due to this small sample size, we should interpret with caution the relationship between connectivity and patch size found when analysing the sample from the Vera source population.

I expect that this relationship between distance and connectivity generally holds for lynx populations other than the studied one, and connectivity should decrease with increasing distance from a given source. Coto del Rey is connected even with its furthest subpopulation (28.5 km, Marismillas, Table 2) with a low connectivity (0.077). Nevertheless, in other lynx metapopulations, connectivity between subpopulations separated greater distances could be possible. We recorded a dispersing lynx in Doñana that travelled 42.4 km from its tagging location (Palomares et al., pers. commun.).

Dispersing lynx need habitats with cover for travelling (Palomares et al., 2000), and close populations separated by open habitats have low connectivity, as occurs between Vera and Coto del Rey (Fig. 1, Table 2). Connectivity between populations of large kangaroos (*Macropus robustus*) living in fragmented landscapes depends on the existence of patches of native vegetation, which provide cover (Arnold et al., 1993). In the present study, although lynx avoid open habitats when dispersing, they seem able to cross them (as the only option for movement) when areas of suitable habitat are small and fragmented, as occurs in the northern part of the study area (Fig. 1). Lynx use remnants of suitable vegetation as "stepping stones" for travelling in a fragmented landscape, as do metapopulations of large kangaroos (Arnold et al., 1993) and brown kiwis, a flightless bird (*Apteryx australis*, Potter, 1990). Lynx are able to cross the open matrix, although such ability seems limited to short distances, and large distances (up to 16 km) travelled along open habitat by dispersers

have rarely been recorded in Doñana (Palomares et al., pers. commun.). Moderate habitat fragmentation in Doñana, despite negative side effects such as increased mortality (Ferreras et al., 1992), seems to encourage lynx dispersers to travel further and explore larger areas and, in this way, indirectly improves connectivity. Similarly, in an experimental study on the effect of fragmentation and connectivity on space use by root voles (*Microtus oeconomus*), Andreassen et al. (1998) found that the rate of inter-fragment movements increased with habitat fragmentation. Whitcomb et al. (1996) describe how dispersal distance of spruce grouse (*Dendragapus canadensis canadensis*) in a fragmented landscape was greater than in areas of more contiguous habitat. The ability of the Iberian lynx to cross unsuitable habitats can partially explain the lack of fit of patch cohesion and connectivity, even though patch cohesion has proved a better predictor of habitat connectivity than nine other commonly used indices (Schumaker, 1996).

Other factors not considered in these analyses may be important in determining connectivity between local populations. For instance, early movements during the start of dispersal are highly related to the habitat features surrounding the natal area, such as habitat barriers or edges of optimal habitat, and subsequent movements seem conditioned to initial movements (Ferreras, 1994). Initial dispersal movements from Vera are usually directed to the south or west, whereas most lynx start dispersing from Coto del Rey to the north (Ferreras, 1994; Palomares et al., pers. commun.), due to the location of the habitats suitable for dispersal around these sources. Therefore, landscape configuration surrounding sources can indirectly affect connectivity through individual decisions during dispersal , but how this occurs is beyond the scope of the present study.

Although some theoretical and empirical studies suggest that emigration might be inversely related to patch size (Risch, 1981; Bach, 1984; Kareiva, 1985; Turchin, 1986 Bjornstad et al., 1998), I did not found any difference in emigration rate from the two sources, despite their different size (Table 1). However, I detected some differences in their connectivity with other subpopulations (Table 2). These differences can be related to the landscape surrounding each source. The south and west area, where most of the lynx from Vera disperse, is constituted mainly of Mediterranean scrubland and pine and eucalyptus plantations. However, open habitats, mainly croplands, dominate the northeast area (northwards to Coto del Rey population), and opportunities for settlement, likely related to the number of territories, are lower there (six territories) than in the southwestern population (nine territories; Gaona et al., 1998; Ferreras et al., unpublished). Lynx dispersing from Coto del Rey have a smaller region of continuous habitat suitable for dispersing (180 km^2), than those

dispersing from Vera (700 km^2), and they are forced to cross open habitats once they exit this area. As a result, dispersers from Coto del Rey behave as "open crossers" and they cover larger areas during dispersal than those from Vera (Figs. 6 and 7). Because of limitation of habitat suitable for dispersing, they reach southerly and westerly subpopulations relatively easily. A consequence of these differences in connectivity is the asymmetry in the connectivity between northeast and southwest; although several dispersers from Coto del Rey reached southerly subpopulations, during 16 years of study, we only recorded one case of dispersal from Vera to northerly populations.

Asymmetry in connectivity between local populations has been described previously using random walk models in realistic landscapes, both unspecific (Gustafson and Gardner, 1996) and specific for badgers (*Meles meles*, Schippers et al., 1996), and, in both cases it was also related to landscape configuration. The present study is the first where such asymmetry in connectivity is supported by observational data. The landscape differences between the areas surrounding both sources can also explain the different effect of the marsh barrier between Vera and Coto del Rey. Lynx dispersing from Vera seem unable to reach the northeast subpopulations because of the surrounding marsh barrier, and because they suffer a "dilution effect" (Danielson, 1992), engaged in exploring the large area suitable for dispersing beside their source, which prevents them from finding the narrow way to the northeast subpopulations. However, lynx dispersing from Coto del Rey, forced to move through larger areas due to habitat fragmentation, reach the southwest subpopulations usually by circling the marsh barrier to the north.

4.1. Conservation implications

The Doñana lynx metapopulation faces serious threats of extinction in the short term (Gaona et al., 1998), mostly because of its small population size, due to habitat limitation (Ferreras et al., 1997). Moreover, provided the low connectivity from Vera to northeast subpopulations, a real risk exists of permanent isolation between the two groups of local populations in Doñana, if the narrow connection of habitats with cover northwest of the marsh barrier is lost (Fig. 1). Limited connectivity between northeast and southwest Doñana lynx subpopulations could be improved by managing habitats, especially allowing dispersers from the southerly and westerly populations to reach the northerly ones. Physical distance, one of the factors most affecting connectivity, is difficult to manage, although at least size and configuration of usable patches can be modified. Certainly, physical distance can only be altered by adding habitat, which may, in fact, be the most important thing to do for conservation. However, according to the

analyses, the most important factor affecting dispersal success is "effective distance", that is, distance including matrix quality. If more habitat cannot be added, dispersal success could be improved by improving matrix quality. Management measures should include recovery of habitats with cover in the area northwest to the marsh barrier (Fig. 1) for improving cover continuity, or developing a "stepping stones" system in the small area of marsh between Vera and Coto del Rey.

Larger areas covered by dispersers in their movements result in greater distances reached from their origin and, in this way, in improvement of connectivity, as occurs for dispersers from Coto del Rey. Landscape patchiness seems responsible for the large size of dispersing areas in the northern region. However, it is not clear that increased patchiness can be a general recommendation, since open habitats (usually croplands) have some negative side effects such as reduced prey densities, limited shelter, and additional risks of mortality such as roads, shooting or illegal trapping. In this sense, it is generally admitted that dispersal has additional risks of mortality, and this has been shown for the Iberian lynx (Ferreras et al., 1992). Because area covered during dispersal and distance from the source clearly depend on time spent dispersing (Fig. 6), reduced mortality during dispersal would indirectly improve the probability of reaching far populations. Therefore, a clear recommendation to improve effective connectivity would be to reduce additional risks of mortality during dispersal.

However, increasing connectivity, at least as defined in this study, must not be taken as an absolute conservation value. Although connectivity within a metapopulation is a key factor for its persistence (Fahrig and Merriam, 1985), a generalised high connectivity could be a sign of lack of suitable settlement areas. In an extreme situation, dispersing individuals could visit many subpopulations (high general connectivity) and not settle in any of them, either because they are saturated, or because carrying capacity is very low.

According to our field data, lynx connectivity in Doñana is limited to the subpopulations within the studied metapopulation. During 16 years of field work, we have only once recorded a disperser going clearly outside the geographic limits of the metapopulation, reaching the hill steps of Western Sierra Morena Mountains (north of Doñana), but it was not able to reach closer populations some km northwards in these mountains. Distance and extent of open habitats northwards from Doñana seem to be serious barriers for dispersing lynx. Since such barriers have existed for at least several decades, genetic variability is very likely now reduced, as suggested by preliminary genetic results (Delibes et al., pers. commun.). As a possible sign of such genetic impoverishment, lynx from Doñana have lost pelage variation found in other populations, and only a single fur design has been found in Doñana since

1960 (Beltrán and Delibes, 1993). Given the risks of isolation for the persistence of this small population (Gaona et al., 1998), management measures aiming to link it with closer populations (such as habitat restoration for corridors, stepping-stone systems, or even translocations) should be considered. In this sense, there is a project of a "green corridor" to recover the Guadiamar river, after a toxic spill in 1998 which affected its lower section, flowing between the Sierra Morena mountains (to the north) and Doñana. Such a corridor would connect Doñana with these mountains and likely could be used for dispersing lynx, setting up a permanent connection between lynx metapopulations of both areas.

Acknowledgements

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