

Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*

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Most studies on the causes of animal dispersal focus on species of birds or small mammals, but there are few such studies on solitary carnivores. A complete picture of the causes of animal dispersal is not possible without considering cases on a representative set of animals. The Iberian lynx is a medium-size, solitary carnivore that inhabits metapopulations, where dispersal plays a prominent role. Between 1983 and 1998 we studied the proximate and ultimate causes of dispersal in Iberian lynx in the Doñana metapopulation (southwestern Spain), based on radio-tracking of 49 individuals. Saturation of limited breeding areas in this small population leads to high dispersal rates in both sexes. Most lynxes dispersed from their natal area between 12 and 24 months of age. Males younger than 1 year old tended to disperse in a higher proportion than females of the same age. However, high dispersal rates for both sexes by the age of 2 years and the lack of differences in the dispersal distances do not support inbreeding avoidance as an ultimate cause of dispersal. Dispersal mainly started between January and June (24/29 cases), when most social interactions occur, which supports the social subordination hypothesis. Lynxes left the natal range at an earlier age from the local population with higher density, which supports intraspecific competition for resources as a cause for dispersal. However, prey seems not to be the limiting resource because dispersal mostly started during the season of increasing prey density, and individual probability of dispersal increases with prey density in the natal area. Dispersers suffered higher mortality than nondispersing lynxes of the same age, due mostly to anthropogenic causes. About half of the dispersers successfully settled in a territory at distances that differed between areas of origin, but not between sexes. Distances reached, shorter than those reported for other similar-size solitary felids, are limited by anthropogenic barriers that prevent connection with closer metapopulations. *Key words:* dispersal rates, lynxes, *Lynx pardinus*, resource competition, settlement, social subordination, survival. [*Behav Ecol* 15:31–40 (2004)]

Dispersal is a key behavioral process with strong influences at the population level. It has been considered a glue cementing subpopulations and allowing connections between usually isolated populations (Waser et al., 2001). In addition, the study of dispersal is also a glue, as it involves different disciplines such as ecology, population genetics, ethology, evolution, wildlife management, conservation biology, epidemiology, and landscape ecology (Stenseth and Lidicker, 1992b).

Most research on dispersal has emphasized its effects on population processes such as spatial distribution, social organization, population dynamics, and genetic structure (Caughley, 1977; Shields, 1987; Stenseth and Lidicker, 1992a; Wolff, 1994). Also, because dispersal can be vital to a species' persistence (Stacey et al., 1997), some studies have focused on the implications of dispersal for conservation—for instance, for the design of reserves or for preserving rare species (Alonso et al., 1998; Koopman et al., 2000; Van Vuren, 1998). However, dispersal is essentially an individual process, and it deserves to be analyzed by behavioral ecologists.

For the purpose of this article, we follow Howard's (1960) definition of dispersal as the movements by an animal from its point of origin to another area where it might reproduce. This implies that dispersal is a behavioral attribute of certain

individuals that make the decision to move, with important implications for their individual fitness (Van Vuren, 1998). As a general pattern in birds and mammals, dispersing individuals are usually young animals (Greenwood, 1980). In addition, dispersal in mammals is often male biased, in contrast with dispersal in birds, which is female biased (Clarke et al., 1997; Greenwood, 1980; Liberg and Von Schantz, 1985). Many studies have tried to explain the reasons for the predominant dispersal by subadults and the reasons for the sex bias. Three major hypotheses have been proposed to explain the ultimate causes of natal dispersal in a wide range of species: competition for resources, competition for mates, and avoidance of close inbreeding (Greenwood, 1980; Johnson and Gaines, 1990; Pusey and Wolf, 1996). Among several ontogenetic mechanisms acting as proximate factors of the decision to move, aggression from conspecifics (social subordination hypothesis; Christian, 1970), absence of strong enough social ties to the natal group (social cohesion hypothesis; Bekoff, 1977), and attainment of a threshold body mass before dispersal (ontogenetic-switch hypothesis; Holekamp, 1986) have drawn most of the attention from researchers. However, proximate and ultimate causes of dispersal can differ between species, between populations, and even between sexes and individuals (Lidicker and Stenseth, 1992; Moore and Ali, 1984; Waser, 1985; Waser and Jones, 1983). Dispersal behavior may depend on several interacting factors rather than on a single one, and the various hypotheses proposed are not necessarily mutually exclusive (Dobson and Jones, 1985).

Causes of dispersal have been studied on a large number of species of birds (Alonso et al., 1998; Greenwood et al., 1987;

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Kenward et al., 1993; Keppie and Towers, 1992; Negro et al., 1997) and small mammals (Gundersen and Andreassen, 1998; Holekamp, 1986; Lambin, 1994; Waterman, 1992). However, studies on the causes of dispersal of some animal groups, such as small- and medium-size carnivores, are scarce, despite the conservation interest in these animals. Dispersal in carnivores has been studied mainly in social species (e.g., Harris and White, 1992; Harrison, 1992; White and Harris, 1994), but few studies have focused on solitary felids, and most of them were on species of large size (Beier, 1995; Maehr et al., 2002; Poole, 1997; Smith, 1993; Sweanor et al., 2000). To have a complete picture of the mechanisms and function of dispersal, we need to consider data from a representative set of animals. In this sense, ours is one of the first studies on the causes of dispersal of a solitary medium-size felid.

The large majority of dispersal studies, both avian and mammalian, have indicated that dispersers experience higher mortality than residents (e.g., Woolard and Harris, 1990), and hence a fitness cost is usually assumed associated with dispersal (Chepko-Sade and Halpin, 1987). However, this increased mortality may not be attributable solely to the inherent risks of dispersal, but rather, it may also reflect an age-specific difference in survival (Small et al., 1993).

In this study we analyzed the dispersal patterns of the Iberian lynx (*Lynx pardinus*), a critically endangered, medium-size, solitary felid (IUCN, 2002) inhabiting the southwestern Iberian Peninsula (Spain and Portugal; Delibes et al., 2000). We studied dispersal in a small (40–50 individuals) and isolated population inhabiting the Doñana National Park and its surroundings. It is internally structured into several “subpopulations” or “local populations” due to habitat fragmentation, constituting a true metapopulation (Gaona et al., 1998). Most Iberian lynx populations are also small and isolated metapopulations (Rodríguez and Delibes, 1992), in which connectivity between local populations depends on dispersing individuals (Ferrereras, 2001).

Some aspects of Iberian lynx dispersal have been previously analyzed (Ferrereras, 2001; Palomares, 2001; Palomares et al., 2000). Dispersing lynxes may use habitats of lower quality than those used by resident lynxes, although dispersers avoid open habitats such as marshes and croplands (Palomares et al., 2000). Dispersers can use patches that are narrower and have lower prey density than those used by residents, and hence corridors connecting reserves do not need to be prime habitats (Palomares, 2001). Connectivity between local populations resulting from movements by dispersing lynxes is mainly explained by the distance and habitats separating local populations (Ferrereras, 2001). In the present article we describe the decision patterns of the radio-tracked Iberian lynx, facing questions such as when (i.e., age at dispersal), how long (the time dispersing), and how far to disperse (the distance reached) and study the relationships between these variables and their possible causal factors. Specifically, we tested the following predictions: (1) dispersers are subadult individuals (resource competition hypothesis), (2) a strong sex bias in probability of dispersal and in natal dispersal distance should exist (inbreeding avoidance hypothesis), (3) dispersers should be individuals with better body condition than nondispersing individuals (ontogenetic-switch hypothesis), (4) lynxes born in densely occupied areas should disperse more (resource [trophic or not] competition hypothesis), (5) dispersal should occur mainly during the season of lower prey density, (6) lynxes born in areas with lower prey density should disperse earlier and reach longer distances (trophic resource competition hypothesis), and (7) dispersal should mostly occur in the season when most social interactions occur (social subordination hypothesis). The social cohesion hypothesis was not evaluated because the Iberian lynx does

not form cohesive groups (Ferrereras et al., 1997). The hypothesis of a fitness cost associated to dispersal, resulting from an inherent risk of increased mortality, was also evaluated.

METHODS

Study area

Lynx in Doñana range throughout an area of about 1500 km² (Palomares et al., 1991), although most live within the Doñana National Park (DNP, 550 km²), the area that has the highest level of protection within the global Iberian lynx range. This flat area (0–50 m above sea level) is located in the southwest of the Iberian Peninsula (37° 00' N, 6° 30' W) and presents a Mediterranean subhumid climate (566 mm mean annual rainfall) with Atlantic influences and a marked seasonality (Fernández-Delgado, 1997). Three main ecological units can be distinguished within the DNP: Mediterranean shrubland, marshland, and sand dunes. Iberian lynxes mainly occupy Mediterranean shrubland and prefer the ecotone with marshland, where the highest densities of rabbits *Oryctolagus cuniculus* L., the lynx's staple prey, are found (Palomares et al., 2001).

Both natural and human-created barriers currently confine the population. It is naturally limited to the east by the marshes of the Guadalquivir River, to the south and west by the Atlantic Ocean, and to the north by a 50-km wide area of croplands. Iberian lynxes in Doñana are distributed in discontinuous patches of suitable habitat, made by Mediterranean shrublands and pine forests with patchy undergrowth (Palomares et al., 1991). Patches inside the park are separated by a “friendly” matrix of natural and safe habitats with no human settlements, but they are unsuitable for lynx establishment and reproduction (e.g., sand dunes, marshes, pine and eucalyptus plantations; Palomares et al., 2000). The matrix area surrounding the DNP suffers high levels of human pressure, particularly due to agriculture and tourism developments, including highly traveled roads, urban areas, and hunting activities (Ferrereras et al., 1992). This habitat patchiness affects the movements of dispersing lynx and greatly conditions the connectivity among permanent breeding areas (Ferrereras, 2001).

Two main areas for lynx reproduction are found in Doñana: Reserva Biológica (RB) and Coto del Rey (CR). The first one (RB) is a core area of about 50 km² within the DNP, with moderate rabbit densities (Beltrán, 1991). The second area (CR) is an 8-km² area to the northern edge of DNP with optimal conditions of habitat structure and rabbit densities for lynx. This small area supports the highest density of lynx within the whole population (0.72–0.88 adults/km²; Palomares et al., 2001), several times higher than the density in RB subpopulation (0.1–0.2 adults/km²; Ferreras, 1994; Rau et al., 1985) and probably one of the highest densities in the whole Iberian lynx geographic range (Rodríguez and Delibes, 1992).

Data collection

We studied the dispersal process through tracking radio-tagged lynxes. Lynx were captured in RB between 1983 and 1992 and in CR between 1991 and 1997 using standard procedures (Delibes and Beltrán, 1986). We determined their age according to body size, tooth wear, and date of capture (in relation to the seasonal peak of births), supported by information from known-age lynxes (Beltrán and Delibes, 1993; Zapata et al., 1997).

We captured and radio-tagged a total of 65 Iberian lynx from 4 February 1983 to 24 November 1997. On first capture 14 females and 14 males were juveniles (<12 months old),

7 females and 8 males were subadults (12–24 months old), and 8 females and 14 males were adults (>24 months old). Thirty-five lynxes were first captured and radio-collared in RB, 28 lynxes in CR, and 2 lynxes in an area close to RB, called Acebuche. Additionally, between 1993 and 1997, we tagged kittens with electronic passive identification tags (model ID100, TrovanTM, Germany) at natal dens, which together with previous accounts of mother's movements allowed us to age them later with an error of approximately ± 1 week and to know their natal range when captured for radio-collaring. For the purposes of this study we used data from 49 radio-tracked lynxes, including predispersing and dispersing individuals. We obtained animal locations between 1983 and 1998 by triangulation from a vehicle, and aircraft searching was occasionally used when radio contact with dispersing animals was lost. The sampling scheme was intended to gather five independent location fixes per week, but ample movement during dispersal sometimes resulted in lower frequencies of fixes.

Age at start of dispersal

We considered that lynxes started dispersal when they left their natal area and they did not return in at least 1 month. We first radio-tagged most of the lynx included in this study when accompanying their mother, before dispersal, which allowed us to establish the natal area and the time of dispersal onset. If the natal area was not known, lynx were considered to be dispersing once they did not show site fidelity during their movements. We determined lack of site fidelity using a computational method that compares short-term home range size and location with computer simulations, coupled with inspection of graphical representations of distances between sequential home ranges and distance from the point of capture (see Palomares et al., 2000).

We were able to establish the true age at start of dispersal when lynxes were being radio-tracked previously to the moment of dispersal onset. For lynx already dispersing since their radio-tracking start, true age at starting dispersal was not known, and instead we used as a surrogate the age of first capture for radio-collaring, which we called "age dispersing," which overestimates the true age at start of dispersal.

Since the age of start of dispersal can be biased by uneven representation in the radio-tracked sample, we calculated the probability that an individual would disperse for a given age period using the Trent-Rongstad maximum likelihood estimator (White and Garrott, 1990). We used the program MICROMORT (Heisey and Fuller, 1985), substituting the event death for the event dispersal (Arthur et al., 1993). The probability of dispersal by a given date was $1 - \text{residency rate}$, or dispersal rate. Age-specific rates of dispersal were calculated as the probability of dispersing during a given period of age, using the data of young lynx radio-tracked before dispersal. Dispersal rates were compared between sexes or areas of origin using the test proposed by Heisey and Fuller (1985), which employs a Z statistic based on rates, their variances, and the covariance, and that fits into a Z -normal distribution. When multiple comparisons were performed between rates, we used standard Bonferroni corrections for calculating threshold p values.

Season of dispersal and social factors

We considered four seasons characterized by different breeding and social events. The first quarter of the year (January–March) mostly coincides with mating and pregnancy of females, the second quarter (April–June) coincides with births and lactation, the third quarter (July–September)

coincides with trophic dependence of cubs from their mother, and the last quarter (October–December) coincides with independence of cubs (Aldama, 1993; Ferreras, 1994; Ferreras et al., unpublished data). We compared the observed number of lynxes dispersing during each of the seasons with the expected number of dispersers according to the total radio-days of lynxes of dispersal-prone age gathered during each season.

Dispersal and prey abundance

We performed two analyses to evaluate the potential effect of prey (rabbit) abundance on lynx dispersal. First, we used correlation analysis between average monthly dispersal rates (independently by groups of sex, subpopulation, and sex \times subpopulation) and average monthly prey density. Rabbit density in the area has marked seasonal variations, having its annual minimum between September and November (Beltrán, 1991; Palomares et al., 2001; Villafuerte et al., 1997) and steadily increasing until it peaks in May–July. For the first analysis, we calculated an average prey density index for each calendar month (January–December) in the two subpopulations. We obtained data for RB subpopulation from Beltrán (1991), Villafuerte et al. (1997), and S. Moreno (personal communication), and data for CR from Palomares et al. (2001). In a second analysis, we used logistic regression to model individual probability of dispersal during a specific year as a function of minimum annual density of rabbits (in September–November) in the subpopulation of origin. Other independent variables used in the logistic regression were the gender, the sampling effort (i.e., the time in days each lynx was radio-tracked for a given year as potential disperser), and the subpopulation of origin. We only included in the model individuals radio-tracked for more than 60 days to reduce noise from early death or radio-collar failure. We used the LOGISTIC procedure of SAS software (SAS Institute, 1990). We set p for entrance of the variables in the model at .1. We evaluated goodness of fit of the model by $-2\text{Log likelihood estimator or deviance}$ (SAS Institute, 1990).

Dispersal and body condition

On each capture, we weighed lynxes to the nearest 50 g, and we measured head–body length to the nearest millimeter. We assessed body condition as the residual value obtained in a reduced major axis regression (Sokal and Rohlf, 1995) of log mass on log head–body length. Reduced major axis regression is recommended instead of ordinary least squares regression when residuals are used as an index of body condition because both x and y variables are subject to error (Green, 2001). Regressions were fitted separately for females and males, producing high correlation indexes (>.99) in both cases.

We tested the index of body condition (IBC) as a predictor of dispersal at a given age. We only considered data from lynx weighed and measured between 7 and 12 months old, reducing possible effects due to age. We used ANOVA to compare the IBP of dispersers versus nondispersers by the age of 12 months, and we performed an independent similar analysis for dispersal by the age of 18 months.

Survival during dispersal

We compared survival rates between dispersing and philopatric lynxes of similar age using the same likelihood methods as for dispersal. We controlled in this way for the effect of inherent age-specific differences in survival (Small et al., 1993). To make rates comparable between dispersers and

philopatric lynxes, we computed equivalent annual survival rates (i.e., corresponding to a year), even if dispersal had a different duration. We used standard Bonferroni corrections for threshold p values when we performed multiple comparisons between rates. We also compared the frequency of causes of mortality between dispersing and philopatric lynxes using G tests.

Settlement, duration of dispersal and distance reached

We considered dispersal to have finished when the disperser settled—that is, showed site fidelity—using the same analytical approach described for the start of dispersal (see Palomares et al., 2000). We defined total duration of dispersal as the time between start of dispersal and settlement. We also calculated minimum duration of dispersal, including not only cases of known date of start and end of dispersal, but also those lynxes that were dispersing when first captured and those that died or whose signals were lost before having settled in a stable home range.

We calculated the distance to the end of dispersal based on one of the following combinations: natal home-range arithmetic center (NAC) or capture site (CS) for animals dispersing when first captured, to establishment home-range center (EAC), last location while dispersing (LLD), or mortality site (MS). When information on settlement was known, we determined distance of settlement as straight-line distance between NAC or CS to EAC. We analyzed the effects of subpopulation, sex, and their interaction on duration of dispersal and dispersal distances. We estimated the rate of dispersal success as the proportion of dispersers which established a home range after dispersing, and we evaluated whether this rate differed among area of origin, sex, age or body condition.

Statistical analysis

We used generalized linear models with type III sum of squares to identify the factors that explain the variation of age of dispersal, distance to the end of dispersal, and distance of settlement. We used the Akaike Information Criterion (AIC), modified for small sample size when necessary (Burnham and Anderson, 1998), for selecting the model best explaining the dependent variables with the lowest number of parameters.

RESULTS

Age at start of dispersal: effects of sex and subpopulation of origin

All the dispersers were younger than 28 months old when they left their natal range (natal dispersal), and most of them (8/11 females and 11/16 males) were between 13 and 24 months old. Only two females and four males dispersed during their first year of life (Table 1). Moreover, two adult lynxes (one female and one male) older than 3 years dispersed after they had been radio-tracked as resident adults (postbreeding dispersal). Some other lynxes, one female (18 months old) and six males (between 8 and 26 months old), were dispersing when first captured (Table 1). Ten females and three males had not dispersed at ages 8–24 months when their monitoring finished, either because of radio failure or death of the animal.

Age at the start of dispersal (overall mean \pm SE: 17.8 ± 1.2 months) was best explained by a model including only the area of origin, although the effect was only marginally significant ($F = 4.090$, $df = 1$, $p = .054$). The model best explaining age dispersing included only the area of origin ($F = 5.518$, $df = 1$, $p = .025$) but not sex nor the interaction

of these terms (all $P \geq .875$). Lynxes from CR dispersed at younger ages (15.7 ± 1.4 months) than those from RB (20.4 ± 1.4 months).

Natal dispersal rates were calculated using data from 41 lynxes (21 females and 20 males), all of them less than 2 years old when first radio-tagged in their natal area. Eighteen lynxes (10 females and 8 males) were first captured in RB, 22 lynxes (11 females and 11 males) in CR, and 1 young lynx was marked in an area (called Acebuche) close to the RB subpopulation; the latter was included in the analyses with those from RB. The curves of age-specific dispersal rates differ in shape for the two areas (Figure 1). Cumulative dispersal rates for both sexes from RB increase slowly between 12 and 18 months of age and sharply increase between 18 and 24 months (Figure 1b). However, most lynx from CR had dispersed by the age of 18 months, and dispersal rates increased slowly between 18 and 24 months (Figure 1a). Rates were higher for males than for females for any age within both areas, although comparisons between sexes were not significant for any age (all $Z \leq 2.758$, $p \geq .009$; the Bonferroni corrections advise a threshold p value of .0062). Most lynxes had dispersed by the age of 2 years (probability $\geq .779$ for either sex \times area combination; Figure 1).

Season of dispersal

Dispersal events were not evenly distributed along the year, even after considering the seasonal differences in radio-tracking effort ($G = 11.421$, $df = 3$, $p = .012$; Figure 2). Dispersal mostly started in the first half of the year (January–June, 22/27 cases). Seasonality in dispersal was more marked in RB, where only 1 out of 14 dispersers left its natal area between July and December. Seasonality was most marked for females from RB, all six dispersers started the process in the first or the second quarters of the year ($G = 11.23$, $df = 3$, $p = .011$; Figure 2).

To test a possible direct relationship between dispersal and breeding of the resident parents, we focused on those young lynxes for which we had information concerning dispersal and reproduction (either positive or negative) of the lynx's mother in the first breeding season after the cub's birth. Yearlings still living in their natal territory dispersed during years when their mother bred in a proportion (6 out of 11) similar to years when their mother did not breed (4 out of 10; Fisher's Exact test: $p = 1.000$). However, test power was low (0.095 for $\alpha = 0.05$) due to reduced sample size.

Dispersal and prey abundance

Monthly variations of prey density were not correlated with monthly dispersal rates, either when considering all individuals or when grouping them by gender, subpopulation, or gender \times subpopulation (Pearson correlation, all $p > .121$). The bulk of lynx dispersal (between January and June; see Figure 2) coincided with increasing rabbit numbers.

We also tested whether the probability of dispersal in a given year was associated with prey density in the subpopulation of origin. The logistic model including minimum annual density of rabbits and time radio-tracked was significant ($\chi^2_{(-2\log L)} = 24.61$, $df = 1$, $p = .0001$). Associations of predicted probabilities were 90% concordant and 10% discordant. Time radio-tracked and minimum annual density of rabbits entered as significant terms in the model (Wald $\chi^2 = 9.94$, $df = 1$, $p = .0016$, and Wald $\chi^2 = 3.42$, $df = 1$, $p = .065$, respectively), but sex and subpopulation of origin did not (all $p \geq 0.143$). Probability of dispersal increased with rabbit density (Figure 3). It is notable that none of the six subadult lynx radio-tracked in 1990, the year with the lowest rabbit

Table 1

Known age at start of dispersal for those lynx radio-tracked in their natal range before dispersing and age of those lynx already dispersing when first captured

Area	Sex	Mean \pm SE (months)	<i>n</i>	Range (months)
Age at start of dispersal				
CR	Females	15.4 \pm 4.5	5	9–24
	Males	15.5 \pm 4.3	8	10–22
RB	Females	20.8 \pm 6.2	6	8–28
	Males	19.3 \pm 6.5	8	9–28
Age when first captured while dispersing				
CR	Males	16.7 \pm 7.4	3	8–26
RB	Females	18.0	1	18–18
	Males	24.5 \pm 0.5	2	24–25

density due to an outbreak of a new rabbit disease (Villafuerte et al., 1994), dispersed during that year. Therefore, Iberian lynx mostly disperse in months with increasing prey density and in years with higher prey density, rather than dispersing when prey density is low or decreasing.

Dispersal and body condition

The index of body condition (IBC) did not differ either between subpopulations ($F_{1,23} = 0.150$, $p = .0702$) nor between sexes ($F_{1,23} = 0.658$, $p = .508$). Dispersing and nondispersing lynxes by the age of 12 months did not differ in their IBC ($F_{1,18} = 0.132$, $p = .721$). Similarly, IBC did not differ between dispersing and nondispersing lynxes by the age of 18 months ($F_{1,14} = 0.054$, $p = .820$).

Survival during dispersal

Overall, dispersers had lower survival than lynxes of the same age that remained in their natal area (philopatric lynxes), with the differences between annual survival rates (ASR) being significant for the second ($Z = 2.601$, $p = .005$) and third years of life ($Z = 2.691$, $p = .004$), but not for the first year ($Z = 1.551$, $p = .060$; see Table 2), when lowest ASRs occurred (0.164 and 0.592 for dispersing and philopatric lynxes, respectively). Only one nondispersing lynx died during the second year of life (ASR = 0.915), and none died during the third year (ASR = 1), whereas six (ASR = 0.480) and three dispersers (ASR = 0.442) of similar ages died. This pattern was maintained when considering groups of sex or area of origin separately, except for females from CR 1 year or younger, but differences were not significant for any group (all $p \geq .005$, threshold p values of $<.00625$ with Bonferroni corrections; Table 2).

Mortality during dispersal was clearly related to human activities. Most deaths of dispersers were caused by illegal hunting (8/11), either direct shooting (three cases) or illegal traps (five cases), such as leg-hold traps or snares. This significantly differs from the causes of death of nondispersing lynxes: none of the four recorded deaths was attributable to illegal hunting ($G = 5.244$, $df = 1$, $p = .023$). Road accidents, another cause of death also related to human activities, were responsible for one mortality of each of dispersing and nondispersing lynxes. Moreover, we were not able to determine the cause of death for three nondispersing lynxes, but natural causes (disease or starvation) were likely involved.

Duration of dispersal, distance reached, and settlement

Both total duration of dispersal (mean \pm SE: 184 \pm 51 days) and minimum duration of dispersal (149 \pm 26 days) were

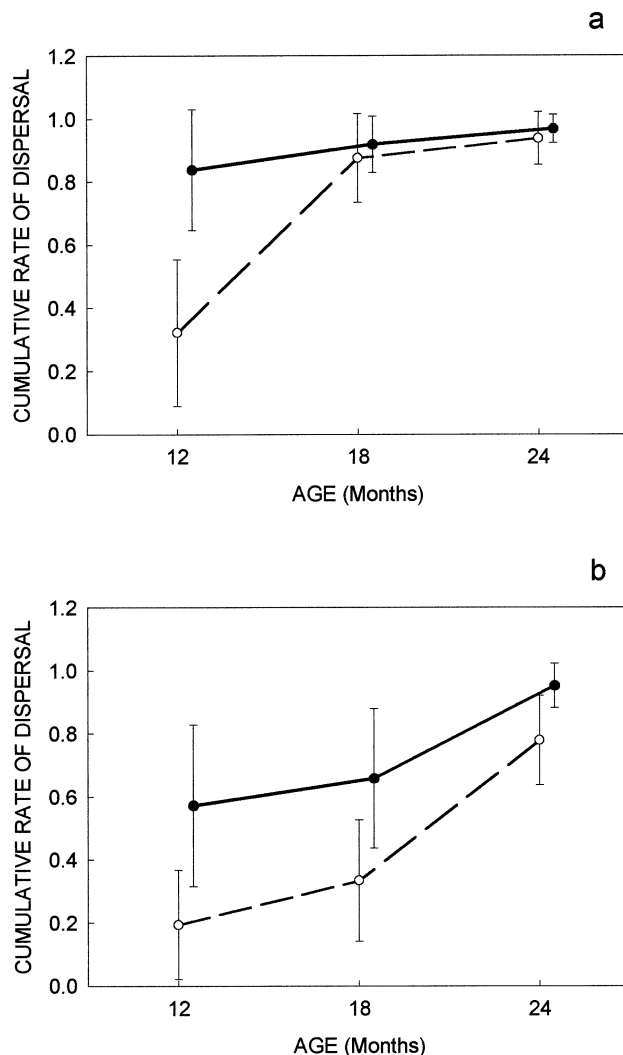


Figure 1

Age-specific cumulative rates of dispersal for lynx according to area of origin and sex (dashed lines for females, solid lines for males). (a) Coto del Rey, (b) Reserva Biológica. The value for each age represents the estimated probability of a lynx of a given age to have dispersed by such age, and error bars indicate standard deviations of the estimates.

unaffected by subpopulation, gender, or their interaction (all $p \geq .128$ and all $p \geq .490$, respectively).

Distance to the end of dispersal was best explained by a model including only subpopulation of origin ($F_{1,25} = 12.412$, $p = .002$) but was not affected by gender, the interaction gender \times subpopulation, nor time dispersing (all $p \geq 0.196$). Lynxes dispersing from CR were, on average, farther (21.5 \pm 2.5 km, $n = 11$) from the point of origin at the end of dispersal than those from RB (10.0 \pm 2.1 km, $n = 16$; Table 3).

At least 48% (13/27) of the dispersers successfully ended the process and settled in a territory after dispersal. Additionally, the fate of seven dispersers was unknown because their contact was lost or they were still radio-tracked when this study finished. Dispersers from the two subpopulations settled in similar proportions (45.5% from CR, 50% from RB; $G = 0.050$, $df = 1$, $p = .816$). Although dispersing females settled in a higher proportion (66.7%) than males (38.4%), these differences were not statistically significant ($G = 0.909$, $df = 1$, $p = .816$). Body condition and age when

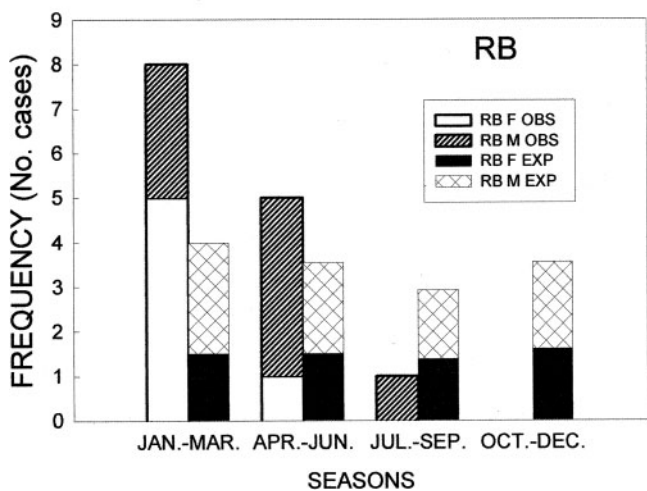
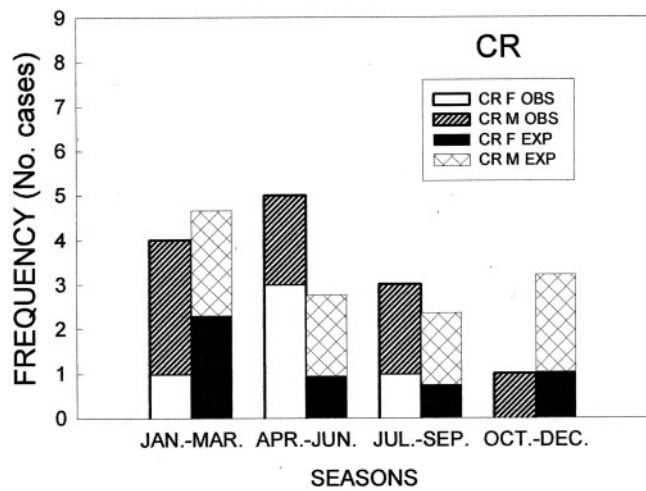
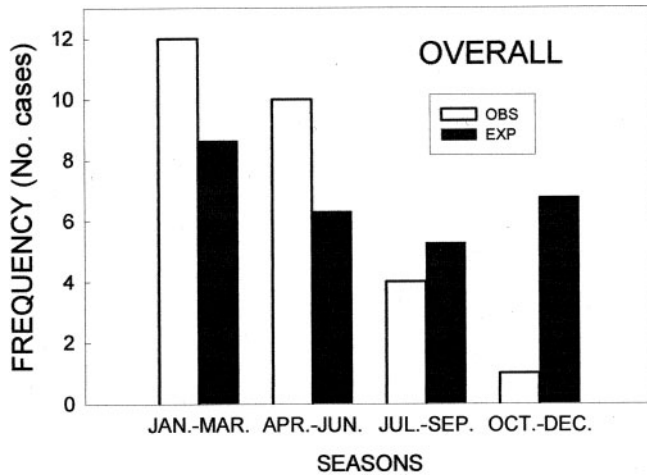


Figure 2
Seasonal pattern of observed (“obs”) and expected (“exp”) dispersal events, according to radio-tracking effort (proportion of radio-days during each season), in the overall sample (top), and in each area of origin (CR, middle graph; RB, bottom graph). Sexes are shown separately for each area. Observed frequency significantly differs from expected frequency for the overall dataset ($G = 11.019$, $df = 3$, $p = .012$) and for females from RB ($G = 11.230$, $df = 3$, $p = .011$), but not for the remaining data sets (all $p > .1$).

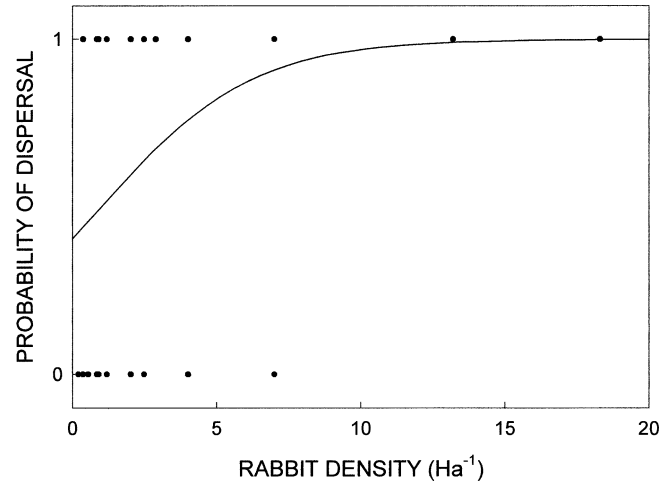


Figure 3
Effect of annual minimum rabbit density (rabbits/ha) on lynx probability of dispersal, once the effect of time radio-tracked was controlled. Line is fitted through logistic regression [$\text{Logit} = 1.8049 + 0.3826 \times (\text{rabbit density}) + 0.0163 \times (\text{time radio-tracked})$] adjusted for average time radio-tracked per year (134 days).

first detected dispersing did not differ significantly between successful and unsuccessful dispersers (all $p \geq .474$).

The best model explaining the variation of distance of settlement included only subpopulation of origin ($F_{1,11} = 6.565$, $p = .026$) but not gender nor their interaction ($p \geq .169$). Lynxes from CR established after dispersal at farther distances (25.8 ± 4.3 km, $n = 5$) than those from RB (11.9 ± 3.4 km, $n = 8$; Table 3). Only two females from RB subpopulation settled after dispersal close (< 5 km) to their natal ranges.

DISCUSSION

We have examined dispersal from a behavioral ecological approach, which allowed us to investigate the factors influencing several decisions involved in the dispersal process and provided information for the development of conservation tools (Van Vuren, 1998). Dispersal in the Iberian lynx is mostly restricted to individuals less than 2 years old, which corresponds with the pre-reproductive age for the species (Aldama, 1993; Ferreras et al., 1997). Such dispersal fits, therefore, within the definition of “natal dispersal” (Greenwood and Harvey, 1982) and follows the general pattern of subadult dispersal in most birds and mammals (Greenwood, 1980). Our results support the hypothesis of intraspecific competition for resources, as subadults are less competitive than adults in acquiring resources (Ferreras et al., 1997; Greenwood, 1980; Johnson and Gaines, 1990). Only two resident adults (one female and one male) dispersed after having settled in a stable home range and thus could be qualified as “postbreeding dispersers” (*sensu* Greenwood and Harvey, 1982).

Factors promoting dispersal in the Iberian lynx

Interpopulation variations in dispersal age and rates also support competition for resources as a cause of dispersal: lynx from the subpopulation with higher lynx density (CR, where competition for resources is expected to be higher) dispersed at younger ages than lynx from RB. The high dispersal rates for Iberian lynx in Doñana may be related to the saturation of

Table 2

Annual survival rates, specific to groups of sex and area of origin, and overall rates for philopatric (nondispersing) and dispersing lynx according to age

Area	Sex	Age								
		4–12 Months			12–24 Months			24–36 Months		
		Philopatric	Dispersing	<i>p</i>	Philopatric	Dispersing	<i>p</i>	Philopatric	Dispersing	<i>p</i>
CR	Female	0.418	1.000	.055	1.000	0.577	.092	1.000	1.000	1.000
CR	Males	0.493	0.177	.251	0.597	0.433	.330	ND	0.164	ND
RB	Female	0.623	0.001	.018	1.000	1.000	1.000	1.000	1.000	1.000
RB	Male	1.000	1.000	1.000	1.000	0.339	.005	1.000	0.339	.036
Overall		0.592	0.164	.060	0.915	0.480	.005	1.000	0.442	.004

Differences were evaluated with the Z test proposed by Heisey and Fuller (1987), and resulting probabilities (*p*) are shown (a threshold *p* value of <.00625 is considered for comparisons within age and sex classes according to Bonferroni corrections). ND, no data available for estimating this value.

the breeding areas (Ferrerás et al., 1997; Gaona et al., 1998), where competition for breeding resources, such as mates or territories, are high. All the young lynx tagged for this study were born within the highly protected Doñana National Park, where survival rates of adults are high (Ferrerás et al., 1992; see Table 2). In such a situation, territory vacancies rarely happen as a consequence of death of the territory owner, but, instead, access to territories often results from aggressive contests among adult lynxes (Ferrerás et al., 1997). Only adult, full-grown lynx are able to challenge territory owners, and young lynx are forced to leave their natal area looking for a territory, resulting in high dispersal rates.

Food does not seem to be the limiting resource causing competition. Seasonal patterns of dispersal do not respond to trophic constraints because the bulk of seasonal lynx dispersal (first half of the year; see Figure 2) coincides with increasing prey availability. Rather, dispersal during the season of increasing prey can have evolved as a strategy to increase the chances of surviving dispersal and finding an area for settlement in the most favorable period. The increase in the probability that individuals will disperse with increasing rabbit density in the natal area (see Figure 3) could be related to this adaptation to disperse when food is abundant. A similar pattern, although at a different temporal scale, has been described for the Canadian lynx (*Lynx canadensis*), adapted to the interannual cyclic fluctuations of its main prey, the snowshoe hare (*Lepus americanus*; Breitenmoser et al., 1993b).

Alternatively, the higher dispersal probability in years of higher rabbit density (Figure 3) could be interpreted in accordance with the ontogenetic switch hypothesis (Holekamp, 1986). In such case, a better body condition should be expected from lynx that grew up in years when rabbit densities were high. Yet the lack of differences in the index of body condition between dispersing and nondispersing lynxes does not support this hypothesis.

Social factors could determine the start of dispersal (Christian, 1970) and explain the interpopulation variations in dispersal age and rates. Aggressiveness of resident adult males toward subadults in other solitary felids, such as the Florida panther (*Puma concolor coryi*) and the tiger (*Panthera tigris*) has been cited as a proximate cause of male dispersal (Maehr et al., 2002; Smith, 1993). Although land tenure contests among adult lynxes of the same sex in the study population sometimes result in aggressive encounters (Ferrerás et al., 1997), we never recorded recent evidence of direct aggression of resident lynx toward dispersers. In a literature review, Wolff (1993) found that only in 4 of 49 mammalian species did juvenile dispersal result from adult aggression.

Dispersal in solitary felids is usually male biased, and dispersal distance is commonly larger for males than for females (Beier, 1995; Breitenmoser et al., 1993b; Maehr et al., 2002; Ross and Jalkotzy, 1992; Smith, 1993; Sweanor et al., 2000). This pattern, common among most mammals, is less clear for the Iberian lynx in Doñana. Although males have a higher probability of dispersing during their first year than females, most lynx of either sex have dispersed by 2 years of age (see Figure 1). In our study we did not find sex differences in the distance of settlement from the natal territory nor in the distance traveled until dispersal ended. These results do not support inbreeding avoidance as an ultimate cause of dispersal in the Iberian lynx. It has been hypothesized that sex-biased dispersal is linked to the mating system (Greenwood, 1980). Polygyny, the predominant mating system among mammals, favors the evolution of male-biased dispersal because of intrasexual competition among males for mates (Dobson, 1982; Greenwood, 1980; Moore and Ali, 1984). The mating system in our study population tends to monogamy, possibly as a result of the high saturation of territories. Because of the high competition for the territories, males are forced to have small but defendable territories, which results in a mating system close to monogamy (Ferrerás et al., 1997). Also as result of the high competition, both males and females disperse, which agrees with the hypothesis of competition for mates or breeding sites as a cause of dispersal (Dobson, 1982).

The first half of the year, when most dispersal events occurred, coincided with the breeding season in the lynx: mating peaks in January–February, births mainly occur in March–April, and lactation extends up to June (Aldama, 1993; Ferrerás, 1994; Ferrerás et al., unpublished data). Time of dispersal in other solitary felids such as tigers and Florida panthers is related to reproduction of the mother, who does not allow previous offspring onto her territory (Maehr et al., 2002; Smith, 1993). However, according to our case-by-case analysis, the decision of whether to disperse by young Iberian lynxes in a given year seems unaffected by whether their mother was rearing a new litter, although this result is not conclusive because of the limited sample size.

The risks of dispersal in the Iberian lynx

The risks associated with dispersal are widely recognized for mammals because dispersers must move through unfamiliar terrain, and when doing so they become vulnerable to predation, aggression, stress, and malnutrition (Gaines and McClenaghan, 1980; Harris and Trehwella, 1988; Waser et al.,

Table 3
Distances (km) to the end of dispersal of lynx from the two subpopulations studied in Doñana (Coto del Rey and Reserva Biológica), according to different estimators

	Female dispersal distance (km)			Male dispersal distance (km)		
	Mean \pm SE	<i>n</i>	Range	Mean \pm SE	<i>n</i>	Range
Coto del Rey						
Distance of settlement	29.5 \pm 8.5	2	21–38	23.3 \pm 6.8	3	16–37
NAC to LLD	—	—	—	13.5 \pm 8.7	2	4–23
NAC to MS	25.0	1	25–25	18.3 \pm 5.9	3	12–23
Any estimator	28 \pm 5.1	3	21–38	19 \pm 3.4	8	4–37
Reserva Biológica						
Distance of settlement	7.0 \pm 2.1	4	3–12	16.8 \pm 4.9	4	6–25
NAC to LLD	10.5 \pm 5.3	2	6–15	11.5 \pm 5.3	2	8–15
NAC to MS	—	—	—	6.3 \pm 2.2	3	4–9
CS to LLD	—	—	—	2.0	1	2–2
Any estimator	8.2 \pm 1.9	6	3–15	11.1 \pm 3.3	10	2–25

Distance of settlement: natal home range arithmetic center (NAC) or capture site (CS) to establishment home range arithmetic center (EAC); MS, mortality site; LLD: last location while dispersing.

1994). Moreover, in the case of the Iberian lynx in our study area, survival of dispersers is reduced because of human-related factors. Due to the saturation of the safe breeding areas, most dispersers leave the protected national park and find increased risks of mortality in the surrounding area. As a consequence, dispersers face significantly lower survival than philopatric lynxes, although once established they increase their chances of reproducing. We recorded at least three cases of females established after dispersal that actually reproduced; reproduction of males is more difficult to ascertain. Therefore, although risks of dying during dispersal are high, benefits obtained after gaining access to a vacant territory probably pay for these risks (Bélichon et al., 1996; Van Vuren and Armitage, 1994).

Only half of the dispersers settled in a postdispersal home range, due to the high mortality during dispersal and habitat limitations for the lynx in Doñana. Even though dispersers explore large extensions and reach distances from their natal range of up to 42 km (Ferrerias, 2001), areas for settling are very limited (Palomares et al., 2000). A similar process, referred to as “frustrated dispersal,” has also been described for another endangered felid, the Florida panther (Maehr et al., 2002).

Distances to the end of dispersal in the studied populations are shorter than those reported for other solitary felids of close size, such as the Canadian lynx (Poole, 1997; Slough and Mowat, 1996), the bobcat (*Lynx rufus*; Knick, 1990; Knick and Bailey, 1986), and the Eurasian lynx (*Lynx lynx*; Breitenmoser et al., 1993a; Schmidt, 1998). This is probably related to limitations of suitable habitat for lynx dispersal in the area (Ferrerias et al., 2001; Palomares et al., 2000). Both natural and human-related barriers hinder dispersal movements: there are marshes to the east, the Atlantic Ocean to the south and west, and a wide area of croplands to the north (Ferrerias et al., 2001). Larger distances can be expected, therefore, in other Iberian lynx populations with wider habitat availability, such as in the Sierra Morena Mountains (Rodríguez and Delibes, 1992). Intrapopulation differences in dispersal distances in Doñana are probably related to habitat configuration surrounding each area (CR and RB), rather than to intrinsic demographic differences. Farther distances reached after dispersal by lynx from CR seem related to effects of landscape on the dispersers’ movements: patchy habitat structure surrounding CR promotes wider movements during dispersal than those of lynxes dispersing from RB (Ferrerias, 2001).

Conclusions

Dispersal in the Iberian lynx is a generalized process that affects most individuals less than 2 years old. However, this could be partially due to the high saturation of breeding territories in the studied population. Our results do not support inbreeding avoidance as a strong ultimate cause of dispersal because both males and females disperse in high proportion, and no significant differences were found in the distances of settlement. This may be related to the mating system in the studied population, which is close to monogamy. Neither is competition for trophic resources supported by our data as an important ultimate cause of dispersal, as temporal and spatial scarcity of the main prey does not lead to more dispersal. Competition for other resources, such as mates or territories, is possibly the ultimate cause of dispersal in the Iberian lynx, as supported by the earlier age of dispersal in the more dense area. The attainment of a physical threshold does not appear to be a requirement triggering dispersal onset, and the ontogenetic switch hypothesis is not supported as a proximate cause of dispersal. Social subordination of dispersers seems to be a proximate cause of dispersal, as supported by the season when most dispersal events occur, coinciding with most social interactions, although direct aggression from adults to young lynxes were never detected. Dispersal in the studied population results in increased mortality, as proved by reduced survival of dispersers when compared to non-dispersers of the same age. However, high human disturbance in the areas used by dispersers can be the reason for this increased mortality and could hide natural risks associated with dispersal. Short dispersal distances, when compared to close species, are probably related to landscape constraints.

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