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Reproduction and pre-dispersal survival of Iberian lynx in a subpopulation of the Doñana National Park

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Abstract

Little is known about the reproduction of the Iberian lynx (*Lynx pardinus*) even though it is the most endangered felid in the world. We studied during 9 years several reproductive parameters of the Iberian lynx in one of the subpopulations situated in Doñana National Park (south-western Spain), by means of radio-tracking, direct observations and photo-trapping. The potential breeding subpopulation was usually composed of 3 adult females, which bred 83% of the total possible 29 female-reproductive year. The minimum total number of cubs born during the study was 64 (7.7±0.69 per year). There was no correlation between the number of cubs born or number of breeding females and population size of European rabbit (*Oryctolagus cuniculus*, the main prey of the lynx). All known births ($n = 16$) occurred in March except one in April and another in June. Mean litter size was 3.0 ± 0.16 ($n = 16$, range = 2–4). Sex-ratio ($n = 59$ cubs) was 1.03:1.00 (females:males). Nevertheless, the commonest picture was a female with 2 cubs older than 3 months. Altogether, at age of 3 months, 75% of cubs survived. Number of lynx alive at 10 months old and before dispersing was 69% and 57%, respectively. Sex did not affect survival for any age. Normally, it was not possible to know the causes of the death of cubs younger than 3 months. Survival at this age was not related with mother, mother age, or rabbit abundance. All females that bred were older than 3 years. The age of last reproduction was 9 years. For 3 females that were tracked during almost their complete reproductive life, the life time reproductive output was between 11 and 19 cubs. Iberian lynx reproductive parameters did not respond to wide changes in prey abundance during the study. Conservation plans considering the extraction of cubs with a low survival probability should be considered by managers, for instance, in translocation campaigns.

Keywords: Litter size; *Lynx pardinus*; Mortality; Reproductive success; Sex ratio

1. Introduction

Information on reproductive parameters is essential to understand population demography and to plan management measures in species of concern. For instance, changes in reproductive rate, age at first reproduction, or cub-juvenile survival can alter the stability of wildlife populations, especially if they have low reproductive potential as it is the case of many carnivore mammals (Laurenson, 1995; Weaver et al., 1996; Carter et al., 1999; Loison et al., 2001). Therefore, the study of reproductive biology of free-ranging populations is needed, for example, to establish quotas in potentially harvestable species (Brand and Keith, 1979; Frost et al., 1999), or to plan translocation programs in endangered species (Miller et al., 1999).

The Iberian lynx (*Lynx pardinus*) is the felid species most vulnerable to extinction in the world (Nowell and Jackson, 1996), and now considered as critically endangered by the Word Conservation Union (IUCN, 2002).

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Its overall population size may not be larger than 200 individuals, and individuals are probably located in only 2 metapopulations isolated from each other in the south of Spain (Palomares et al., 2002; Guzmán et al., 2002). Reproductive biology of the Iberian lynx is little known (Delibes et al., 1975; Aldama, 1993) with the only exception of partial results published on den site characteristics and use as part of this long term study presented here (Fernández and Palomares, 2000; Fernández et al., 2002). Here, we studied several reproductive parameters in a lynx subpopulation of Doñana National Park during 9 years and relate some of them with the abundance of European rabbit (*Oryctolagus cuniculus*), the main prey of Iberian lynx (Delibes et al., 1975; Palomares et al., 2001). The Doñana lynx metapopulation is the best known since it has been intensively studied for 20 years (e.g., Ferreras et al., 1997; Palomares et al., 1991, 2000, 2001). Using a viability model for this metapopulation, Gaona et al. (1998) found that the second, third, and fourth most sensitive parameters were reproductive rate and cub and juvenile mortality, respectively.

2. Study area and methods

2.1. Study area

The study was carried out in the north of the Doñana National Park and surroundings (about 50 km^2), in an area called Coto del Rey (south-western Spain; 37°9′N 6°26′W), between December 1992 and August 2001. The Doñana National Park is a flat sandy area containing 3 main biotopes: scrubland, dunes, and marsh (Valverde, 1958). The climate is Mediterranean sub-humid, with mild, wet winters, and hot, dry summers, and an average annual rainfall around 550 mm.

Coto del Rey is characterized by a mixture of relatively well conserved areas of Mediterranean scrubland and ash stands where mastic shrubs (*Pistacia lentiscus*), dominate, plantations of mainly (*Pinus pinea*), and cleared areas for cattle grazing with isolated trees (*Quercus suber* and *Olea europaea*). Marsh extends to the south of the study area. In Coto del Rey, lynx reach the highest density of Doñana and there are also other carnivore species such as red foxes (*Vulpes Vulpes*), Eurasian badgers (*Meles meles*), Egyptian mongooses (*Herpestes ichneumon*), and European genets (*Genetta genetta*) (Palomares et al., 1996).

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

2.2. The studied lynx population

Lynx in Coto del Rey were studied continuously from 1992 to 1999 by trapping and radio-tracking (e.g., Palomares et al., 2001). Between 1999 and 2001, lynx were studied using track censuses, direct observations, and automatic photographic cameras. The lynx population in the study area was usually composed of 3 adult pairs plus juvenile individuals. On occasion, an extra adult female and/or male was also present (Palomares et al., 2001). All lynx activity was concentrated mainly in a small patch of Mediterranean scrubland (700 ha), thus monitoring of the population was relatively easy.

2.3. Location of litters

Litters were mainly located by radio-tracking females between 1993 and 1999. In 1999–2001, litters were located by searching known sites where females had bred in previous years, and in potential sites by systematic searching according to the characteristics of known dens. In the study area, females give birth in hollow trees, which can be easily recognized because their diameter is >0.9 m and have a hole large enough to accommodate the female and the cubs (Fernández and Palomares, 2000).

Adult females were radio-tracked daily during the reproductive season. When a female was located on 2–3 consecutive days in the same place, the observer approached her position to check what the exact place was. When we identified the exact place, we waited for the female to go hunting to check for cubs. Two or 3 weeks later, and before females moved cubs from the natal dens (Fernández et al., 2002), we tagged the cubs with transponders, took their weight and body measurements, and recorded their sex.

When females were not radio-tracked, we looked in known dens of previous years in March or April. In the same time, teams of 4–6 people looked for potential breeding sites by walking on the study area. After a litter was found, we try to see and photograph the female. She was recognized by the color of the radio-collar and the pictures.

2.4. Survival at different ages

Information on survival is presented as the percentage of lynx alive for individuals: (1) <3 months, (2) <10 months, and (3) before dispersing or <2 years (see below). Until 2–3 months old, cub remain in dens and do not accompany to the mother (Fernández et al., 2002). At about 3 months old, young lynx start to travel with the mother, and frequently remain with her until 10 months old (Aldama, 1993; Fernández et al., 2002). Finally, young or subadult (i.e., between 1 and 2 years old) lynx may stay in the mother’s home range until dispersal, which normally occurs between 12 and 24 months of age (Ferreras et al., 2004). Lynx not dispersing at 2 years old generally obtain a territory in the subpopulation (Ferreras et al., 2004). Because we were interested in survival of lynx born in this particular subpopulation, which, occupy a very small area (Palomares et al., 2001), dispersal here was considered when lynx left the subpopulation as described in Palomares et al. (2000).

Survival of cubs <3 months age was based on observations, captures and radio-tracking. When the female was radio-tracked, we tried to observe her and her cubs at least once per week after cubs were 2 months old. In most cases, captures of the lynx for radio-tagging allowed us to know the individuals that survived. Because in 1999 radio-tracking activities ceased, in 1999–2001 we set camera-traps with scent (Iberian lynx urine) and visual lures (feather and tinsel) to know the number of cubs surviving. Attractants were set together on a platform covered by sand so that when trodden upon by lynx the camera was triggered.

Survival between 10 months of age and dispersal was determined through captures, radio-tracking, observations, and photos of individuals undertaken by us and the staff of Doñana National and Natural Parks, and the Delegación of Consejería de Medio Ambiente of Huelva. All lynx born in the study area between 1994 and 1997 were captured and radio-tracked except one which was identified from pictures. Due to logistic problems, there was no information for the year 1998, and for 1999–2000, 3 lynx were captured and radio-tracked and the remainder ($n = 14$) were determined to be in the area from pictures.

Generalized linear mixed models (using SAS macro GLIMMIX; vs. 8.00; Littell et al., 1996) was used to test if probability of a lynx being alive at ages <3 and <10 months (i.e. when cubs and young depend of the mother) was affected by mother identity (random effect), age of mother, and rabbit density. We considered spring and autumn rabbit density for survival at age <3 and <10 months, respectively. Age of the mother was known by counting the cementum annuli of incisors extracted from anesthetized lynx (Zapata et al., 1997) or because the age of birth for the mother was known.

2.5. Reproductive success

Reproductive success (number of breeding females, number of cubs born and number of cubs surviving to 3 months old) was correlated to European rabbit density in the study area. Rabbit density was estimated by line transect sampling in the times of higher (end of spring) and lower (autumn) rabbit density in the area from autumn 1993 to spring 2001. Details on the methods and information on rabbit densities in the study area can be found in Palomares et al. (2001) and Palomares (2003).

3. Results

3.1. Breeding population and productivity

During the entire study period, 7 known females plus an unidentified female gave birth at least once. Six out of the 7 known females were marked with radio-collars, and the other was known through repetitive photos since she was young. The minimum number of females in breeding condition per year (i.e., between 3 and 9 years old, see below) was 3 for 7 years and 4 for other 2 years. Over 9 years, 83.3 ± 5.4% of the adult females bred per year (range = 66.7–100). In 4 out of 9 years all females in the population gave birth. Considering all 29 cases of female-year data, female bred in 24 occasions (83%). The observed breeding pattern in the 3 most tracked females was different. One bred every year until she was 9, another bred every 2 years, and the third bred every year until 9, except when she was 4 years old (the previous year she had raised 5 cubs). There was no significant correlation between either the total number of potentially breeding females or actually breeding females with rabbit density in spring ($r_s = 0.31$ and -0.28, $n = 8$, $p = 0.457$ and 0.460, respectively; Spearman rank order correlation) or the previous autumn ($r_s = 0.52$ and -0.28, $n = 8$, $p = 0.182$ and 0.460, respectively).

At least 64 cubs were born during the study, or 7.7 ± 0.69 ($n = 9$, range = 5–11) per year. There was no significant correlations between the number of cubs born and rabbit density in spring ($r_s = 0.06$, $n = 8$, $p = 0.839$) or rabbit density in the previous autumn ($r_s = -0.04$, $n = 8$, $p = 0.885$).

3.2. Timing of the birth

Most births occurred in March, one in April and another in June ($n = 16$). These 2 cases were for the same female. The first was after she had lost her territory and was living in a surrounding marginal area, and the second was in a year when she apparently had a pseudo-pregnancy in March (she was inside a hollow tree for 3 days, but there were no cubs).

During all years with records, timing of the births for all females present in the study area spanned no more than 2–3 days, except in 1999 when there were 2 weeks between each of the 3 births, and in 2000 when 1 litter was born about 1 week later than the other 2. In both years, the litters that were born later were of females that did not hold a territory of optimal quality.

3.3. Litter size and sex ratio

The mean litter size was 3.0 ± 0.16 ($n = 16$, range = 2–4). There were 3 cubs per litter in 10 cases of the 16 in which we were able to see the cubs before

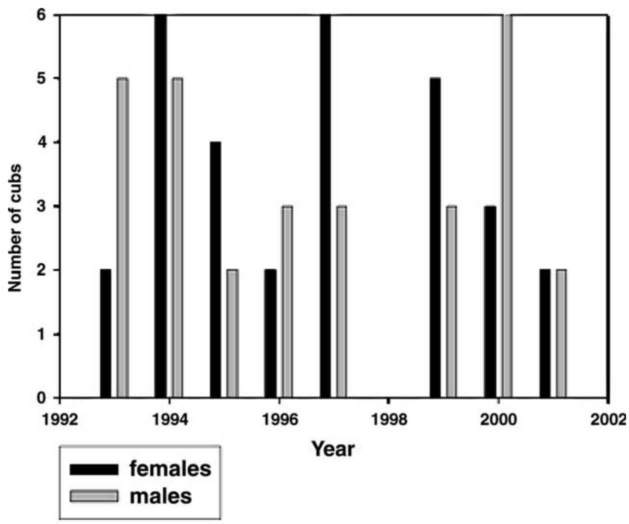

Fig. 1. Total number of male and female cubs of Iberian lynx born every year between 1993 and 2001 in the area of Coto del Rey, Doñana National Park. There was no data for 1998.

they were 4 weeks old. Two and 4 cubs/litter occurred twice each. There was a case of a female that was able to raise 5 cubs, although we could not know to how many cubs she gave birth. Considering this female with 5 cubs, the mean litter size would be 3.1 ± 0.19 (n = 17, range = 2–5).

For 59 cubs from 20 litters we knew the sex. Sex-ratio was 1.03:1.00 (females:males). For the 8 years with data on sex of cubs, female cubs were dominant on males in 4 years, males on females in the other three, and in one year the number of male and female cubs was the same (Fig. 1). In 6 out of 20 litters, cubs were of the same sex (3 litters of 3 cubs each were all females, and 3 litters of 2 cubs each were all males). Six out of the 7 breeding females gave birth more females than males (Fig. 2).

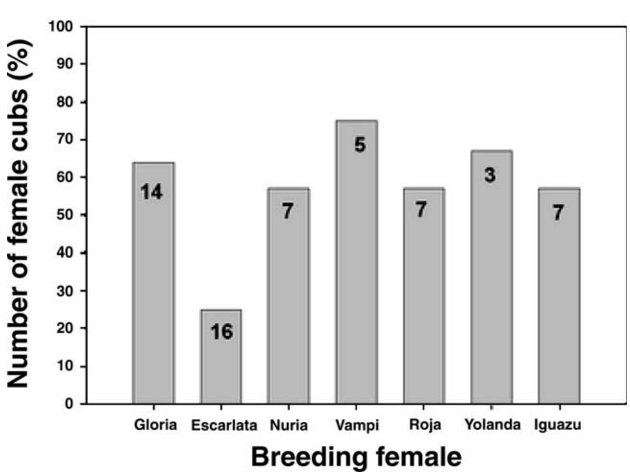

Fig. 2. Percentage of female cubs from each known Iberian lynx female studied in Coto del Rey, Doñana National Park. Numbers in bars are the total number of cubs.

Table 1
Percentage of Iberian lynx born in the study area that survive to different ages in Coto del Rey, Doñana National Park

Age	Males	Females	Total
<3 Months	73 (n = 26)	73 (n = 26)	75 (n = 63[a])
<10 Months	70 (n = 23)	68 (n = 22)	69 (n = 45)
Before dispersal	59 (n = 22)	55 (n = 20)	57 (n = 42)

Sample size (i.e., individuals which it is known if they were alive or death for a given age) is between brackets.
[a] Sex of 11 cubs was not known

3.4. Survival of the lynx born up to dispersal

There was only one case in which females lost a complete litter before cubs were 3 months old. There were four cases where females reared all cubs to age older than 3 months (litters of 3, 3, 4 and 2 cubs). In 5 cases of litters of 3 cubs where survival until 3 months was known, female lost one cub, and in 2 other cases they had lost 2 cubs (litters of 3 and 4 cubs). Thus, typically females raised 2 cubs to ages older than 3 months; by age of 3 months, 75% of cubs (n = 63) had survived (Table 1).

We did not detect any lynx death between 3 and 10 months old, and only 4 lynx died between 10 months and dispersal (we did not know the fate of 18 and 21 lynx for each period, respectively). Therefore, number of lynx alive <10 months and before dispersing was 69% and 57%, respectively (Table 1). Sex of the lynx did not affect survival for any age (P always >0.571 for any age class, Z test; Table 1). For the 52 cubs for which we had information, GLIMMIX did not detect any effect of mother age (F = 0.0, d.f. = 1, p = 0.9888) or rabbit density (F = 0.85, d.f. = 1, p = 0.3615) on probability of surviving <3 months (we did not perform any GLIMMIX for age <10 months because we did not detect any dead lynx aged 3–10 months).

Normally, it was not possible to know the causes of death of cubs younger than 3 months. Twice we found bodies of cubs. One case was a 5 weeks old female that the mother had covered partially the body with sand and leaves. There was no apparent sign of trauma but the cub was the smallest in the litter. In 3 litters with known cub deaths, it was the smallest that died; in the other 2 cases the heavier cub died. The other cub found dead was an 1 week old male that had never suckled. In the same litter, there was another cub in poor body condition presumably due to starvation. It was removed from the field and, once artificially fed, recovered fully. This case coincided with the lowest rabbit density recorded during the study. Nevertheless, GLIMIX did not detect any relationship between the number of cubs <3 months alive and rabbit density in the study area (see above). Only in 2 cases, we know the causes of the death for lynx between 10 months and dispersing. One was killed by dogs and other run over by a car.

3.5. Age of first and last reproduction

Any female bred before 3 years of age. Of known-age females ($n = 6$), first breeding was known to have occurred at 3 years of age for 3 females.

We could be sure of the age of the last reproduction for only 2 females. One died by unknown causes when she had cubs at age of 9 years. The other one disappeared from the study area when she was 11, and had not breed since she was 8 years old. Another female still alive at the end of the study was 10 years old, and she had bred the last time when 9 years old.

3.6. Life time reproductive output

The lifetime reproductive output per female was between 2 for a female with data only for one year, and 19 for a female that bred in 6 years. For the 3 females that were studied between 5 and 8 years, reproductive outputs were at least 14, 8, and 19 (one female was still alive when the study ended, but she was older than 9 years and unlikely to breed thereafter). Two of these females had been studied only since they were 4 and 5 years old, thus they could have bred previously. Assuming that they bred for the first time when they were 3 years old, and that one bred every year when she was monitored until she was 8, and that the other bred every 2 years until she died when 9 years of age, the total number of cubs that they might have produced would be 18 and 11, respectively.

4. Discussion

Females exhibited clearly different breeding patterns that differed from one another. While some of them bred every year, others bred in alternative years, producing a general pattern close to that observed in other lynx species. Seventy five percent of Eurasian (*Lynx lynx*), or Canadian lynx (*Lynx canadensis*), females bred during years of normal prey abundance (Brand and Keith, 1979; Breitenmoser et al., 1993). We have no ecological explanation for the observed differences in individual breeding pattern, because animals used territories of similar quality, there were breeding males available (Palomares et al., 2001), and there was no significant correlation between the main prey (European rabbit) abundance and lynx reproduction. In contrast, Canadian lynx, pregnancy rates decreased to 33% in years of prey scarcity (Brand and Keith, 1979). Furthermore, except in the case of a female that produced 5 cubs 1 year and the following year did not breed, litter size was identical for females that regularly bred and those that did not regularly bred when they gave birth. Thus, the reproductive pattern seems to be related to characteristics of the female.

Usually, parturition dates were concentrated into a few days of March (also see Fernández et al., 2002). The synchrony in parturition could be related to the apparent monogamy that lynx exhibit in this population, where normal adult population consisted of 3 pairs (Palomares et al., 2001). However, when there was an extra female, she gave birth a few weeks later than the other females. If females need to be stimulated by males to induce ovulation, this might explain this pattern since males would be limiting.

Parturition coincided with the time of the year when European rabbits, the main prey of the lynx, start to increase abundance in the study area (Palomares et al., 2001), hence facilitating the feeding of the litters, which during the first months of breeding is very demanding for the female in terms of energy and prey requirements (Aldama et al., 1991; Aldama, 1993).

The most common litter size was similar to those of Eurasian lynx and bobcat (*Lynx rufus*) (Kvam, 1991; Jedrzejewski et al., 1996; Crowe, 1975), but was lower than that of the Canadian lynx, which seems to show higher plasticity for this trait (Brand and Keith, 1979; Mowat et al., 1996). Nevertheless, the most common litter size when cubs start to accompany females (i.e., around 3 months old; Fernández et al., 2002) was 2, also close to the litter size reported by Breitenmoser et al. (1993) for the Eurasian lynx. This means that generally 1 cub died in the first months of life, although there were some exceptions. Again lack of a relationship between cub survival and prey abundance, suggests that although rabbits declined in the study area during the study period (Palomares, 2003), the decline was not enough to provoke failure in the reproduction. Nevertheless, the observed rabbit abundance at the end of the study (4 rabbits/ha in spring; the lowest recorded for the study period; F. Palomares, unpubl.) might be close to critical for lynx reproduction. In the last year of study, 1 cub was found death of starvation and another in poor condition for the first time. It is interesting to note that rabbit decline in the study area neither affected lynx home range, daily movements, habitat use or diet (Palomares et al., 2001).

We could not know the cause of death for some cubs that died before 3 months of age. The only 2 known cases suggest that it might be starvation, but not always the smaller cub died, suggesting that could have other different causes. In the Eurasian lynx, aggressions between siblings may lead to the death of some of them (Sokolov et al., 1994).

We did not record any case of a breeding Iberian lynx female younger than 3 years of age yet this is relatively common in other lynx species (Kvam, 1991; Mowat et al., 1996; Stehlík, 2000). Although there is no study on the reproductive tracts of Iberian lynx that could confirm if females are physiologically capable of breeding at younger ages, it would seems reasonable. In fact, second year females have similar body size and weight as older females. The strong intrasex territorial behavior of Iberian lynx in Doñana (Ferreras et al., 1997), and the limited available space (Palomares et al., 1991), could be preventing younger females from breeding because they can not successfully compete with older females for quality territories.

Iberian lynx appears to have little sensibility to respond to changes in prey abundance as occurs in other species (e.g., Brand and Keith, 1979; Mowat et al., 1996). The studied population did not respond to large changes in prey abundance from 4 to 55 rabbits/ha during the study, by changing either litter size and cub survival.

Females often were able to raise only 2 cubs to >3 months of age. Although starvation could be the reason of the death of the third and fourth cubs (when litters were of 4), it seems that the problem was not associated with an insufficient number of rabbits. It seems that these cubs might have died in any circumstance. If this is the case, these cubs might be extracted from the field in order to be artificially reared for captive breeding or translocation programs. Nevertheless, if this is considered, population viability models should be performed to test effects of these extractions on the donor populations. Additionally effects of extractions on breeding success of target females should be monitored. If intralitter aggression was responsible for the deaths as sometimes is the case for the Eurasian lynx (Sokolov et al., 1994), it might continue independently of the extraction of any cub.

This study provides information on reproductive parameters that are important in models of viability of the lynx population at Doñana. However, this study was carried out in one subpopulation situated inside the protected area. Here, the mortality of lynx is very low (Ferreras et al., 1992), and the population is a source where productivity clearly exceeds mortality. Furthermore, the study area holds the highest density of rabbits in the area of Doñana (Palomares et al., 2001; Villafuerte et al., 1994; Fernández, 2003), therefore, the reproductive output of lynx may also be the highest of the entire Doñana metapopulation. Thus, caution should be taken before considering the results obtained here as general for the Doñana area. In fact, other source populations of Doñana reported in Gaona et al. (1998) appear to have had during last years lower reproductive output (authors unpubl.). Reproduction in these areas (both inside and outside of the national park) should be studied.

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