J. Zool., Lond. (1997) **243**, 163–189

Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*)

P. Ferreras[1], J. F. Beltrán[1], J. J. Aldama[2†] and M. Delibes[1]

[1] *Estación Biológica de Doñana, C.S.I.C., Apdo. 1056, 41080 Sevilla, Spain*

[2] *Centro de El Acebuche, ICONA, Parque Nacional de Doñana, Almonte, Huelva, Spain*

(*Accepted 29 November 1996*)

(With 7 figures in the text)

The spatial organization of the endangered Iberian lynx, *Lynx pardinus* (Temminck, 1827), was studied in Doñana National Park, south-western Spain, between 1983 and 1992. Thirty-six individuals (19 males and 17 females), including 24 adults (13 males and 11 females) were radio-tracked, providing 13,950 locations during 17,111 radio-tracking days. Iberian lynxes were essentially solitary (95.9% of simultaneous locations apart) and interactions were restricted to rearing activities by females. Adult associations were uncommon. Seasonal (four months) home ranges were larger for adult resident males (10.3 ± 1.9 km^2; $n = 5$) than for females (8.7 ± 2.4 km^2; $n = 5$). Lynxes used a central portion of the home range intensively ('core area', 50% Harmonic Mean) with similar size for males (3.7 ± 0.7 km^2) and females (3.2 ± 0.8 km^2), representing, on average, a 37.6 ± 1.5% and 36.6 ± 4.5% of male and female home ranges, respectively. Intrasexual home-range overlap was usually low between same-sex neighbours (15.1 ± 6.6% males and 22.1 ± 3.3% for females), but some instances of high overlap (>25%), both among males and females, were recorded, corresponding to spatial interactions between neighbours which usually ended with the displacement of one of the contenders. Core areas were mainly exclusive except during these spatial interactions. Actual fights resulting from these interactions seem more frequent than previously reported for other medium-sized solitary felids, likely promoted by high competition for optimum territories due to saturation of the population. The Iberian lynx spatial organization in Doñana works as a land tenure system, as described for other solitary felids. Although the mating system tends to monogamy, with male home range overlapping mainly that of one female, individual variations to polygyny were also found.

Introduction

A social system has been defined as the manner in which individuals position themselves in space and time in relation to other conspecifics and some features of the environment (Morrison & Menzel, 1972). Most of the Felidae species (except the lion, *Panthera leo*, Schaller, 1972; the cheetah, *Acinonyx jubatus*, Caro & Collins, 1987; Caro, 1994; and the domestic cat, *Felis catus*, Macdonald *et al.*, 1987) have an essentially solitary life, intraspecific contacts being limited to those associated with reproduction (mating in adults, and rearing of the cubs by females; Kleiman & Eisenberg, 1973). However, even the usually solitary species have social relationships of different kinds, for example with their neighbours (Leyhausen, 1965), and numerous studies have revealed the complex social organization of apparently solitary species (Macdonald *et al.*, 1987; Kruuk & Moorhouse, 1991). The social systems of solitary felids are very flexible, since many intraspecific variations have been described in degree of sociability (Bailey, 1974; Sunquist, 1981), home-range size and exclusivity (degree of inter- and intrasexual overlap), both in time and geographically (Ward & Krebs, 1985;

[†] This paper is dedicated to Dr Aldama who sadly died on 29 November 1996

Eisenberg, 1986; Hopkins, Kutilek & Shreve, 1986; Anderson, 1987; Knick, 1990; Breitenmoser, Slough & Breitenmoser-Würsten, 1993*b*).

On the other hand, a species social system can act as a natural regulation mechanism, limiting the proportion of the population reproducing and, consequently, the rate at which the population can increase (Seidensticker *et al.*, 1973; Sunquist, 1981; Hornocker & Bailey, 1986; Beier, 1993). Understanding the social organization of endangered species and the factors that influence their social behaviour is therefore particularly important for their management and conservation.

Recognized as a separate species from the Eurasian lynx (*Lynx lynx*; Honacki, Kinman & Koeppl, 1982), the Iberian lynx (*Lynx pardinus*) is a medium-sized felid inhabiting the south-western quarter of the Iberian Peninsula (Rodríguez & Delibes, 1992). Adult specimens weigh between 9 and 16 kg, males being bigger than females (Beltrán & Delibes, 1993). It has been identified as the most vulnerable of all the Felidae species (Nowell & Jackson, 1996). The aim of this study is to determine the social organization of a naturally occurring population of Iberian lynx and the effects on its population dynamics. We carried out a long-term intensive study of the Doñana National Park population, during which we radio-tracked a total of 36 individuals (19 males and 17 females) in 10 years (between 1983 and 1992). The main questions asked were: 1) How solitary are Iberian lynx? 2) Are there different social classes among adult males and females? 3) What is the home-range size for each sex? 4) How are neighbouring individuals organized (inter- and intrasexual overlap between ranges, number of contacts, defence of home ranges, etc.), and does this suggest a territorial or land tenure system? 5) How and when are territories acquired and lost? and finally 6) What is the Iberian lynx mating system?

The study area and the Doñana lynx population

The study was carried out between 1983 and 1992 in the Doñana National Park (500 km^2), located in the south-west of the Iberian Peninsula (37° 00′ N, 6° 30′ W; see Fig. 1), which presents a Mediterranean subhumid climate with Atlantic influences and a marked seasonality, with hot, dry summers and mild, wet winters (for a general description of the ecology of Doñana, see Valverde, 1958; Rogers & Myers, 1980).

The Iberian lynx is a rather poorly known species. Also, its social organization at the study area must be influenced by the population size and population structure, demography, available food and habitat. Hence, it seems important to indicate some of the species traits and the population characteristics of the Iberian lynx in the Doñana area, to make readers familiar with the species and the location.

The species total world population, under one thousand individuals, is distributed in nine spatially and genetically isolated populations in the south-western quarter of the Iberian Peninsula (Rodrígue & Delibes, 1992). Each of these populations is fragmented in separate breeding nuclei (subpopulations) connected among them by dispersing individuals, corresponding to demographically rea 'metapopulations' (Rodríguez & Delibes, 1992).

The best known of these metapopulations is partially included in the Doñana National Park, an are where the existence of a lynx population has been recognized for a long period (Valverde, 1963). A present this metapopulation is made up of no more than 50–60 lynxes (in a total area of abou 1000 km^2) distributed among four to six subpopulations connected by variable numbers of dispersin individuals (Palomares *et al.*, 1991; Gaona, Ferreras & Delibes, In prep.). This situation was probabl different before the mid century, when lynx had a continuous distribution throughout the Doñana are (Valverde, 1957). During the last 40 years, human persecution and, above all, habitat losses hav caused the fragmentation of the original population into the discontinuous nuclei of today.

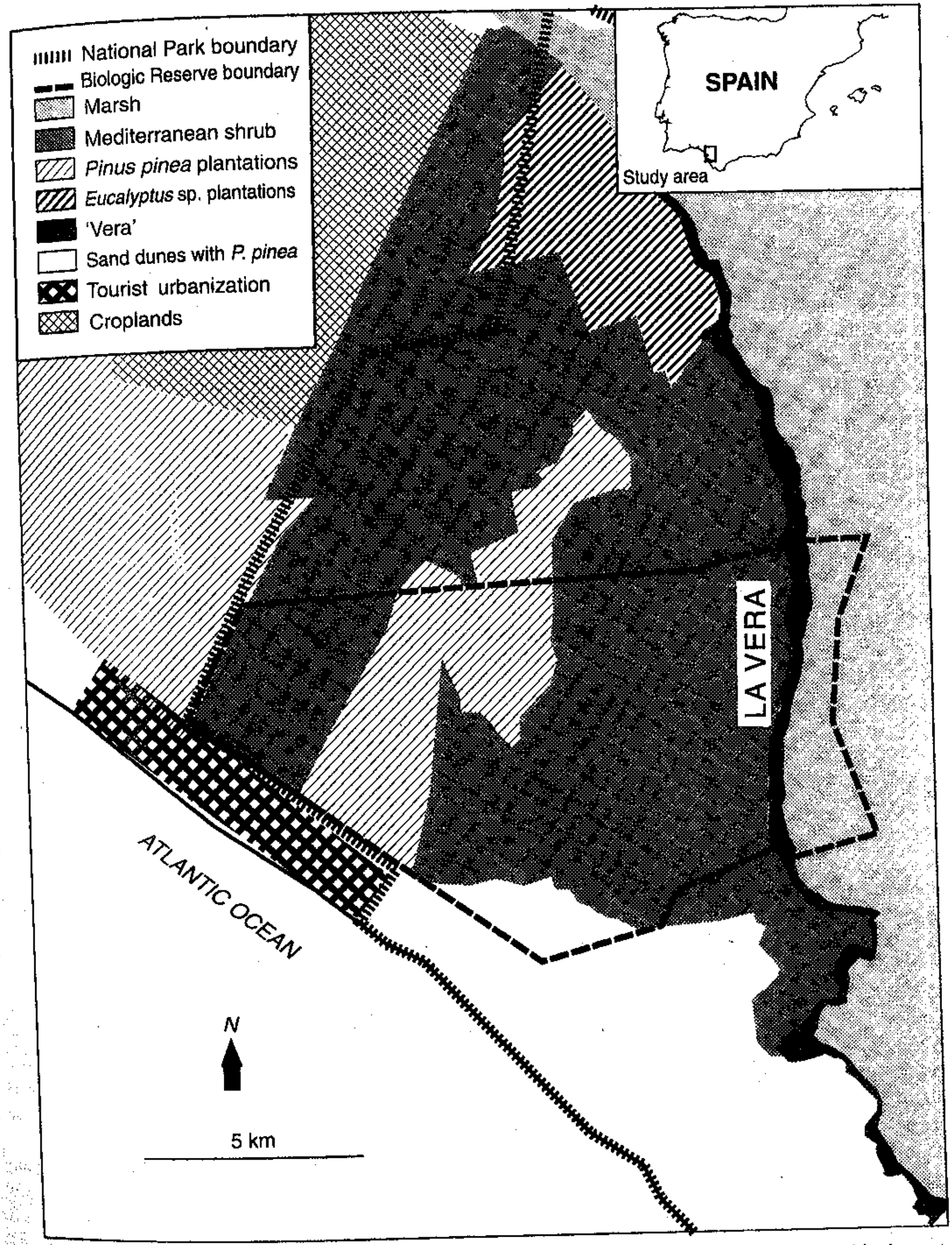

FIG. 1. Location of the study area in south-western Spain. Main lynx population and study area are centred in the ecotone between the mediterranean shrub and the marsh ('LA VERA') at and around the Biologic Reserve. Unfavourable habitats are also shown: marshes, croplands, sand dunes and a tourist urbanization.

Most individuals and breeding nuclei of this metapopulation are living within the Doñana National Park, the most protected area in the whole Iberian lynx range, while some other smaller breeding nuclei are outside the National Park, some of them in a peripheral and less protected Regional Park The density of human habitation in the area surrounding the National Park, due to agriculture and tourism developments, makes the whole Doñana lynx population spatially restricted to the scarce suitable habitat, mainly inside the National Park. High mortality occurs outside the National Park primarily as a result of human-related factors, while few lynx die inside (Ferreras *et al.*, 1992) where a presumably high intraspecific competition may occur.

Our study has been centred in one of the high-density nuclei located in a zone called 'La Vera', i.e. the ecotone between the dry scrubland and the humid marsh, at the core of the Doñana National Park and partially inside its Biological Reserve, established in 1964 (see Fig. 1). This zone has good shelte and high, but declining, rabbit (*Oryctolagus cuniculus*) numbers (Beltrán, 1991; Villafuerte *et al.* 1994; Moreno & Villafuerte, 1995), the staple prey of the Iberian lynx (Delibes, 1980; Beltrán & Delibes, 1991). Rabbit density and dense cover decrease as distance to this ecotone increases (Moreno & Villafuerte, 1995). Also, rabbit populations in Doñana oscillate during the year, density in June being up to five times that in October (Beltrán, 1991). Here, lynxes are active mainly at dusk and dawn (Beltrán & Delibes, 1994) and use preferably scrub areas, avoiding marshlands, dunes and *Eucalyptu* sp. plantations (Palomares *et al.*, 1991; Beltrán, Aldama & Delibes, 1992). Breeding occurs mainly in early spring (births peak occurs between March and April), but it can take place in every month of the year (Valverde, 1957; authors unpubl.). Usually, two or three cubs per litter are born.

Lynx density in 'La Vera' has been estimated as between 0.1 and 0.18 individuals (excluding cubs dependent on their mother) per square kilometre (Rau, Beltrán & Delibes, 1985), but it could be locally even higher. Between three and five adult females simultaneously occupied the area during our study with a trend to decrease following the above reported rabbit decrease, which probably is reducing the Doñana carrying capacity for lynx.

Material and methods

Capture, immobilization, radio-tagging and radio-tracking

Lynxes were captured with 2 types of traps: baited home-made box-traps and baited or unbaited padded coil spring traps (Victor #2, Woodstream Co., Pennsylvania, U.S.A.; Delibes & Beltrán, 1986). Thirty-six differen individuals (19 males and 17 females) were captured a total of 84 times (including recaptures). Once captured, th animals were immobilized with an intramuscular injection of Ketamine hydrochloride (50 mg/ml, Ketolar, Parke Davis) and Xylazine hydrochloride (23.32 mg/ml, Rompun, Bayer). Drug doses, induction and recovery times ar described in Ferreras *et al.* (1994).

Three age categories were distinguished according to the capture date (in relation to the seasonal peak of births) body size and tooth wear, which were also supported by information from known-age lynxes (Beltrán & Delibes, 1993). These 3 age classes were: juveniles or individuals less than 1 year old; subadults, between 1 and 2 years old and adults, individuals older than 2 years (for a detailed description see Beltrán & Delibes, 1993).

Captured lynxes were fitted with radio-collars (*c.* 200 g for adult individuals, lifespan 12–18 months), mainl from Wildlife Materials Inc. (Carbondale, Illinois), although some transmitters from AVM Instrument Co (Livermore, California), Telonics (Mesa, Arizona) and Biotrack (Dorset, U.K.) were occasionally used (Delibes Beltrán, 1986). Locations of the animals were obtained by triangulation from a vehicle. Radio-tracking followed basic schedules: approximately daily locations at different times of the day, and intensive tracking sessions of 2 (1 fix/hour) or 48 hours (1 fix/3 or 4 hours). Triangulation bearings were usually obtained less than 1 km from th animal, and the distance fix error, estimated using test transmitters, was usually less than 100 m (Beltrán, 1988)

We obtained 13,950 locations during 17,111 radio-tracking days of the 36 tracked individuals (Fig. 2). Each individual was radio-tracked, on average, on 475 ± 77 ($\bar{x}$ ± S.E.) days (range 7–2547) providing 387 ± 77 fixes per individual (range 3–2481).

Seasonal intervals considered for analyses were periods of 4 months, so-called 'spring' (March–June), 'summer' (July–October) and 'autumn–winter' (November–February). These periods reflected differences in climate, daily activity, and prey eaten by lynx (Delibes, 1980; Beltrán & Delibes, 1994).

Solitariness

A 'coefficient of spatial association' was used to estimate the time spent by each individual in proximity to each neighbour. This coefficient was calculated as the proportion of simultaneous locations (time span less than 2 hours) of both individuals in which the distance between them was less than twice the triangulation error (100 m). The value of this index was estimated for each possible different combination of sex-age pairs.

The index R of Clark & Evans (1954; herein referred to as RCE) was also employed to analyse the spatial arrangement of the individuals radio-tracked simultaneously. This index compares the average distance of each individual to its nearest neighbour (r_A) with the value expected if the distribution of all the radio-tracked animals were random (r_E). A value of R ($R = r_A/r_E$) greater than one means that the distribution of the animals

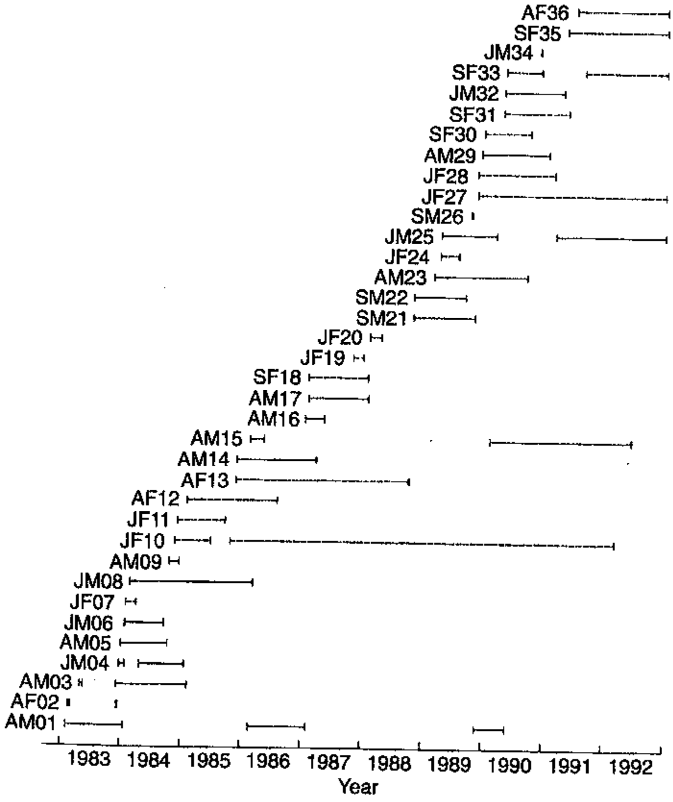

FIG. 2. Radio-tracking periods for 36 lynx marked between 1983 and 1992. Males are represented by full lines and females by dashed lines. The first letter for each individual corresponds to the age when first captured (J = juvenile; S = Subadult; A = Adult), the second one to the sex (F = Female; M = Male) and the number is unique for each individual.

is dispersed (distances greater than expected by random), and values lower than one would point to an aggregated distribution.

Social categories

Individuals showing relatively small and temporarily stable home ranges between at least 2 consecutive seasonal periods were considered residents, whereas those showing no stability (which was usually accompanied by large range sizes) have been considered transients or non-resident. The majority of the study focused on the resident adult individuals.

Home ranges and territoriality

Independent radio-fixes (defined as those at less than 6 hours apart; Ferreras, 1994) were used to analyse home-range size and stability with the program RANGES-IV (Kenward, 1990). Here, 'home range' is used to refer to the area used by an animal (Brown, 1975: 50), and 'territory' is defined as a more or less exclusive area defended by an individual (Burt, 1943; Brown & Orians, 1970). Home-range size was estimated by: a) the minimum convex polygon including the total of locations (Mohr, 1947; here referred to as MCP100), or 'total range', broadly used in the bibliography; and b) the area defined by the minimum convex polygon excluding the most external 5% of the locations (MCP95 or 'home range' s.s., Knick, 1990; Breitenmoser *et al.*, 1993*a*). The excluded locations would correspond mostly to irregular movements outside the usual range (White & Garrott, 1990; Poole, 1995). We used cumulative-area curves (Odum & Kuenzler, 1955; Harris *et al.*, 1990) to evaluate the number of independent locations required to estimate seasonal home ranges. On average, seasonal home-range size versus cumulative fix number reached an asymptote after approximately 60 independent fixes, when estimated as either MCP100 or MCP95. For this reason, only seasonal periods with more than 60 independent fixes for each animal were included in the home-range size analyses. The core areas of each home range were identified as the areas of the 50% probability isopleth resulting from the harmonic mean method (Dixon & Chapman, 1980) using a 200 m size grid.

The stability of the home range was evaluated using the index of Cole (1949), which estimates the coincidence between 2 areas by the equation:

$$C\% = \frac{2AB}{A+B} \times 100 \tag{1}$$

where A and B are the home-range sizes in 2 consecutive periods (usually seasons) and AB is the area common to them. This index can take values between zero (no coincidence at all) and 100 (total coincidence).

We estimated the home-range overlap of neighbouring adult resident individuals, as the proportion of one individual home range which is shared by the overlapping one. When a no-directional measure of the coincidence between 2 individuals' home ranges was required, instead of the overlap index, we used a coincidence index, calculated using the Cole (1949) equation, referred to above.

The index of Mitani & Rodman (1979) was used to estimate the defendability of the home range against conspecific neighbours as the ability of travelling between the furthest points of the home range during a daily cycle. This index (referred to as DI) is calculated as the ratio between the mean total distance travelled during a day and the diameter of the home range, supposed to be circular.

As an index of home-range patrolling activities, we employed the percentage of the seasonal home range overlapped by the area (minimum convex polygon) covered during 24 h sessions of intensive radio-tracking. A high proportion of the seasonal home range covered in one day would suggest an intense activity of patrolling.

Statistics

Throughout the paper mean values are presented ± 1 Standard Error (S.E.). Data were analysed using standard parametric tests (Zar, 1984) when possible. We considered the individual as a sample unit in most of the tests, which usually implies small sample size. The effect of season on range size and core area size was tested using 2-way analysis of variance fitting terms for the individual and the season. Since the different individuals were not equally represented for all the seasons (unbalanced design), this was carried out using the PROC GLM option of SAS system (SAS Institute, 1988). Sample sizes were denoted by *n* when referring to number of individuals and by *N* when referring to some other sampling unit.

Results

Solitariness: spatial association between individuals

Iberian lynxes were principally solitary; only on 4.1% of simultaneous locations were two radio-tracked lynxes found in close proximity ('spatial association', see Table I). Adult individuals were the most solitary (coefficient of spatial association: 3.6% and 2.0% for females and males, respectively), while juvenile and subadult females were the most sociable (9.5 and 7.4%). The interactions of adult females with juvenile individuals, both females and males, resulting from rearing activities, produced index values among the highest in the population (12.9 and 12.1%; Table I). Interactions between adult individuals were infrequent, those between males and females being more frequent than those between adult individuals of the same sex (2.2% males–females, 1.3% females–females, and 0.6% males–males; Table I).

Considering all the individuals radio-tracked at one time, the mean value of the RCE index was

TABLE I

Number and frequency of spatial associations (simultaneous locations closer than 200 m) between lynxes of different sex and age classes throughout the study. The values corresponding to adult individuals are marked in bold. M = male; F = female; J = juvenile; S = Subadult; A = adult.

Pair composition	N. spatial associations	N. simultaneous locations	Coefficient of spatial association(%)
FJ–FJ *	26	122	21.1
MJ–FA	53	411	12.9
FS–FS	71	583	12.2
FJ–FA	32	264	12.1
MS–MS	10	105	9.5
FS–FA	87	915	9.5
MS–FJ	4	66	6.1
MJ–MS	1	22	4.5
MA–FJ	20	446	4.5
MS–FA	28	779	3.6
MS–FJ	4	119	3.4
MS–FS	15	542	2.8
MA–MS	14	524	2.7
MA–FA	**79**	**3520**	**2.2**
MA–FS	17	844	2.0
FS–FJ	1	65	1.5
FA–FA	**21**	**1564**	**1.3**
MJ–FJ	1	87	1.1
MA–MA	**4**	**622**	**0.6**
MA–MJ	0	311	0.0
MJ–MJ	0	0	—

* Simultaneous locations of juvenile females were from two pairs of siblings

0.988 ± 0.103 for 19 dates randomly chosen from all the study. According to this measure, the radio-tracked lynxes were situated, on average, randomly with respect to the others, although the dates included cases of females and juveniles still dependent on their mother or that became independent recently. In order to isolate such effects, this index was calculated for only adult females and adult males. Considering only the distances between adult females, the value of the average RCE index for seven random dates (with three or more simultaneously tracked females) indicated a trend towards a dispersal distribution, although not significantly different from a random distribution ($\bar{x} \pm$ S.E. $= 1.304 \pm 0.301$, $t = 1.01$, 6 *d.f.*, $P = 0.351$). Average values obtained for 16 random dates of simultaneous tracking of adult males were significantly higher than 1 ($\bar{x} \pm$ S.E. $= 1.427 \pm 0.195$; $t = 2.20$, 15 *d.f.*, $P = 0.044$), meaning dispersed spatial arrangements.

According to these results, adult Iberian lynxes tended to spread further away from conspecifics than expected by random movement, in agreement with the solitary condition shown above by the low levels of spatial association.

Social classes

We have defined resident individuals as those with a relatively small and stable seasonal home range, although the spatial behaviour before and after the period considered was also taken into account when classifying an individual as resident. By plotting graphically home-range size against stability (as percentage of coincidence between successive seasonal periods, see Fig. 3), we observed that most adult individuals fit our definition of resident, although some juvenile and subadult animals also showed similar spatial behaviour. These juveniles (all 7 months or older) and subadults were partially or totally independent from their mothers, and although they were still living in or nearby their mothers' home range, they moved together only occasionally. Most subadult, some adult and some juvenile individuals, however, cannot be considered as resident and they were individually qualified as either: 'dispersers' (mainly juveniles and subadults leaving their natal area, see Ferreras, 1994) or as 'transients', formerly resident adults who abandoned their previous home ranges. Most of the rest of the paper will focus on resident adult individuals as the main portion of the social system, and will exclude both non-adult (juvenile and subadult) and the adult dispersers and transients.

Home range and territoriality

Owing to the different resource requirements affecting the space use for each sex in solitary cats (prey for females and females for males; Eisenberg, 1986; Sandell, 1989), we first analysed each sex separately and then we examined the relationships between them.

a) Females' home-range size and use

The size of the seasonal home range for the resident females (MCP95) showed values between 1.7 and 21.0 km^2, with an individual-weighted average for five females of 8.7 ± 2.4 km^2 ($\bar{x} \pm$ S.E.; Table II). The lowest values were reported for females during the first months following parturition, and the highest values for females residing in peripheral parts of the study area. The absolute minimum value, 1.7 km^2, corresponds to female AF10 in spring 1989, during the first months of life of her cubs. Female AF13 also showed a reduction in home-range size (4.3 km^2) during pregnancy and the first few weeks after parturition. Despite the broad range of variation, the home-range size (MCP95) was less than 10 km^2 in 87% of the considered cases ($N = 32$; Fig. 4). There were no significant differences

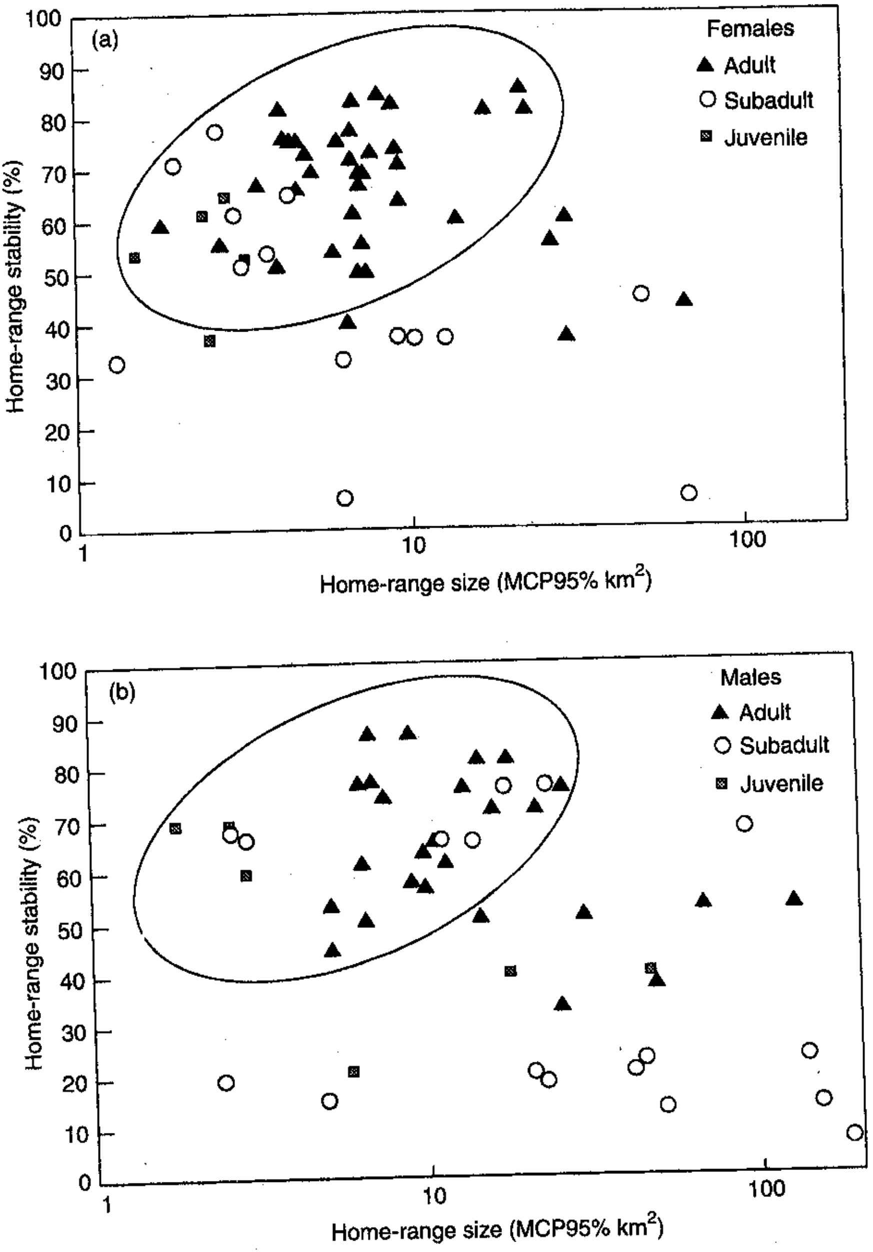

FIG. 3. Seasonal home-range sizes versus stability (as percentage of coincidence between successive seasonal periods) for (a) females and (b) males radio-tracked during at least two consecutive seasonal periods. The ellipse-shaped area contains those cases classified as residents, according to our definition.

between seasons of the year ($F_{(2,6)} = 1.43$, $P = 0.311$). The average stability of the seasonal home ranges (as the coincidence between ranges of consecutive seasons) was 68.9 ± 3.3% ($n = 5$; range of individual averages: 59.7–82.1%), a high value as a result of our definition of resident individuals. The total range or minimum convex polygon of 100% of locations (MCP100) for each season had an average value for all the adult resident females of 11.6 ± 3.6 km^2 (Table II). In Table II, we also show annual home-range and core-area sizes for comparison with other studies where these values instead of seasonal ranges are calculated (annual MCP95: 12.6 ± 4.0 km^2, $n = 4$ females). Body size of resident females seemed not to influence home-range size (linear regression of MCP95 on weight: $F_{(1,3)} = 2.56$, $P = 0.579$). According to DI values of Mitani & Rodman (1979), which were on average higher than one (2.73 ± 0.11, $n = 2$ females), the radio-tracked females would be able to defend their home ranges by means of their daily movements (daily distance travelled 6.4 ± 0.7 km; Table III).

The core areas (50% harmonic mean isopleth) had a mean size of 3.2 ± 0.8 km^2 ($n = 5$ females; Table II), varying between 0.3 and 8.8 km^2, indicating how little of the home range (37.6 ± 1.5% of the MCP95, on average) was used intensively, particularly in spring (30.5 ± 2.3%), although season did not have a significant effect ($F_{(2,6)} = 1.462$, $P = 0.304$).

In spite of the solitary character of the resident adult females (see 'Solitariness'), their seasonal home ranges were not completely exclusive intrasexually. MCP95 overlap exceeded 20% in 42% of the cases, and was greater than 30% in 25% of them. The cases where overlap was higher often included females who changed location soon afterwards (see below). Season had a significant effect on the variations in overlap index between resident females ($F_{(2,49)} = 4.198$, $P = 0.0161$ percentages arcsin-transformed), spring being the season with higher average overlap (percentage: 31.9 ± 8.1%, $N = 14$ dyads of adjacent females × season). Although home ranges overlapped highly, core areas of the resident adult females were mainly exclusive; only in 6% of the cases reported was the overlap 25% or more, corresponding to agonistic interactions between females, described below.

b) Males home-range size and use

Seasonal home-range sizes (MCP95) of five resident adult males showed an individually weighted average of 10.3 ± 1.9 km^2, with absolute minimum and maximum values of 5.3 and 21.8 km^2, and individual averages ranging between 6.0 and 16.7 km^2 (See Table II). Despite the lack of significant differences between the home-range sizes of resident males and resident females (MCP95, $t = 0.52$, 8 *d.f.*, $P = 0.616$), the males distribution is skewed towards higher values than those of females (Fig. 4). The effect of the season on male home-range sizes (MCP95) is not significant ($F_{(2,8)} = 0.59$, $P = 0.577$). Body weight seemed not to influence male home-range size ($F_{(1,3)} = 3.22$, $P = 0.171$). The seasonal total range (MCP100) for resident males had an average value of 15.6 ± 4.0 km^2 (Table II). The stability of the seasonal home ranges is high (weighted average 65.3 ± 4.4% for 5 males, range 51.3–80.7%), and therefore similar to the females. Annual home ranges were on average 16.9 ± 3.1 km^2 for five males (MCP95, see Table II). Subsequent descriptions will refer to seasonal home ranges, although values corresponding to annual total ranges (MCP100) and annual core areas (HM50) are also supplied in Table II to allow comparisons with other studies.

Male seasonal core areas had a mean size of 3.7 ± 0.7 km^2, similar to those of females ($F_{(1,8)} = 0.208$, $P = 0.665$). This intensively used area represents a reduced part of the seasonal home range (36.6 ± 4.5%, as average). Males seem not to change the way they use their core areas through the year, as indicated by the absence of significant seasonal variations of this percentage ($F_{(2,8)} = 0.453$, $P = 0.651$).

TABLE II

Average size (km^2 ± S.E.) of the seasonal and annual home ranges (MCP95), total ranges (MCP100) and core areas (HM50) of resident lynxes. Extreme values of seasonal MCP95 for each sex are marked in bold. Weighted averages by individuals are presented (N = number of seasonal periods for each individual; ***n*** *= number of individuals).*
** = Low number of fixes during a year prevented reliable annual home range estimations*

		SEASONAL							ANNUAL		
				MCP95							
INDIV.		N	Number of fixes (x̄ ± S.E.)	(x̄ ± S.E.)	MIN.	MAX.	MCP100 (x̄ ± S.E.)	HM50 (x̄ ± S.E.)	MPC95 (x̄ ± S.E.)	MCP100 (x̄ ± S.E.)	HM50 (x̄ ± S.E.)
FEMALES	AF10	16	96 ± 6	6.7 ± 0.8	**1.7**	15.0	9.0 ± 1.1	2.2 ± 0.3	9.7 ± 2.2	13.4 ± 2.0	2.5 ± 0.4
	AF13	9	109 ± 7	5.7 ± 0.7	2.9	8.7	8.0 ± 1.2	2.4 ± 0.6	7.5 ± 1.1	13.7 ± 2.8	2.3 ± 0.3
	AF12	3	105 ± 17	7.6 ± 1.5	4.6	9.4	8.7 ± 1.8	2.6 ± 0.4	8.5	11.7	3.0
	AF36	1	68	5.6	5.6	5.6	6.5	2.3	—*	—*	—*
	AF18	3	102 ± 23	18.1 ± 1.9	14.0	**21.0**	25.9 ± 1.3	6.6 ± 1.2	24.6	42.6	5.5
	MEAN	*n* = 5	96 ± 7	8.7 ± 2.4			11.6 ± 3.6	3.2 ± 0.8	12.6 ± 4.0	20.4 ± 7.4	3.3 ± 0.7
MALES	AM23	3	100 ± 14	6.0 ± 0.7	**5.3**	7.3	8.2 ± 0.9	2.0 ± 0.1	8.5	12.4	2.3
	AM15	4	76 ± 5	7.9 ± 0.9	5.5	9.5	11.3 ± 1.3	2.2 ± 0.2	11.8 ± 0.6	18.6 ± 3.8	3.5 ± 0.4
	AM01	4	80 ± 9	8.7 ± 0.9	6.4	10.7	11.7 ± 1.9	4.2 ± 0.7	22.3 ± 10.4	31.2 ± 10.2	4.5 ± 0.3
	AM17	3	106 ± 22	12.3 ± 3.1	6.5	17.3	15.8 ± 1.2	5.5 ± 1.2	17.0	26.1	5.1
	AM25	2	62 ± 2	16.7 ± 5.1	11.6	**21.8**	30.9 ± 14.1	4.7 ± 2.5	25.0	34.8	5.9
	MEAN	*n* = 5	85 ± 8	10.3 ± 1.9			15.6 ± 4.0	3.7 ± 0.7	16.9 ± 3.1	24.6 ± 4.1	4.3 ± 0.6

TABLE III

Average daily distance travelled (DIST), defendability index (DI) and daily home range patrolling by adult resident individuals. Average daily distances travelled were estimated as the sum of distances between hourly locations during 24-hour radio-tracking sessions; DI as the ratio between DIST and the seasonal home-range axis length, supposed to be circular and patrolling as the percentage of the seasonal home range (MCP95) covered in each session of intensive radio-tracking of 24h (daily minimum convex polygon)

Individual	Number of 24h sessions	DIST $\bar{x} \pm$ S.E. (km)	DI $\bar{x} \pm$ S.E.	Patrolling $\bar{x} \pm$ S.E. (%)
FEMALES				
AF10	10	5.7 ± 0.5	2.85 ± 0.34	18.6 ± 3.8
AF13	7	7.1 ± 0.5	1.62 ± 0.45	21.7 ± 8.2
Average		**6.4 ± 0.7**	**2.74 ± 0.12**	**20.2 ± 1.6**
MALES				
AM01	15	9.2 ± 0.9	2.68 ± 0.25	39.4 ± 4.0
AM23	4	8.2 ± 0.9	3.17 ± 0.33	37.8 ± 6.6
Average		**8.7 ± 0.5**	**2.93 ± 0.25**	**38.6 ± 0.8**

As a measure of extraterritorial activity, we have considered the proportion of the total range (MCP100) not contained in the MCP95. The weighted average of this proportion for five males is 28.9 ± 3.5%. Males engaged in this explorative activity equally throughout the year, since no significant changes among seasons existed ($F_{(2,8)} = 0.287$, $P = 0.758$; proportions arcsin-transformed).

The home ranges of males overlapped an average of 15.1 ± 6.5% ($N = 20$ dyads), 75% of the cases being less than 20%. The cases with higher overlap were interpreted as the results of interactions between neighbouring resident males, and they always lasted less than four months (see below). The

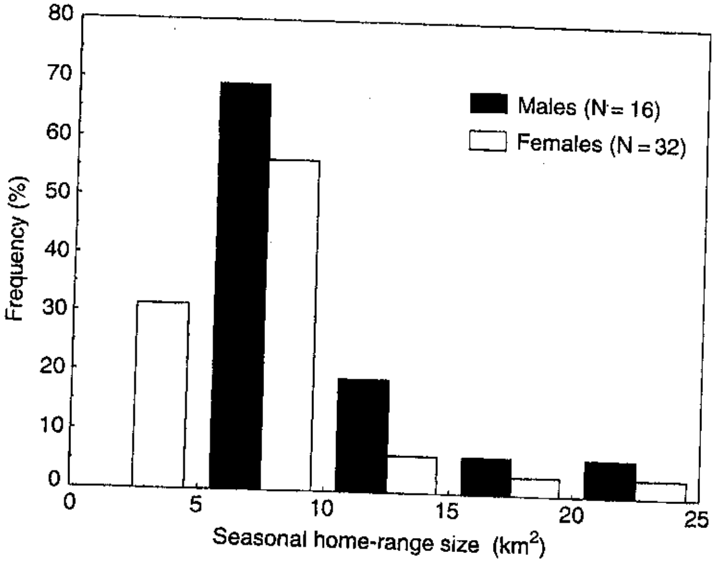

FIG. 4. Frequency distribution of seasonal home-range sizes (minimum convex polygon of 95% of locations) for adult resident females and males. N represents the total number of individual-season cases for each sex.

season of the year had no significant effect on the overlap between males ($F_{(2,17)} = 0.861$, $P = 0.440$, percentages arcsin-transformed). As with the females, the core areas of the males' home ranges were highly exclusive, and the average overlap percentage between adjacent males was 4.4 ± 2.1 ($n = 20$).

The values of the defendability index for two resident males were, on average, greater than one (2.68 ± 0.25 and 3.17 ± 0.33 for AM01 and AM23, respectively; Table III). Therefore, their home ranges could be defended through their daily movements (average daily distance travelled 8.7 ± 0.5 km, $n = 2$ males). On the other hand, resident males covered daily a higher proportion of their home range (38.6 ± 0.8%) than females (20.2 ± 1.6%, $t = 9.39$, 2 *d.f.*, $P = 0.011$, arcsin-transformed percentages), which indicates a greater patrolling activity of the males (Table III).

Territory acquisition and loss

The observed mechanisms of territory acquisition by adult females were: a) to expel an established female from her territory and take it over; b) to inherit her mother's territory; c) to fill a vacancy left by a dead female; and d) to disperse and settle in a vacant area not currently occupied far from the natal range. Males were seen to establish or expand their home ranges in three ways: a) to occupy empty peripheral territories after dispersing from the natal area; b) to settle in an empty territory due to the death of a resident male; and c) to expel a resident adult male from his territory and to take it over.

Female AF10 first acquired a territory in May 1986 after expelling AF12 from her territory (Fig. 5). This female (AF10) subsequently acquired a new territory by a different mechanism, inheriting her mother's (AF13) territory when she died in autumn-winter 1988. Female AF35 established residency in a marginal area of Doñana, in October 1991, after dispersing 23 km from her natal area. Female AF33 first became resident in a suboptimal area surrounding the vera optimal habitat in August 1991, after dispersing 5 km from her natal area.

Three males (AM08, AM21 and AM25), previously captured and followed as either juvenile or subadults, acquired a territory far away from their natal area after dispersing. Moreover, male AM29, first captured during his dispersal process, established as a resident 27 km from his first capture location. Dispersal seems, therefore, a common mechanism by which males acquire their first territory. A special result of dispersal is the establishment of a territory in suboptimal areas surrounding the 'vera' optimal habitat, as recorded for AM25. Another adult male (AM15) enlarged his territory in winter 1990–91, when he took over the vacant territory of a dead resident male (AM23; see Fig. 6).

Age of first acquisition of a territory for three females was: 25 months old for AF10 and AF33 and about 24 months old for AF35 (the last one followed in a northern marginal nucleus of the population). The age at which males first acquired territories is known in four cases: AM08 AM21, AM25 and AM29 established after dispersing when they were 24, 25, 26 and 29 months old, respectively.

Females successively occupying the same territory used it in a similar way. After AF10 replaced AF12, in spring 1986, her home range coincided extensively (70.4%; index of Cole, 1949) with the previous home range of AF12. Similarly, the home range of AF13 in spring 1988 was occupied by AF10 with high coincidence (77.4%) in spring 1989, after AF13 died in winter 1988. Four males (AM01, AM03, AM15 and AM17) occupied successively the same territory in different periods throughout the study (1983, 1984, 1986 and 1987, respectively). Their home ranges were highly coincident (81.9, 80.8 and 73.0% between consecutive occupiers). This remarkable coincidence between home-range boundaries of successive occupants suggests that territories have defined size and location, independently of their owners. Boundaries between home ranges of neighbouring males, as well as between females, were usually located along significant features of the terrain, such as some sand roads and firebreaks located transversely to the 'vera' optimal habitat. These roads were intensely

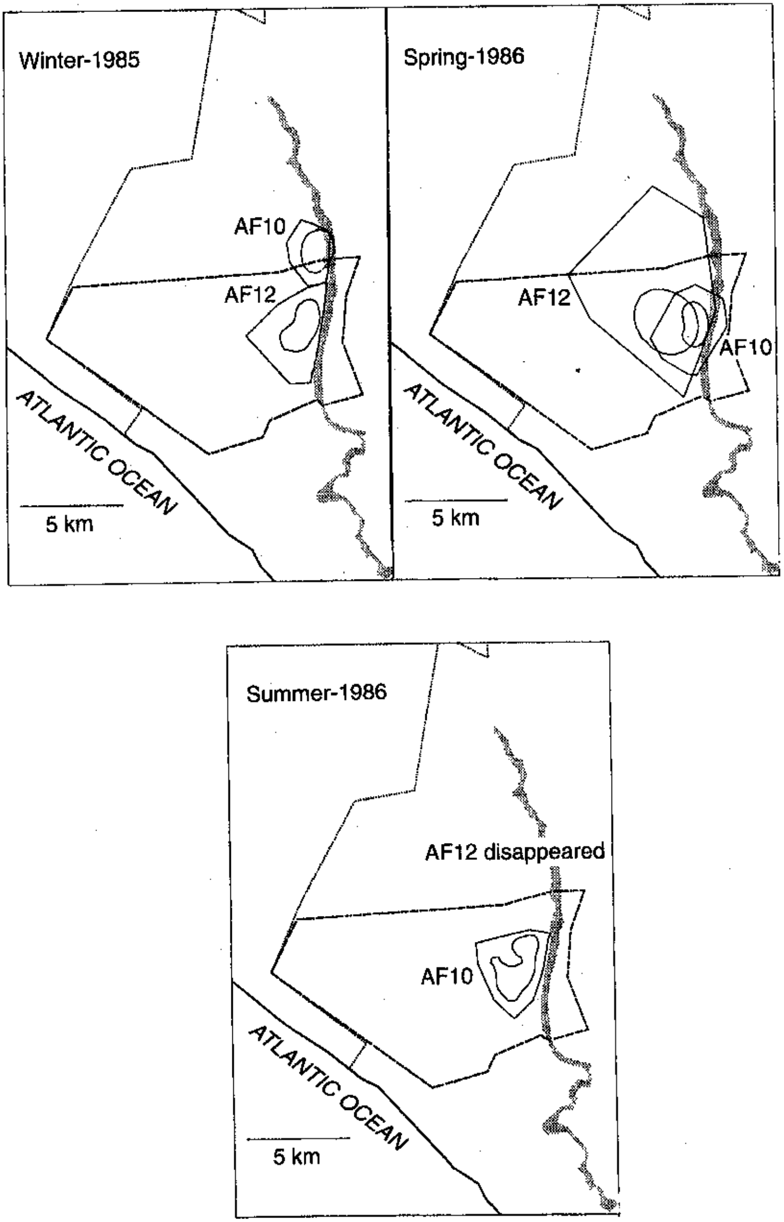

FIG. 5. Spatial interaction between females AF10 and AF12 between winter 1985 and summer 1986. Doñana National Park (dotted line) and Biological Reserve (dashed line) limits are shown as in Fig. 1. Home-range boundaries (as MCP95) and core area (as HM50) are shown for both females. As a result, AF10 displaced AF12 from her territory, and AF12 disappeared from the study area after the interaction.

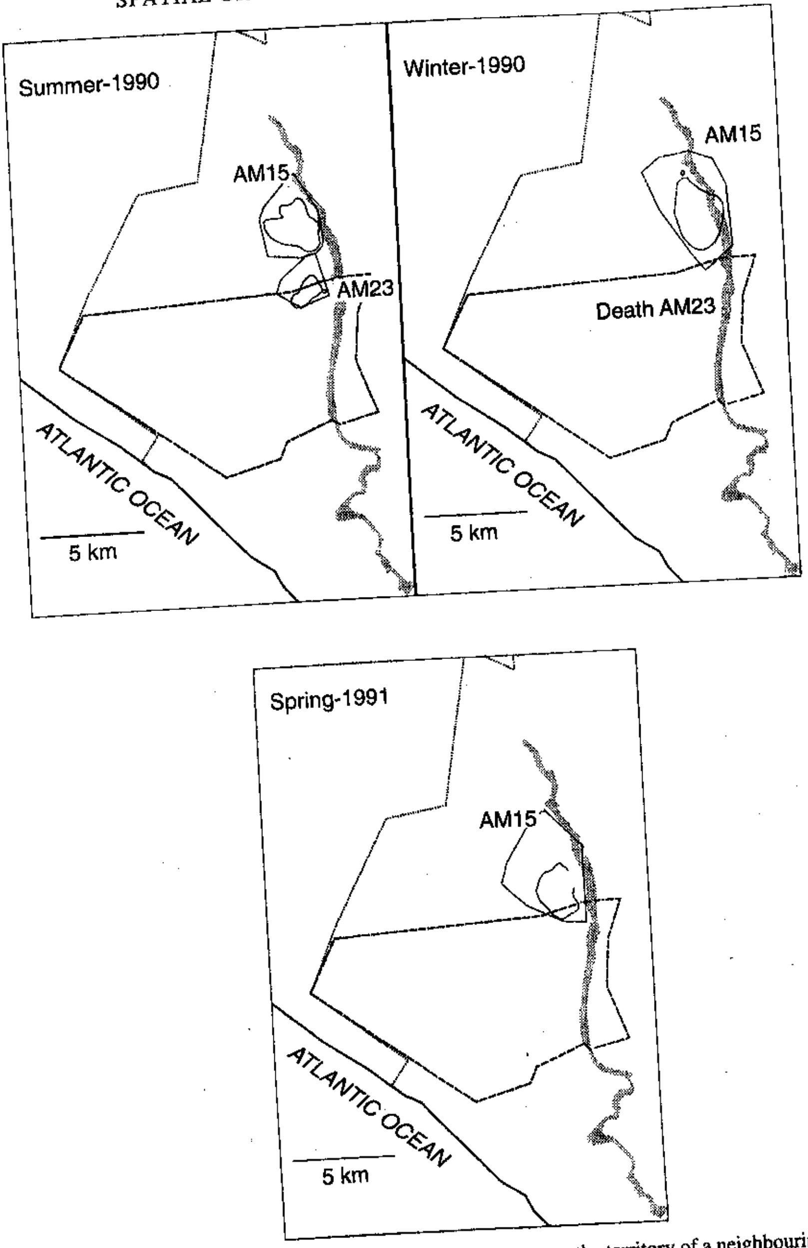

FIG. 6. Enlargement of resident adult male (AM15) territory by taking over the territory of a neighbouring dead resident male (AM23; home-range contours as MCP95; internal lines are core areas as HM50). Doñana National Park (dotted line) and Biological Reserve (dashed line) limits are shown as in Fig. 1. We lost radio-contact with AM23 in September 1990, after he had occupied the same territory for at least one-and-a-half years. In winter 1990–91, when AM23 was presumed to have died (based on the dating of his remains found later), we observed a displacement of AM15's territory which changed to occupy both territories in spring 1991.

marked by both sexes with scats, acting as limits for the neighbouring individuals (Robinson & Delibes, 1988).

The total period of territory occupancy for female AF10, the only one with known dates of tenure, was 5.2 years. For five other females, the minimum occupancy time was 2.3 ± 0.8 years. We know the total period of territory occupancy for male AM21, who died from unknown causes after 1.4 years of tenancy. Partial data for those for whom we do not know the exact time of starting or ending of territory occupancy, indicate some longer times (4.0 years for AM01 and 2.6 for AM15 as minimum occupancy spans). However, the average minimum value is similar to that reported for AM21 (1.5 ± 0.8 years, $n = 9$ individuals). According to these minimum values, annual rate of residence seems to be higher for females (0.74) than for males (0.64). Conversely, annual rate of turnover (probability of territory holder change in a given year) would be faster for males than for females (maximum annual rate 0.36 and 0.26, respectively).

The relatively high levels of overlap between the home ranges of adjacent same-sex residents (see above) were interpreted as the result of land contests, since some of them (five out of nine) ended with the displacement of one of the contestants from its territory (Table IV). Five out of nine interactions started between December and March. The spatial interactions lasted up to six months, those of males being shorter (average 1.7 ± 0.3 months, $N = 3$) than those of females (average 3.8 ± 0.5 months, $N = 6$). These spatial interactions did not necessarily involve direct contact. Only two interacting pairs of females were located in close proximity during the spatial contest (see Table IV). Moreover, two pairs of interacting males (AM15 and AM01, and AM15 and AM16) and one of interacting females (AF36 and AF10), which were never located in close proximity during their interactions, were captured with clear signs of recent fights (Table IV). When AF10 was captured in August 1991, she had injuries to the sides of her forelimbs, probably the result of a fight with another lynx. Since this time coincided with the moment when AF36 intruded on AF10's territory, such injuries were presumably the result of a fight between them. In January 1992, AF10 left her territory which was occupied by AF36 afterwards. Males AM15 and AM01 were captured on 20 February 1986, less than one kilometre from each other, both showing wounds on the outer side of their forelimbs, probably as a result of a recent fight between them. Their home ranges overlapped extensively (Table IV) in February–March 1986, but their exclusive core areas showed a remarkable pattern, with AM01's core area split into two centres of activity, between which was AM15's core area. Their spatial interaction ended in April 1986, when they showed adjacent and exclusive home ranges, that of AM15 keeping the same initial position. A similar spatial pattern of avoidance of core areas was also found in January 1984 during the spatial interaction between AM01 and AM03; AM01's core area was located between the AM03's two distinct activity centres. This interaction ended with the displacement of AM01 by AM03. During the interaction between AM17 and AM16, in March 1987 (Table IV), it is remarkable that AM16, the heaviest male ever captured in Doñana (15.9 kg), was unable to expel AM17 (11.8 kg) from his territory.

Although first acquisition of a territory seems to occur around two years of age for both sexes (see above), the outputs of the contests shown in Table IV indicate that acquisition and successful defence of a territory in the optimal area ('vera' habitat) occur at older ages both for females (3–7 years) and for males (4–7 years). An exceptional case seems to be AF10 who, when two years old, displaced AF12 (about four years old) from her territory.

Access of females to territories and reproduction

Only resident females inhabiting the ecotone between the marsh and the scrubland were observed to breed during the study. Six resident females were monitored by telemetry during 14 reproduction

TABLE IV

Characteristics of the spatial interactions between adult resident individuals of the same sex when competing for territories in the 'vera' optimal area and relationship of dominance between their ages. Ages ranking coding: m >> n : an individual m years old displaced an individual n years old; m > n: an individual m years old was not displaced by an individual n years old

Indiv. A	Age A (years)	Indiv. B	Age B (years)	Month start	Duration (months)	Monthly HR coincidence % range	N Fixes close proximity (Total)	Fight evidence	Result	Ages ranking
FEMALES										
AF10	2	AF12	4	Feb. 86	4	21–44	2 (77)	No	A displaces B	2 >> 4
AF13	7	AF12	4	Feb. 86	3	8–42	0 (93)	No	A not displaced by B	7 > 4
AF10	3	AF18	2	May 87	2	8–22	0 (46)	No	A not displaced by B	3 > 2
AF13	8	AF18	2	Jun. 87	4	2–23	0 (80)	No	A not displaced by B	8 > 2
AF10	4	AF13	9	May 88	6	17–51	6 (114)	No	A displaces B	4 >> 9
AF36	4	AF10	7	Jul. 91	4	7–18	0 (53)	Yes	A displaces B	4 >> 7
MALES										
AM03	8	AM01	7	Dec. 83	2	29–33	0 (59)	No	A displaces B	8 >> 7
AM15	4	AM01	9	Feb. 86	2	18–29	0 (34)	Yes	A displaces B	4 >> 9
AM17	4	AM16	7	Mar. 87	1	33	0 (26)	Yes	A not displaced by B	4 > 7

periods. Moreover, we obtained additional information about their reproduction during previous years through observation of juveniles or subadults occupying their home range and meeting them occasionally, which was interpreted as son–mother bonds. During a total of 16 reproduction-years, the six females combined bred on six occasions (Table V). Moreover, AF10 apparently failed to breed in spring 1990, after she had been in an advanced state of pregnancy, possibly due to an abortion or to the early litter death. Apart from that, she successfully raised two cubs (JF27 and JF28) to independence in 1989. Female AF02 bred in 1983 and successfully raised at least two cubs (JM04 and JF07), according to their spatial relationships in winter 1983–84. At least two juveniles were produced by female AF13, both in 1983 (JM06 and another juvenile male captured but not marked) and in 1984 (JF10 and JF11). She also bred successfully in 1985, producing at least one juvenile (JM14) and in 1988, although on the last occasion her two kittens probably died when four months old as a consequence of the sudden death of AF13.

Intersexual relationships and mating system

An analysis of the relationships between adult males and adult females was carried out through the overlap of seasonal home ranges of simultaneously tracked individuals. Home ranges of adult females were overlapped on average 73.4% ± 5.1 ($N = 22$ female × season) by the area of one male. All the females' home ranges were overlapped by the range of a male by at least 30%, and in 77% of the cases the percentage of overlap was more than 50%. A large percentage of each male home range usually overlapped one female, although it commonly overlapped secondarily with other females. There were no significant differences between season of the year in intrasexual overlapping ($F_{(2,19)} = 0.206$, $P = 0.816$, percentages arcsin-transformed).

The core areas of females were overlapped by 39.5 ± 7.1% ($N = 22$ female × season), on average,

TABLE V

Reproduction of female Iberian lynxes in Doñana between 1983 and 1992. RT: Radio telemetry. [1] AF10 failed to breed in 1990 after being pregnant. [2] AF13 gave birth in 1983 to JM06 and another male, captured but not marked. [3] AF13 produced two kittens in 1988 but they died after AF13's sudden death

Female	Year	RT	Breeding	Juveniles in winter
AF02	1983	+	+	JM04, JF07
AF10	1986	+	—	
	1987	+	—	
	1988	+	—	
	1989	+	+	JF27, JF28
	1990	+	+[1]	—
AF12	1985	+	—	
	1986	+	—	
AF13	1983	—	+	JM06, JM[2]
	1984	—	+	JF10, JF11
	1985	—	+	JM14
	1986	+	—	
	1987	+	—	
	1988	+	+	2 unknown[3]
AF18	1987	+	—	
AF36	1992	+	—	

by the core area of a male. The season of the year did not affect significantly the variation in core area overlap ($F_{(2,19)} = 0.272$, $P = 0.765$, percentages arcsin-transformed).

The coefficient of spatial association (proportion of simultaneous locations closer than 200 m) between resident males and females showed a positive regression with home-range overlap ($F_{(1,38)} = 25.24$, $P < 0.001$, $y = -0.06 + 0.20x$), and core-area overlap ($F_{(1,38)} = 32.20$, $P < 0.001$, $y = 0.22 + 0.20x$, arcsin-transformed variables). In order to isolate the effect of seasonality on the intrasexual association from the variability due purely to variation of home-range overlap, we conducted a stepwise regression including seasons as dummy variables. The model explaining most of the variability ($R^2 = 43.9\%$, $F_{(2,37)} = 16.26$, $P < 0.001$) includes the dummy variable corresponding to summer ($t = 2.186$, 37 *d.f.*, $P = 0.035$). According to this analysis, spatial associations were more frequent in summer than in spring or winter, controlling for the home-range overlap.

The mass of resident adult males does not seem to influence the proportion of spatial associations with females ($F_{(1,20)} = 0.610$, $P = 0.440$). According to this, heavier males seem not to have access to more females than lighter males. However, heavier males had territories closer to the ecotone marsh-scrubland than lighter ones ($r = -0.515$, 14 *d.f.*, $P = 0.041$), and therefore of better quality (rabbit density—lynx main prey—and dense cover decrease as distance to this ecotone increases; Moreno & Villafuerte, 1995). All the radio-tracked females recorded to have bred during this study were established in this ecotone, therefore heavier males also occupied the most productive territories for females.

Male–female interactions are highly flexible and dynamic, as shown in Fig. 7 by the seasonal variation of the percentage of spatial association between males and females. Extreme cases were those of AM17, who in the summer of 1987 was frequently located close to three females and AM23, who between spring of 1989 and summer of 1990 was very frequently associated with a single female.

Discussion

This is the first description of the social organization of the Iberian lynx, being the result of a long-term and intensive study, which Hornocker & Bailey (1986) postulated as the only way to understand the complexity of felid social systems. This kind of study is, however, uncommon in the literature on felids owing to its technical complexity and expense (but see: Smith, McDougal & Sunquist, 1987; Maehr, Land & Roof, 1991; Ross & Jalkotzy, 1992). Few studies on felid social organization are based on such long intensive radio-tracking (10 years with a nearly daily-location basis) of so large a number of individuals, which allowed us to gather valuable data about individual life histories (Eisenberg, 1986). We have shown how the Iberian lynx can be considered as a solitary felid, with associations between individuals being restricted to rearing of young by females and to mating activities among adult lynx. Adult resident home ranges were, in general, exclusive with respect to same-sex individuals, overlapping occurring only when neighbouring individuals apparently competed for the possession of the land. The home ranges of resident males and females home ranges overlapped highly throughout the year.

The Iberian lynx as a solitary felid

Although we could not estimate the frequency of spatial associations of radio-tracked individuals with other untagged individuals, it can be considered as very rare. According to the intensive trapping carried out throughout the study, the proportion of un-marked individuals in the study must be low. The average coefficient of spatial association for the Iberian lynx in Doñana (4.1%) was similar to

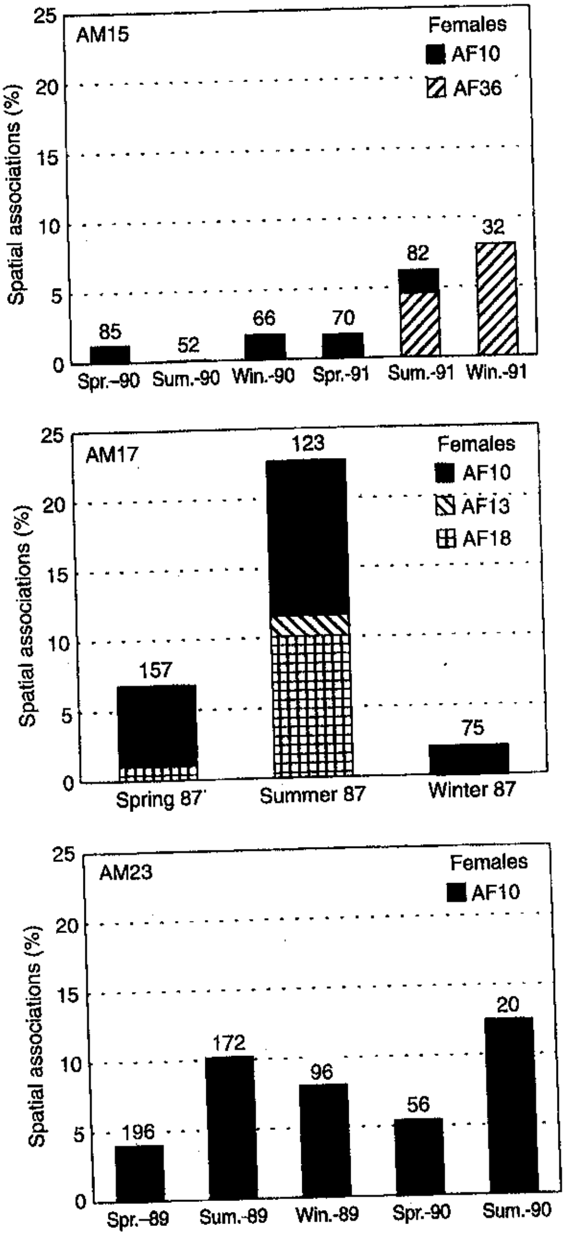

FIG. 7. Seasonal variations of the percentage of spatial association (simultaneous locations less than 200 m apart) between three males (AM15, AM17 and AM23) and those females simultaneously radio-tracked to them. Total number of locations of each male simultaneous to any female during each season are shown above each bar.

those reported by Bailey (1993) for the leopard (*Panthera pardus*, 4–6% in Kruger National Park), which is recognized as a solitary felid. Our values are, on the other hand, lower than those reported for two other solitary felids: the tiger (*Panthera tigris*) in Chitawan National Park (11%, Sunquist, 1981) and the mountain lion (*Puma concolor*) in Idaho (10%, Seidensticker *et al.*, 1973). The RCE index also supports the solitariness of the Iberian lynx, the values obtained being similar to those reported by Seidensticker *et al.* (1973) for the mountain lion. The Iberian lynx most closely related felid species, the bobcat (*Lynx rufus*), the Eurasian lynx and the Canadian lynx (*Lynx canadensis*) are also generally accepted to be solitary (Bailey, 1974; Anderson, 1987; Breitenmoser *et al.*, 1993*a*; Poole, 1995).

Multiple associations occasionally occurred in the population in special circumstances, when several individuals shared large prey (Aldama & Delibes, 1991). However, it seems reasonable that these multiple associations probably only occur among directly related individuals. Bailey (1974) reported a multiple association of two adult males and two female bobcats, supposedly not related, in a rocky refuge during inclement weather conditions, which made cover extremely scarce in the area.

According to their low interaction index, contacts between adults are infrequent even between individuals of different sex (2.2% of simultaneous locations), in which case they are probably limited to those associated with reproduction. Hemker, Lindzey & Ackerman (1984) reported a similar figure (1.8%) of association between adult mountain lions in Utah.

Home ranges; is the Iberian lynx a territorial species?

The observed values of intrasexual overlap of seasonal home ranges were in some cases higher than 10%, the value proposed by Sandell (1989) as maximum for considering two home ranges exclusive. However, we have shown for the Iberian lynx through the monthly analysis how this high overlap usually lasted only a few months and how it corresponded to unstable agonistic interactions, which usually ended with the displacement of one of the interacting individuals (Table IV). This brings to question the validity of Sandell's (1989) figure of home-range overlap as a territoriality criterion considered alone, in short-term studies, or when individuals are tracked on a low-frequency location basis. We also warn about the limitation of such short-term studies as a method for describing complete social systems in carnivores, although we concede they are sometimes the only feasible way to obtain basic information. Although low overlapping between same-sex neighbours has been repeatedly proposed as a clear index of territoriality in solitary felids (Seidensticker *et al.*, 1973; Smith *et al.*, 1987; Bailey, 1993), other factors must also be considered when trying to determine the existence of territoriality. The high values of the defendability index, always above unity (Table III) means, according to Mitani & Rodman (1979), that lynxes would be able to defend their territories through their mere daily movements. Scent-marking has been described as a means of individual advertisement and avoidance in felids (Smith, McDougal & Miquelle, 1989; Mellen, 1993) and in mammals in general (Richardson, 1993). In the Iberian lynx, Robinson & Delibes (1988) showed how scent-marking with faeces is a potentially effective system of advertizing the presence of the territory owners to competitors and it would act as a complement to the patrolling as a mechanism of territory defence. Both scent-marking and active patrolling seem to be necessary to defend the territories effectively, owing to the high intraspecific pressure in the saturated optimal area. During this study, we have observed adult males and females marking with urine along sand pathways when travelling, and fixed stations of marking with faeces which were periodically renewed. The defence of the territories in most felid species is also based on scent-marking, the aggressive encounters between potential competitors being unusual (Griffith & Fendley, 1986; Sandell, 1989). However, for large felid species, avoidance and aggressive behaviour have also been reported as characteristics of territorial systems (Seidensticker *et al.*, 1973, for the mountain lion; Smith *et al.*, 1987, for the tiger; Maehr *et al.*, 1991 for the Florida panther, *Puma concolor coryi*, Bailey, 1993, for the leopard). The three fights between adult individuals of the same sex reported during the present study show how aggressive behaviour occurs in the population associated with territorial contests. In addition to these fights, a female radio-tracked during this study (AF33) was later found dead, with wounds indicating that she had died from a fight (Fedriani, Ferreras & Laffitte, 1995). The explanation of these unusual aggressive encounters between Iberian lynxes is perhaps related to the particular conditions observed in the Doñana lynx population. Owing to the limitation of the optimal habitat for the species in the study area to the ecotone between the scrubland and the marshland ('vera'), adult lynxes suffer high competition for the best territories. This can be the cause of the high intrasexual overlap levels and the relatively high frequency of aggressive encounters. Prior rights in the studied population seem useless as a means to avoid such encounters, as opposed to other Felidae studies (Seidensticker *et al.*, 1973; but see Smith *et al.*, 1987). The same argument of limited opportunities for territory in a confined area was proposed by Maehr *et al.* (1991) to explain intraspecific strife in the Florida panther. However, prior rights seem to have a role in gaining and maintaining territories, as supported by the case of AM16, the heaviest male lynx ever trapped during the study (15.9 kg), who was unable to displace AM17 (11.8 kg) from his territory and was obliged to leave the optimal area (see Table IV).

As shown in the results, many criteria for territoriality were found to occur in the studied population, and the spatial organization of the Iberian lynx in Doñana, therefore, can be classified as territorial.

Minimum values of female home-range size during the first months of raising cubs has been reported previously for bobcats (Zezulak, 1980), mountain lions (Hemker *et al.*, 1984), tigers (Sunquist, 1981), servals (*Leptailurus serval*, Geertsema, 1985) and ocelots (*Leopardus pardalis*, Laack, 1991). In all these studies, females reduced their movements to a small area around the den in order to protect and frequently feed their kittens. This can also be the cause of the small proportion of the home range contained in the core area during spring, the period in which kitten raising mainly occurs (Aldama, 1993).

The greater home-range overlap of females in spring could also be related to birth and raising of cubs (Aldama, 1993). Breeding females reduce their patrolling activities during lactation and weaning breeding phases (Aldama, 1993). Other females could profit from this situation, trying to take over the territories of the breeding females, and resulting in high home-range overlap.

The fact that we have not detected the reproduction of any non-resident female seems to support the hypothesis that only resident females can reproduce successfully. On the other hand, reproduction by resident females was not observed in some years during their radio-tracking, which means that being resident is not enough for a female to reproduce and other factors must influence the process, such as variations in prey availability between years.

Assuming that females adjust their home-range size to their energetic requirements, as generally accepted in solitary felids (Sandell, 1989), we have tested whether males do so or, if other factors affect male home-range sizes (e.g. a tendency to access to more females). Since metabolic home-range size (home-range size/weight$^{0.75}$; Litvaitis, Sherbourne & Bissonette, 1986) was similar for both sexes ($1.57 \pm 0.32\,\mathrm{km}^2/\mathrm{kg}^{0.75}$, weight $= 12.9 \pm 0.8$ kg, $n = 5$ males; $1.57 \pm 0.39\,\mathrm{km}^2/\mathrm{kg}^{0.75}$, weight $= 10.0 \pm 0.1$ kg, $n = 5$ females; Mann–Whitney test $U = 13$, $P = 0.999$), no other factor seems to be necessary to explain the small differences observed between male and female home-range sizes in the study area.

The territories of males, despite small variations in size, are maintained throughout the year without significant differences between seasons, perhaps because it is not advantageous to increase the home range during the mating season, as sometimes happens in other species of carnivores (Erlinge & Sandell, 1986). Seasonal variations of staple prey of lynxes seem not to induce significant changes in male home-range size, perhaps because such size is adjusted to the requirements during the season with the lowest prey density. As another possible explanation of constant male home-range sizes throughout the year, the mating season in the study area may not be predictable enough to make profitable an increase of the home range in a specific period of the year, as supported by the records of new-born litters almost throughout the year. However, according to Beltrán (1988), a detailed analysis of the monthly variations of home-range size for two adult males yielded significant variations throughout the year, although these results agree with the tendency observed in our study (not significant) to larger home ranges in spring.

The most frequent mechanisms of access to the territories by males and females are also affected by the saturation of the population, where vacant territories are uncommon. This is probably due to the high survival rate of the resident adult animals (Ferreras *et al.*, 1992). In this situation, the establishment after the dispersal process away from the natal area (as reported for AM08, AM21, AM29 and AF35) is a possible way of acquiring a vacant territory. Dispersing individuals can also temporarily settle in peripheral suboptimal areas, waiting for a vacancy in the main nucleus, while they reach the required body condition to contest the established residents successfully, as described for AM25 and previously reported for tigers (Sunquist, 1981) and wolves (Packard & Mech, 1983). Other, apparently common, mechanisms of acquisition of a territory involve spatial interaction with territory owners, and sometimes physical contact (fights) with the defendant, as reported for AM01 and AM15 in February 1986, and for AF10 and AF36 in August 1991. Smith *et al.* (1987) found displacement of previous territory owners as a common mechanism of acquisition of a territory by tigresses, and even reported a female who expelled her mother from her territory after being settled next to it for two years, a case similar to that of AF10 and her mother, AF13. Emmons (1988) also described a displacement of an old female ocelot by her middle-aged daughter who had previously established a territory adjacent to her mother's, but during the 6 or 7 months they were next door, they never met. Inheritance of the mother's territory is a mechanism of acquisition by females, although this seems to be less common in our study population (one case during 10 years) than in other solitary felids, as in an unhunted mountain lion population in southern Utah, where 5 out of 10 resident female replacements were by their independent daughters (Laing & Lindzey, 1993). A female inheriting her mother's territory can profit from familiarity with the territory where she was raised, as shown by female AF10 who bred for the first time in spring 1989 when she occupied her mother's previous territory, and showed a pattern of space use similar to that of AF13 before she died. AF10 even gave birth in a den used by AF13 for the same purpose, and perhaps where AF10 herself was born.

Age of first acquisition of a territory for both males and females (about 2 years old) seems to occur at the start of their physiological reproductive capacity (Aldama, 1993). However, acquisition and successful defence of a territory in the 'vera' optimal area is delayed both for females (3–7 years) and for males (4–7 years; see Table IV), which is probably related to the saturation of reproductive territories.

Periods of territory occupancy for Iberian lynx in Doñana (18 and 28 months, average minimum for males and females, respectively) were shorter than those reported for the core area of a reintroduced and expanding population of Eurasian lynx in the Swiss Jura mountains (average minimum of 28 and 33 months, respectively; Breitenmoser *et al.*, 1993*a*). Moreover, replacement of resident lynxes resulted usually from human factors and territorial contests were not reported for Swiss lynxes, perhaps because home ranges were much larger than in our study (264 and 168 km^2 vs. 10.3 and 8.7 km^2, for males and females in Switzerland and Doñana, respectively), making less likely the encounter between neighbouring lynxes.

The social organization of the Iberian lynx may be described as a dynamic land-tenure system, based on prior residency rights, possibly acting as a mechanism of density regulation, as described for untrapped populations of bobcat (Bailey, 1974), mountain lion (Seidensticker *et al.*, 1973; Hemker *et al.*, 1984), tiger (Sunquist, 1981) and Canadian lynx (Poole, 1995). A difference of the Iberian lynx system with those previously described is that prior residency rights seem sometimes not to be enough to prevent fights between the owner and the contender (but see AM17–AM16 case in **Results**), which can eventually decide who will own the territory afterwards.

Intersexual relationships and mating system

The degree of home-range overlap and the proportion of spatial associations between males and females indicate, in general, that the area of each male overlapped extensively with that of a female, with whom he made contact more frequently, and to a lesser extent with those of other neighbouring females. This suggests the existence of a mating system close to monogamy, although some tendency to polygyny was also detected in some males (Fig. 7). This agrees with the adjustment of home-range size to the trophic requirements as shown by similar metabolic home-range size (home-range size/weight$^{0.75}$) for males and females. As we lack information about the fathering of the new-born kittens, we cannot evaluate the efficiency of the monogamous and polygynous strategies employed by the males. This result contrasts with the generalized pattern in other lynx species, which seem to have polygynous systems, where monogyny is seldom reported (Anderson, 1987; Breitenmoser *et al.*, 1993*a*; Poole, 1995). However, Wassmer, Guenter & Layne (1988) reported a similar mating system for bobcats in Florida to that of the lynx in Doñana, where the range of each male contained usually the range of only one female, and they maintained social interactions throughout the year, suggesting that such a relationship could fit Kleiman's (1977) definition of 'facultative monogamy'. The general tendency to a monogamous mating system in our case can be related to the high competition for the best territories (because of the high density) and the constraint of males to have small but defendable territories. This could lead to smaller male territories, corresponding to their trophic requirements, as shown above, resulting in a nearly monogamous system. As a consequence, we propose as a hypothesis to be tested in further studies, that in situations of male saturation, the adjustment of home-range size to trophic requirements could be applied not only to females, as proposed by Sandell (1989), but also to males.

Although there are no seasonal variations in intrasexual home-range overlap, the proportion of spatial associations between males and females are higher in summer, once the effect of home-range overlap is accounted for (Fig. 7). Although not proved to exist in the Iberian lynx, infanticide has been reported in other species of Felidae (lion: Packer *et al.*, 1988; farm cats: Macdonald *et al.*, 1987) and the increase of locations of males in proximity to females in summer could be related to an attempt by the males to avoid infanticide of their fathered cubs by other males. Wassmer *et al.* (1988) provided observations which suggest that a male bobcat kept other males from his female with young, thereby protecting his own young from predation, including cannibalism, from other males.

Body mass of males seems not to be related to total proportion of spatial association with females. However, heavier males own the best territories in the 'vera' habitat, and therefore they have access to the reproductive females. This means that body weight in males is indirectly determining reproductive success. This also agrees with the general pattern described by Sandell (1989) for solitary carnivores, in which females are distributed according to prey and males follow the distribution of the females.

Current research on the Iberian lynx population in Doñana focuses on the consequences of the social system on population dynamics and its implications for population persistence (Gaona *et al.*, In prep.).

The effects on the social system of ongoing processes such as a Lynx Management Plan, operational in the National Park since 1988 (Aymerich, 1992), and the reduction of rabbit populations due to a new disease (Villafuerte *et al.*, 1994) are also under study. Finally, owing to the importance of dispersal as a factor of structuring populations (Smith, 1993) and as the only natural way of connecting this population with others in the future, current research in Doñana is also focused on space use and behaviour during dispersal.

We gratefully acknowledge the suggestions made by C. D. FitzGibbon and the English corrections made by S. H. Cousins. We also acknowledge P. Johnson for helpful support for some statistical analysis. U. Breitenmoser and an anonymous referee critically reviewed and improved the manuscript. We thank R. Laffitte for capturing most of the lynx. This study was funded by Dirección General de Investigación Científica y Técnica (projects 944, PB87–0405 and PB90–1018), and Asociación para la Defensa de la Naturaleza (ADENA-WWF). The first author was provided with two pre-doctoral grants by the Ministerio de Educación y Ciencia and Fundación Caja de Madrid, and one post-doctoral fellowship by the first institution.

REFERENCES

Aldama, J. J. (1993). *Ecología energética y reproductiva del lince ibérico (**Lynx pardina**, Temminck 1824) en Doñana*. PhD thesis, Complutense University, Madrid.

Aldama, J. J. & Delibes, M. (1991). Observations of feeding groups in the Spanish lynx (*Felis pardina*) in the Doñana National Park, SW Spain. *Mammalia* **55:** 143–147.

Anderson, E. M. (1987). *A critical review and annotated bibliography of literature on the Bobcat*. Colorado: Colorado Division of Wildlife.

Aymerich, M. (1992). Management of a lynx population in the Doñana National Park. In *The situation, conservation needs, and reintroduction of Lynx in Europe. Environ. Encounters* No. 11: 33–35. Convention on the Conservation of European Wildlife and Natural Habitats. Strasbourg: Council of Europe Press.

Bailey, T. N. (1974). Social organization in a Bobcat population. *J. Wildl. Manage.* **38:** 435–446.

Bailey, T. N. (1993). *The African leopard: Ecology and behavior of a solitary felid*. New York: Columbia University Press.

Beier, P. (1993). Determining minimum habitat areas and habitat corridors for cougars. *Conserv. Biol.* **7:** 94–108.

Beltrán, J. F. (1988). *Ecología y conducta espacio-temporal del lince ibérico, **Lynx pardina** Temminck 1824, en el Parque Nacional de Doñana*. PhD thesis, University of Sevilla.

Beltrán, J. F. (1991). Temporal abundance pattern of the wild rabbit in Doñana, SW Spain. *Mammalia* **55:** 591–599.

Beltrán, J. F., Aldama, J. J. & Delibes, M. (1992). Ecology of the Iberian lynx in Doñana, southwestern Spain. In *Global trends in wildlife management*: 331–334. Bobek, B., Perzanowski, K. & Regelin, W. (Eds). Krakow–Warszawa: Swiat Press.

Beltrán, J. F. & Delibes, M. (1991). Ecología trófica del lince Ibérico en Doñana durante un período seco. *Doñana Acta Vertebr.* **18:** 113–122.

Beltrán, J. F. & Delibes, M. (1993). Physical characteristics of Iberian lynxes (*Lynx pardinus*) from Doñana, Southwestern Spain. *J. Mammal.* **74:** 852–862.

Beltrán, J. F. & Delibes, M. (1994). Environmental determinants of circadian activity of free-ranging Iberian lynxes. *J. Mammal.* **75:** 382–393.

Breitenmoser, U., Kavczensky, P., Dötterer, M., Breitenmoser–Würsten, C., Capt, S., Bernhart, F. & Liberek, M. (1993*a*). Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. *J. Zool. (Lond.)* **231:** 449–464.

Breitenmoser, U., Slough, B. G. & Breitenmoser-Würsten, C. (1993*b*). Predators of cyclic prey: is the Canada lynx victim or profiteer of the snowshoe hare cycle? *Oikos* **66:** 551–554.

Brown, J. L. (1975). *The evolution of behavior*. New York: Norton, W. W. & Co. Inc.

Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* **1:** 239–262.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24:** 346–352.

Caro, T. M. (1994). *Cheetahs of the Serengeti plains: group living in an asocial species*. Chicago: University of Chicago Press.

Caro, T. M. & Collins, D. A. (1987). Male cheetah social organization and territoriality. *Ethology* **74:** 52–64.

Clark, C. K. & Evans, F. E. (1954). Distance to nearest neighbour as a measure of spatial relationship to populations. *Ecology* **35:** 445–453.

Cole, L. C. (1949). The measurements of interspecific association. *Ecology* **30:** 411–424.

Delibes, M. (1980). Feeding ecology of the Spanish Lynx in the Coto Doñana. *Acta Theriol.* **25:** 309–324.

Delibes, M. & Beltrán, J. F. (1986). Radio-tracking of six species of carnivores in the Doñana National Park, S W Spain. *Mesogée* **46:** 113–120.

Dixon, K. R. & Chapman, J. A. (1980). Harmonic mean measure of animal activity areas. *Ecology* **61:** 1040–1044.

Eisenberg, J. F. (1986). Life history strategies of the Felidae: variations on a theme. In *Cats of the world: biology, conservation and management*: 293–303. Miller, S. D. & Everett, D. D. (Eds). Washington, D.C.: National Wildlife Federation.

Emmons, L. H. (1988). A field study of ocelots (*Felis pardalis*) in Peru. *Rev. Ecol. Terre Vie* **43**: 133–157.

Erlinge, S. & Sandell, M. (1986). Seasonal changes in the social organization of male stoat, *Mustela erminea*: An effect of shifts between two decisive resources. *Oikos* **47:** 57–62.

Fedriani, J. M., Ferreras, P. & Laffitte, R. (1995). Iberian lynx dead in Doñana by an intraspecific attack. *Quercus* **Apr. 1995:** 19.

Ferreras, P. (1994). *Patrones de dispersión del lince ibérico (**Lynx pardina**) en Doñana e implicaciones para su conservación.* PhD thesis, Autónoma University, Madrid.

Ferreras, P., Aldama, J. J., Beltrán, J. F. & Delibes, M. (1992). Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck, 1824. *Biol. Conserv.* **61:** 197–202.

Ferreras, P., Aldama, J. J., Beltrán, J. F. & Delibes, M. (1994). Immobilization of the endangered Iberian lynx with Xylazine- and Ketamine- hydrochloride. *J. Wildl. Dis.* **30:** 65–68.

Gaona, P., Ferreras, P. & Delibes, M. (In prep.). Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*).

Geertsema, A. A. (1985). Aspects of the ecology of the serval *Leptailurus serval* in the Ngorongoro Crater, Tanzania. *Neth. J. Zool.* **35:** 527–610.

Griffith, M. A. & Fendley, T. T. (1986). Influence of density on movement behaviour and home range size of bobcats on the Savannah River Plant. In *Cats of the world: biology, conservation and management*: 261–275. Miller, S. D. & Everett, D. D. (Eds). Washington, D.C.: National Wildlife Federation.

Harris, S., Cresswell, W. J., Forde, P. G., Trewella, W. J., Woollard, T. & Wray, S. (1990). Home-range analysis using radio-tracking data—A review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* **20:** 97–123.

Hemker, T. P., Lindzey, F. G. & Ackerman, B. B. (1984). Population characteristics and movement patterns of Cougars in Southern Utah. *J. Wildl. Manage.* **48:** 1275–1284.

Honacki, J. H., Kinman, K. E. & Koeppl, J. W. (1982). *Mammal species of the world: a taxonomic and geographical reference.* Kansas, U.S.A.: Allen Press, Inc. and Association of Systematics Collections.

Hopkins, R. A., Kutilek, M. J. & Shreve, G. L. (1986). Density and home range characteristics of mountain lions in the Diablo Range of California. In *Cats of the world: biology, conservation and management*: 223–235. Miller, S. D. & Everett, D. D. (Eds). Washington, D.C.: National Wildlife Federation.

Hornocker, M. G. & Bailey, T. N. (1986). Natural regulation in three species of felids. In *Cats of the world: biology, conservation and management*: 211–220. Miller, S. D. & Everett, D. D. (Eds). Washington, D.C.: National Wildlife Federation.

Kenward, R. E. (1990). *RANGES IV. Software for analysing animal location data.* Cambridge: ITE NERC.

Kleiman, D. G. (1977). Monogamy in mammals. *Q. Rev. Biol.* **52:** 39–69.

Kleiman, D. G. & Eisenberg, J. F. (1973). Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* **21:** 637–659.

Knick, S. T. (1990). Ecology of bobcats relative to exploitation and a prey decline in Southeastern Idaho. *Wildl. Monogr.* **108:** 1–42.

Kruuk, H. & Moorhouse, A. (1991). The spatial organization of otters (*Lutra lutra*) in Shetland. *J. Zool. (Lond.)* **224:** 41–57.

Laack, L. L. (1991). *Ecology of the ocelot (**Felis pardalis**) in South Texas.* MSc thesis, A & I University, Kingsville, Texas.

Laing, S. P. & Lindzey, F. G. (1993). Patterns of replacement of resident cougars in Southern Utah. *J. Mammal.* **74:** 1056–1058.

Leyhausen, P. (1965). The communal organization of solitary mammals. *Symp. zool. Soc. Lond.* No. 14: 249–263.

Litvaitis, J. A., Sherbourne, J. A. & Bissonette, J. A. (1986). Bobcat habitat use and home range size in relation to prey density. *J. Wildl. Manage.* **50:** 110–117.

Macdonald, D. W., Apps, P. J., Carr, G. M. & Kerby, G. (1987). Social dynamics, nursing coalitions and infanticide among farm cats, *Felis catus. Adv. Ethol. (Suppl. to Ethology)* **28:** 1–64.

Maehr, D. S., Land, E. D. & Roof, J. C. (1991). Social ecology of Florida Panthers. *Res. Explor.* **7:** 414–425.

Mellen, J. D. (1993). A comparative analysis of scent-marking, social and reproductive behavior in 20 species of small cats (*Felis*). *Am. Zool.* **33:** 151–166.

Mitani, J. C. & Rodman, P. S. (1979). Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav. Ecol. Sociobiol.* **5:** 241–318.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37:** 223–249.

Moreno, S. & Villafuerte, R. (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biol. Conserv.* **73:** 81–85.

Morrison, J. A. & Menzel, E. W., Jr (1972). Adaptation of a free-ranging rhesus monkey group to division and transplantation. *Wildl. Monogr.* **31:** 1–78.

Nowell, K. & Jackson, P. (1996). *Wild Cats. Status survey and conservation action plan.* Gland, Switzerland: IUCN.

Odum, E. P. & Kuenzler, E. J. (1955). Measurement of territory and home range size in birds. *Auk* **72:** 128–137.

Packard, J. & Mech, L. D. (1983). Population regulation in wolves. In *Proceedings of the Symposium on Natural Regulation of Wildlife Populations* **1978:** 151–174. Bunnell, F. L., Eastman, D. S. & Peek, J. M. (Eds). Moscow: Forest Wildlife and Range Experiment Station, and University of Idaho.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hánby, J. P., Cairns, S. J. & Borgerhoff-Mulder, M. (1988). Reproductive success of Lions. In *Reproductive success: Studies of individual variation in contrasting breeding systems*: 363–383. Clutton-Brock, T. H. (Ed.). Chicago: University of Chicago Press.

Palomares, F., Rodríguez, A., Laffitte, R. & Delibes, M. (1991). The status and distribution of the Iberian Lynx *Felis pardina* in Coto Doñana Area, SW Spain. *Biol. Conserv.* **57:** 159–169.

Poole, K. G. (1995). Spatial organization of a lynx population. *Can. J. Zool.* **73:** 632–641.

Rau, J. R., Beltrán, J. F. & Delibes, M. (1985). Can the increase of fox density explain the decrease in Lynx numbers at Doñana?. *Rev. Ecol. Terre Vie* **40:** 145–150.

Richardson, P. R. K. (1993). The function of scent marking in territories: a resurrection of the Intimidation Hypothesis. *Trans. R. Soc. S. Afr.* **48:** 195–206.

Robinson, I. H. & Delibes, M. (1988). The distribution of faeces by the Spanish lynx (*Felis pardina*). *J. Zool. (Lond.)* **216:** 557–582.

Rodríguez, A. & Delibes, M. (1992). Current range and status of the Iberian lynx *Felis pardina* Temminck, 1824, in Spain. *Biol. Conserv.* **61:** 189–196.

Rogers, P. M. & Myers, K. (1980). Animal distributions, landscape classification and wildlife management, Coto Doñana, Spain. *J. appl. Ecol.* **17:** 517–542.

Ross, P. J. & Jalkotzy, M. G. (1992). Characteristics of a hunted population of cougars in Southwestern Alberta. *J. Wildl. Manage.* **56:** 417–426.

Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behaviour, ecology and evolution*: 164–182. Gittleman, J. L. (Ed.). London: Chapman & Hall.

SAS Institute Inc. (1988). *SAS/STAT^{TM} User's Guide.* Release 6.03 edn. Cary, NC, U.S.A.: SAS Institute.

Schaller, G. B. (1972). *The Serengeti lion.* Chicago: Chicago University Press.

Seidensticker, J., Hornocker, M. G., Wiles, W. V. & Messick, J. P. (1973). Mountain lion social organization in the Idaho primitive area. *Wildl. Monogr.* **35:** 31–60.

Smith, J. L. D. (1993). The role of dispersal in structuring the Chitwan tiger population. *Behaviour* **124:** 165–195.

Smith, J. L. D., McDougal, C. W. & Miquelle, D. (1989). Scent marking in free-ranging tigers, *Panthera tigris. Anim. Behav.* **37:** 1–10.

Smith, J. L. D., McDougal, C. W. & Sunquist, M. E. (1987). Female land tenure system in tigers. In *Tigers of the world: The biology, biopolitics, management and conservation of an endangered species*: 97–109. Tilson, R. L. & Seal, U. S. (Eds). New Jersey: Noyes Publications.

Sunquist, M. E. (1981). The social organization of Tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal. *Smithson. Contrib. Zool.* No. 336: 1–98.

Valverde, J. A. (1957). Notes écologiques sur le lynx d'Espagne *Felis lynx pardina* Temminck. *Terre Vie Rev. Ecol.* **104:** 51–67.

Valverde, J. A. (1958). An ecological sketch of the Coto Doñana. *Br. Birds* **51:** 1–13.

Valverde, J. A. (1963). *Información sobre el lince español.* Madrid: Ministerio de Agricultura.

Villafuerte, R., Calverte, C., Gortázar, C. & Moreno, S. (1994). First epizootic of rabbit haemorrhagic disease in free living populations of *Oryctolagus cuniculus* at Doñana National Park, Spain. *J. Wildl. Dis.* **30:** 176–179.

Ward, R. M. P. & Krebs, C. J. (1985). Behavioral responses of lynx to declining snowshoe hare abundance. *Can. J. Zool.* **63:** 2817–2824.

Wassmer, D. A., Guenter, D. & Layne, J. N. (1988). Ecology of the bobcat in South Central Florida. *Bull. Fla State Mus. Biol. Sci.* **33:** 159–228.

White, G. C. & Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data.* San Diego–London: Academic Press, Inc.

Zar, J. H. (1984). *Biostatistical analysis.* (2nd edn.). London: Prentice-Hall International.

Zezulak, D. S. (1980). *Northeastern California bobcat study.* Draft final report to Calif. Dept. of Fish and Game, State of California: The Resources Agency.