

DYNAMICS AND VIABILITY OF A METAPOPULATION OF THE ENDANGERED IBERIAN LYNX (*LYNX PARDINUS*)

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Abstract. The use of metapopulation models in conservation biology is growing exponentially, but there is a need for empirical studies that support theoretical approaches, especially for species with large and long-lived individuals. In this paper we explore the viability and dynamics of a real metapopulation of an endangered mammal by combining field work and modeling in order to support conservation decisions and evaluate theoretical approaches. The Iberian lynx (*Lynx pardinus*), considered the most vulnerable felid in the world, is restricted to the Iberian Peninsula in southwestern Europe. The persistence of the species is handicapped by the high fragmentation of its populations. Fewer than 1000 individuals are distributed in nine isolated populations, each of them also fragmented but with their patches connected by dispersers, in what could be called metapopulations. One of these metapopulations, including ~60 individuals, inhabits the Doñana National Park (DNP) and its surroundings. Demographic and behavioral data gathered over one decade for this lynx population were employed to develop a spatially realistic structured model with density-dependent fecundity and migration, including demographic and environmental stochasticity. Such a model is used to identify the demographic features that determine the dynamics of this population and to predict its risk of decline under a set of alternative assumptions. A hypothetical lynx metapopulation with values of the parameters such as those observed in Doñana, but without stochastic events, could sustain itself over time. Results of this deterministic model show how females occupy all the potential breeding territories, while males are below the carrying capacity. The metapopulation has a source-sink structure, with the sources internal and the sinks external to the national park. Sinks result from reduced survival rather than reduced fecundity, as generally assumed. High mortality in sink patches is deterministic, deriving both from within-patch risks and from factors related to the landscape matrix among patches. The survival rate of adults with territories in the sources was the most sensitive parameter, leading the dynamics of the metapopulation. When we include demographic stochasticity in the model, the population becomes extinct 22% of the time within 100 yr, and this value increases to 33.8% when environmental stochasticity is also considered. Most of the metapopulation extinctions occurred because of the disappearance of males due to sex differences in demographic parameters related to behavioral aspects (e.g., dispersal rate). Different scenarios were simulated as modifications affecting either within- or between-patch dynamics. Changes in the carrying capacity of source and sink patches would have very different consequences in terms of metapopulation persistence: one breeding territory increase in the largest source reduces metapopulation extinction risk from 33.8 to 17.2% in 100 yr, while an increase of three territories in the largest sink does not modify the extinction risk. In this sense, results suggest that the best management strategy for conservation should be restoring habitat at the source patches and reducing mortality at the sinks. The results of our models emphasize the need for empirical studies to characterize metapopulations in nature and distinguish between such terms as source-sink, mainland-island, nonequilibrium, or even "refuge" metapopulations.

Key words: *carrying capacity; demographic stochasticity; environmental stochasticity; extinction; Iberian lynx; intrinsic dispersal; landscape matrix; Lynx pardinus; metapopulation dynamics; migration; Population Viability Analysis; protected area; refuge; simulation model; source-sink dynamics.*

INTRODUCTION

The Iberian lynx (*Lynx pardinus*) has been recognized as a separate species from the Eurasian lynx (*Lynx lynx*) (Werdelin 1981, Honacki et al. 1982) and

it is considered the most vulnerable of all the Felidae (top priority for conservation, Nowell and Jackson 1996). It is a medium-size felid inhabiting the southwestern quarter of the Iberian Peninsula (Rodríguez and Delibes 1992). Its world population is below one thousand individuals, distributed in nine spatially and genetically isolated populations (Rodríguez and Delibes 1992). Each population is fragmented into sep-



PLATE. 1. The Iberian lynx. Photo by Antonio Sabater.

arate local populations connected by dispersal (Rodríguez and Delibes 1992). As a result, these populations fit the broad definition of metapopulation (Harrison and Taylor 1997).

The classic metapopulation concept, a set of populations in balance between local extinction and colonization (Levins 1969), has been expanded to include many types of spatially structured populations (Harrison 1991, Hanski and Simberloff 1997, Harrison and Taylor 1997). For instance, it is now usual to refer to nonequilibrium metapopulations, in which local extinction occurs in the course of a species' overall regional decline (e.g., Rolstad 1991, Lindenmayer and Lacy 1995, Hanski 1997), or source-sink metapopulations, in which the dynamics of the sources determines the viability of the complete system (e.g., Wootton and Bell 1992, Donovan et al. 1995, Dias 1996). Anyhow, the fragmentation, reduction, and deterioration of habitats are playing a crucial role in the appearance of new metapopulations, and much of the metapopulation research is being motivated by, and applied to, conservation biology (Hanski and Gilpin 1991).

Studies on metapopulation dynamics are becoming more and more frequent, either giving interesting theoretical information (e.g., Hastings 1991, Howe et al. 1991, Davis and Howe 1992, Hanski and Gyllenberg 1993) or modeling real populations (e.g., Wootton and Bell 1992, Beier 1993, Lindenmayer et al. 1993b, Lamberson et al. 1994, LaHaye et al. 1994, Akçakaya et al. 1995, Doak 1995). However, there is only weak evidence that metapopulation structures are common in nature and the knowledge of metapopulation dynamics in real fragmented landscapes is scarce (Harrison and Taylor 1997), specially for large and long-lived animals. Hence, spatially realistic simulation models

of presumed metapopulations may provide useful guides for theory and sound basis for conservation of charismatic endangered species, provided they are well studied in the field (Doak and Mills 1994).

The best known of the Iberian lynx metapopulations is partially included in the Doñana National Park (hereafter DNP; Southwestern Spain; $\sim 37^\circ$ N, $6^\circ 30'$ W), where field data on the species have been collected for decades (e.g., Valverde 1957, Delibes 1980, Palomares et al. 1991, Ferreras et al. 1992, 1997, Beltrán and Delibes 1993, 1994). In this paper we combined the demographic data and information on size and distribution of local populations to make a spatially realistic model of the Iberian lynx metapopulation in the Doñana area. Our purpose was to assess its dynamics, identify the demographic features that determine this dynamics, and predict its viability and risks of decline in a set of alternative scenarios. The results must be useful to the conservation of the species, but also to evaluate the applicability of theoretical concepts (e.g., source-sink and mainland-island systems, nonequilibrium dynamics, refuge dynamics, etc.) to a real metapopulation of an endangered mammal, and to guide new theoretical analyses on population dynamics in fragmented landscapes.

The Doñana lynx population

This lynx population is patchily distributed on an area of ~ 1500 km² (Palomares et al. 1991). It has been isolated from the rest of the Iberian lynx distribution areas at least for the last 50 yr. Nowadays, the contact with the nearest lynx areas (to the north and to the west) seems very unlikely, since a 50 km wide extension, occupied mainly by croplands to the north, and a 28-km wide strip of human settlements with a wide

river to the west, constitute impenetrable barriers (Rodríguez and Delibes 1992).

Lynx distribution censuses, based on intensive search of signs (e.g., tracks and scats) and validated by intensive radio-tracking, were carried out in winter 1986–1987 (Palomares et al. 1991) and winter 1992–1993 (Estación Biológica de Doñana Carnivore Group, Sevilla, Spain [hereafter EBD-Carnivore Group] unpublished report). Both surveys show a total population of 50–60 individuals distributed in discontinuous patches of suitable habitat, made by Mediterranean shrublands and pine forests with patchy undergrowth. The amount of occupied land was rather similar in 1986–1987 and 1992–1993, but the spatial distribution of the occupied patches changed, suggesting a high turnover (extinction and recolonization) in peripheral patches.

This patchy situation was different before the mid-century, when lynx had a continuous distribution throughout the Doñana area (Valverde 1957). During the last 40 yr several human factors have caused the fragmentation of the original population into the discontinuous patches found today.

Most of the Doñana population currently occupies part of DNP, the most protected area in the whole Iberian lynx range (Fig. 1). Patches inside the park are separated by a “friendly” matrix made by natural and safe habitats with null human population, but unsuitable for lynx (e.g., sand dunes and marshes). The matrix area surrounding the DNP suffers a high human pressure, particularly with agriculture and tourism developments, including highly traveled roads, urban areas, hunting activities, etc. As a consequence, to be included or not in the protected area will determine different demographic parameters for each lynx local population (see *Demographic parameters* section below).

Adult Iberian lynxes weigh 9–15 kg, with males being bigger than females (Beltrán and Delibes 1993). They are active mainly at dusk and dawn (Beltrán and Delibes 1994). Their main prey are rabbits, *Oryctolagus cuniculus* (Delibes 1980, Beltrán and Delibes 1991), and they prefer scrub areas, avoiding marshlands, field croplands, and *Eucalyptus* sp. plantations (Palomares et al. 1991, Beltrán et al. 1992). Associations between adults are highly uncommon; interactions are restricted to rearing activities by females (Ferrerías et al. 1997). Adults are intrasexually territorial, as shown by their exclusive home ranges (Ferrerías et al. 1997) and other behavioral characteristics, such as contests over territories and the use of faeces and urine for territory marking (Robinson and Delibes 1988). Rabbit densities likely determine the size of territories, and therefore carrying capacity of a given area. Possession of a territory seems to be required for adults to reproduce (Ferrerías et al. 1997). Usually when 1 yr old, young males and females (mainly the former) disperse through the matrix seeking a suitable patch (Fer-

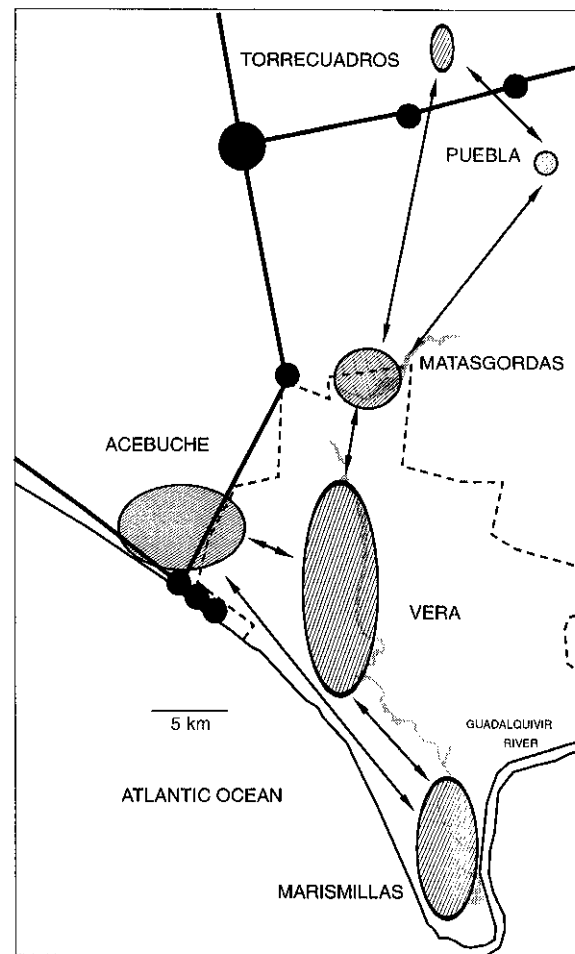


FIG. 1. Spatial distribution of the local populations (shaded areas) making up the Iberian lynx metapopulation of the Doñana area. Arrows indicate migration between local populations, the consequence of dispersal. National park boundaries are marked with dashed lines. Black filled circles represent human settlements, and thick lines represent high-traffic roads.

reras 1994). Adults can also disperse when breeding territories are saturated (Ferrerías 1994). Mortality severely increases during the dispersal process, especially outside DNP (Ferrerías et al. 1992, Ferrerías 1994). Most of the Iberian lynx mortality occurs outside the protected area and is caused by human-related factors such as illegal trapping, road traffic, irrigation wells, and direct killing by poachers, either through gunshots or hound dogs (Ferrerías et al. 1992).

MODEL DESCRIPTION

We developed an age- and space-structured model with density-dependent fecundity and dispersal. Both sexes were included in its formulation, and behavioral aspects and an “Allee effect” (Allee 1931) also were considered. We examined both deterministic and stochastic versions of the model, and both demographic and environmental stochasticities were considered.

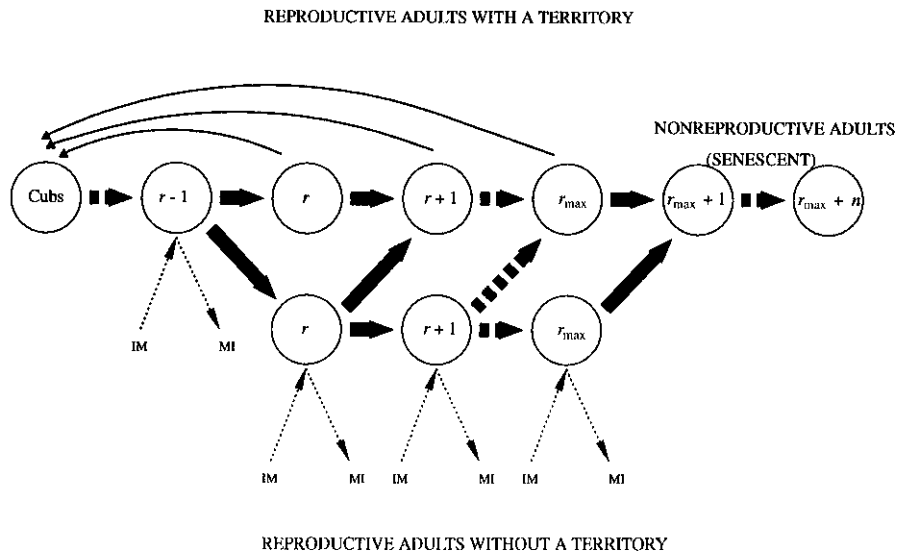


FIG. 2. General life cycle followed in the simulations. Abbreviations are r = age at first reproduction; r_{max} = maximum reproducing age; MI = migrants leaving the age class considered; IM = immigrants joining that age class; and n = maximum number of years a senescent, nonreproductive adult can survive as such. Thick lines represent survival (when dashed, several intermediate age classes can exist in between, depending on the parameter values); thin full lines represent reproduction, and thin dashed lines represent dispersal.

Based on field data (Ferrerás et al. 1997), a minimum and a maximum breeding age were determined for each sex, resulting in three population groups: (a) cubs and juveniles, (b) potentially breeding adults, and (c) senescent, nonbreeding adults. The territorial behavior of lynx limits the number of potential breeders, resulting in a sort of ceiling density dependence for reproduction. When all the available territories in a local population (carrying capacity) were occupied, excess lynxes became part of a floater population without territory. Consequently, we can refer to an age- and stage-structured life history pattern (Fig. 2).

The simulation algorithm in our model was similar for each local population, with differences between them due only to values of the parameters. The formulations for both the deterministic and stochastic versions of the model are summarized in Tables 1 and 2. Environmental stochasticity was incorporated into the model as climatically adverse years in which survival rates are reduced. We assume that climatic variations affect every local population equally, given the small area encompassing the whole metapopulation. Frequency of adverse years was modeled as a normal distribution (see *Demographic parameters* section below). Demographic stochasticity was modeled by sampling the number of survivors, the number of dispersers, the direction of dispersers, and the sex of the cubs from binomial distributions (Akçakaya 1991). The birth process was simulated by generating random numbers to determine the number of reproductive females and the litter size produced for each one (see *Reproduction* below). A simplified statement of the simulation algorithm is as follows.

1. *Annual survival*.—Once the initial parameter values (initial population size, carrying capacities, survival rates, dispersal rates) were read, annual survival was applied. In the stochastic version of the model, survival rates were dependent on environmental stochasticity.

2. *Occupation of vacant territories by individuals of the local population*.—Access to vacant breeding territories for each sex was controlled by a dominance hierarchy based on age and breeding status.

3. *Dispersal*.—Juveniles and adults of both sexes without territories can disperse according to sex- and age-specific density-dependent functions, which are defined below in the *Demographic parameters* section.

4. *Survival and allocation of dispersers*.—The probability of the different local populations being a dispersal destination was dependent on the local population of origin. The stochastic model established some direction priorities, based on these probabilities (Table 3). The risk of mortality associated with dispersal can prevent the dispersers from reaching their destination.

5. *Incorporation of dispersers*.—Surviving dispersers of reproductive age were incorporated into the receiving local population's breeding age class provided there were some vacant territories (this also is influenced by the age and breeding status-based dominance hierarchy). Otherwise, dispersers join the floating nonbreeding population. Juvenile dispersers join the corresponding age cohort in the receiving local population.

6. *Reproduction*.—Scarcity of males can limit the number of females that actually reproduce; only a proportion of the females owning a territory and having

TABLE 1. Algorithms used in the deterministic and the stochastic versions of the model. For parameter and variable definitions see Table 2.

Parameter	Algorithm	
	Deterministic	Stochastic
Annual survival	$L_{a(t+1)} = L_{a(t)} \times P_{sa}$	$L_{a(t+1)} = \text{binomial}(L_{a(t)}, P_{sa(t)})$
Occupation of vacant territories (this sequence is followed for every reproductive age class of both sexes)	$V = N - \sum_{a=r}^{r_{\max}} L_{a(\text{with})}$ $Z_a = \min(L_{a(\text{without})}, V)$ $L_{a(\text{with})} = L_{a(\text{with})} + Z_a$ $L_{a(\text{without})} = L_{a(\text{without})} - Z_a$ $V = V - Z_a$	(same as for deterministic model)
Dispersal	$D_a = L_a \times P_{da}(\text{RBAT})$	$D_a = \text{binomial}[L_a, P_{da}(\text{RBAT})]$
Allocation of dispersers and survival after dispersal	$ID_a^j = \sum_{i=1, i \neq j}^Z D_a^i \times P_{da}^{ij} \times P_{sda}^{ij}$	Distribution, e.g., with three possible destinations, $P_{da}^1 > P_{da}^2 > P_{da}^3$: $D_a^1 = \text{binomial}(D_a^1, P_{da}^1)$ $D_a^2 = \text{binomial}(D_a^1, P_{da}^2)$ $D_a^2 = \min(D_a^1 - D_a^1, D_a^2)$ $D_a^3 = D_a^1 - (D_a^1 + D_a^2)$ Survival: $ID_a^j = \text{binomial}(D_a^j, P_{sda}^j)$
Incorporation of dispersers to the receiving local population	$V = N - \sum_{a=r}^{r_{\max}} L_{a(\text{with})}$ $RI_a = \min(IM_a, V)$ $L_{a(\text{with})} = L_{a(\text{with})} + RI_a$ $L_{a(\text{without})} = L_{a(\text{without})} + (IM_a - RI_a)$ $V = V - RI_a$	(same as for deterministic model)
Reproduction (no. of females with territory)	$F = \min\left(\sum_{a=f}^{f_{\max}} F_{a(\text{with})}, h \times \sum_{a=m}^{m_{\max}} M_{a(\text{with})}\right)$	(same as for deterministic model)
No. and sex of cubs	$C = F \times \text{pr}(\text{RBAFT}) \times \text{als}$ $C_f = C \times \text{sr}$ $C_m = C - C_f$	$C_f = \text{binomial}(C, \text{sr})$ $C_m = C - C_f$

access to a mate eventually breed. This proportion depends on the level of female saturation in the population. In the stochastic version of the model, for every female with a territory and an available mate, a pseudorandom number (0–1) was generated; that female breeds if this number is smaller or equal to the proportion of females that can reproduce [density-dependent variable pr(RBAFT); see Table 2]. Litter size also is randomly assigned following the same method and according to the observed frequencies of the different litter sizes.

The program was written in TURBO-PASCAL and

the simulations were carried out on a microcomputer. The population dynamic was simulated 1000 times for 100 yr in the stochastic version.

The deterministic potential growth and metapopulation structure were assessed through the deterministic model. A sensitivity analysis was used to evaluate the importance of potential biases. The sensitivity analysis was performed by simulating multiple combinations of parameter values (10% above and below their initial values) and analyzing the results through stepwise partial regressions (Rabinovich and Himschoot 1990). Standardized partial coefficients of regression represent

TABLE 2. Definitions of symbols used for parameters and variables in the model.

a	class of age, sex, and/or reproductive status (with or without territory)
als	average litter size
C	number of cubs
C_f	number of female cubs
C_m	number of male cubs
D_a	number of dispersers of class a
D_a^i	number of dispersers of class a of subpopulation i
D_a^{ij}	number of class a dispersers from subpopulation i dispersing to the subpopulation j
f	age of first reproduction for females (years)
f_{\max}	age of last reproduction for females (years)
F	number of females with territory that could reproduce
$F_{a(\text{with})}$	number of females with territory of age a
h	maximum number of females that a male can mate
i	subpopulation from which disperser came
ID_a^i	number of dispersers joining class a in the subpopulation j
ID_a^{ij}	number of dispersers joining class a in the subpopulation j coming from subpopulation i
IM	number of immigrants joining the age class considered
j	destination subpopulation for a disperser
L_a	number of lynxes in class a
$L_{a(\text{without})}$	number of lynxes in class a without a reproductive territory
$L_{a(\text{with})}$	number of lynxes in class a with a reproductive territory
m	age of first reproduction for males (years)
m_{\max}	age of last reproduction for males (years)
$M_{a(\text{with})}$	number of males with territory of age a
MI	number of immigrants joining the age class considered
N	number of reproductive territories in a subpopulation (carrying capacity)
n	maximum number of years a senescent adult can survive
P_{sa}	annual survival rate for class a
P_{da} (RBAT)	probability of dispersal for class a (density-dependent function)
P_{da}^{ij}	probability that class a dispersers from the subpopulation i dispersing to the subpopulation j
P_{da}^{ji}	survival rate of class a dispersers from the subpopulation i dispersing to the subpopulation j
pr (RABFT)	proportion of females with territory that actually produce any cub (density-dependent function)
r	age at first reproduction
r_{\max}	maximum reproducing age
RBAFT	ratio of breeding adult females to number of reproductive territories
RBAMT	ratio of breeding adult males to number of reproductive territories
RBAT	number of adult lynxes per number of reproductive territories
RI_a	number of class a immigrants that occupy a vacant territory
sr	sex ratio of cubs
sr _r	female reproductive rate (proportion of females with territory that actually produces some cubs) at saturation (no. of reproductive females = no. of territories)
t	time (years)
V	number of vacant reproductive territories
z	number of subpopulations in the metapopulation
Z_a	number of lynxes of class a without a territory that occupy a vacancy

the relative importance of each parameter for the dependent variable considered.

Usual outputs in Population Viability Analyses (Gilpin and Soulé 1986) were obtained from the stochastic model. They included: the probability of extinction within specified time intervals for the whole metapopulation and for each local population (for the metapopulation "extinction" means absence of at least one sex, while for local populations it means absence of individuals; senescent individuals are not considered in either of the cases); the mean time to extinction of those simulated metapopulations that went extinct; the mean size of populations not yet extinct; the mean time to first extinction, the mean time to recolonization after first extinction, and the mean time to extinction after first recolonization for each local population; and the mean number of extinctions, and the mean number of recolonizations in 100 yr for each local population.

Finally, the stochastic model was used to develop different scenarios related to changes in the environment and management strategies.

DEMOGRAPHIC PARAMETERS

Estimates of the population parameters (Table 3) come mainly from studies since 1983, primarily using radio-tracking procedures. The model was built with information gathered until 1992. In this period 36 animals (19 males and 17 females), including 24 adults (13 males and 11 females) were radio-tagged and tracked for >17 000 radio-days (Beltrán 1988, Ferreras et al. 1992, Aldama 1993, Beltrán and Delibes 1994, Ferreras 1994, Ferreras et al. 1997). Most of the radio-tracking was carried out on individuals coming from the largest local population ("Vera"). Since 1993, lynx radio-tracking has focused on a different local population ("Matagordas") and the preliminary results are mainly unpublished (EBD-Carnivore Group, *personal communication*), but they have been considered for the estimation of the parameters. Moreover, in 1986–1987 and 1992–1993 presence censuses were carried out in all the potential distribution areas, providing instantaneous "snapshots" of the lynx distribution. These methods allowed collection of basic information on population demography, such as local population size and distribution, survival, and reproductive and dispersal rates. Long-term radio-tracking of a number of individuals (some of them tracked for >6 yr) allowed us to examine individual life histories (Ferreras et al. 1997). These data were taken into account when duration of territory occupancy and reproductive life were considered in the models. Some demographic parameters for the remaining local populations were estimated indirectly, based on those from the most studied ones. Factors such as the particular characteristics of each local population, e.g., protection degree, mortality risks, habitat quality, and prey densities, were also taken into account. Some parameters were supported by published values from populations of other lynx

TABLE 3. Values of demographic parameters considered in the models of the Doñana lynx metapopulation. References are provided for those parameters directly estimated from field data; those values without reference were arbitrarily assigned by the authors, based on the knowledge of particular features of each local population. The column head n refers to the number of lynx-years considered in the estimate.

A) Values of demographic parameters						
Parameter	n	Value (\pm SE)	References			
Age at first reproduction (yr)						
Females (f)		2	1, 2, 3, 4			
Males (m)		3	1, 2, 3, 4			
Age at last reproduction [females (f_{\max}) = males (m_{\max})]		9	1, 4			
Maximum longevity		13	5			
Carrying capacity (number of territories, N ; females = males)			1, 6			
Vera		5				
Marismillas = Acebuche = Matasgordas		3				
Torrecuadros = Puebla		1				
Reproductive rate in situation of female saturation (srr):						
Vera = Marismillas = Acebuche = Puebla	16	0.6 ± 0.12	1			
Matasgordas = Torrecuadros	12	0.8 ± 0.12	1			
Average litter size (als)	9	2.9 ± 0.87	1, 7, 8			
Survival rates (p_{sa})						
Cubs						
Vera = Marismillas = Matasgordas	22	0.5 ± 0.11	1			
Acebuche = Torrecuadros = Puebla	...	0.4				
Nondispersing subadults (females = males)						
Vera = Marismillas	26	0.7 ± 0.04	8, 9			
Matasgordas	...	0.6				
Acebuche = Torrecuadros = Puebla	...	0.5				
Dispersing females	6	0.5 ± 0.20	1, 8, 9			
Dispersing males	13	0.4 ± 0.14	1, 8, 9			
Adults with territory (females = males)						
Vera = Marismillas	27	0.9 ± 0.06	1, 8, 9			
Matasgordas	...	0.8				
Acebuche = Torrecuadros = Puebla	...	0.7				
Adults without territory (females = males)						
Vera = Marismillas	6	0.7 ± 0.19	1			
Matasgordas = Acebuche = Torrecuadros = Puebla	...	0.6				
Old individuals (females = males)						
Vera = Marismillas	...	0.6	1			
Matasgordas = Acebuche = Torrecuadros = Puebla	...	0.5				
Maximum dispersal rates						
Subadult males: density-dependent function		$0.3 + 0.5 \times \text{RBAMT}\dagger$				
Subadult males at saturation	9	0.8 ± 0.13	8			
Subadult females	11	0.7 ± 0.13	8			
Adult males without territory	...	0.5				
Adult females without territory	...	0.4				
B) Percentage of dispersers between subpopulations			1, 7, 8			
		To				
From	Vera	Marismillas	Acebuche	Matasgordas	Torrecuadros	Puebla
Vera	...	45	50	5	0	0
Marismillas	67	...	33	0	0	0
Acebuche	67	33	...	0	0	0
Matasgordas	10	0	0	...	50	40
Torrecuadros	0	0	0	50	...	50
Puebla	0	0	0	50	50	...

Note: References are 1, EBD-Carnivore Group, *personal communication*; 2, Fritts and Sealander 1978; 3, Kvam 1991; 4, Ferreras et al. 1997; 5, Zapata et al. 1997; 6, Palomares et al. 1991; 7, Aldama 1993; 8, Ferreras 1994; 9, Ferreras et al. 1992.

† The dispersal rate of 1-yr-old males is a function of the proportion of male territories occupied (RBAMT_M).

TABLE 4. Initial populations of the simulations.

Sub-population	Females			Males			
	Cubs	Young	Adults	Cubs	Young	adults	Adults
Vera	4	2	5	4	2	1	4
Marismillas	3	2	3	3	1	1	3
Matasgordas	3	2	3	3	1	1	2
Acebucho	3	2	3	3	1	1	2
Torrecaudros	1	1	1	1	0	0	1
Puebla	1	1	1	1	0	0	1

Note: Cubs = 0–1 yr; young = 1–2 yr; subadult = 2–3 yr; adult females, >2 yr; and adult males, >3 yr.

species, such as the European lynx (*Lynx lynx*), the bobcat (*Lynx rufus*), and the Canada lynx (*Lynx canadensis*). When this was done, it is stated in the text. Numeric values obtained for the parameters were rounded to the first decimal and occasionally smoothed when estimates obtained from small samples were clearly biased to nonlogical values.

Distribution and carrying capacity of the local populations

Lynx distribution censuses (Palomares et al. 1991, EBD-Carnivore Group, unpublished report) allowed us to identify six patches supporting local populations. We called them: Vera, Marismillas, Matasgordas, Acebucho, Torrecaudros, and Puebla (Fig. 1). The first three are inside DNP; Vera and Marismillas occupy a core area, while Matasgordas occupies a peripheral one. Acebucho, partially included in the national park, is effectively surveyed by its wardens, who have their headquarters in that area. However, it is crossed by a heavily traveled road and surrounded by intensive agricultural lands, which add strong negative effects such as mortality risks. The remaining two patches (Torrecaudros and Puebla) are outside the protected area (~25 km from the national park). On each of these patches lynxes were detected only in one of the two distribution censuses. Carrying capacity of local populations, defined as the maximum number of territories for breeding females within a patch, was estimated based on radio-tracking data, records of females with kittens and availability of suitable habitats (Table 3). It was considered similar for both sexes in every local population (Ferrer et al. 1997). Initial size for local populations in the simulations was estimated based on observed field data and assumed a stable age distribution (Table 4).

Minimum and maximum ages of reproduction

According to our observations (Ferrer et al. 1997) as well as from data on other lynx species (Fritts and Sealander 1978, Kvam 1991), only females as old as 2 yr could give birth, whereas males could only breed when 3 yr old. Considering the age of the oldest reproductive lynxes in the study area, the maximum age of reproduction for both sexes was 9 yr (Table 3); older

animals were observed to be displaced from their territories by younger individuals (Ferrer et al. 1997).

Adult lynxes were assumed to occupy vacant territories following a preference ranking depending on their age, according to the results of some territorial contests observed in the area (Ferrer et al. 1997). This age ranking was: 4, 5, 6, 7, 3, 8, and 9 yr old for males and 4, 5, 6, 7, 3, 2, 8, and 9 for females.

Reproductive rate

Breeding males of this and closely related species have been reported to retain home ranges large enough to encompass the territories of three females (Anderson 1987, Breitenmoser et al. 1992, Poole 1995), and even occasionally up to five females, although this seems to be very uncommon (Breitenmoser and Haller 1993). We therefore considered that in situations when males were scarce, each male could reproduce effectively with as many as three females.

We have simulated the influence of habitat heterogeneity on reproductive rate (proportion of females with territory and available male that actually reproduce) within local populations assuming that territories are occupied following an order that depends on their quality (Pulliam and Danielson 1991). In this way, reproductive rate is considered to be related to the number of occupied territories on each local population, according to a density-dependent function (Fig. 3). If only a breeding female is present in a local population ($RBAFT = 1/\text{no. territories}$; Fig. 3), she would occupy the best territory where she would breed with a high probability (95% assumed in the model). As female density increases, the average quality of the territories and consequently the mean fecundity decrease. A similar density-dependent response from the Imperial Eagle (*Aquila adalberti*) in Doñana has been reported recently by Ferrer and Donazar (1996). In the saturation

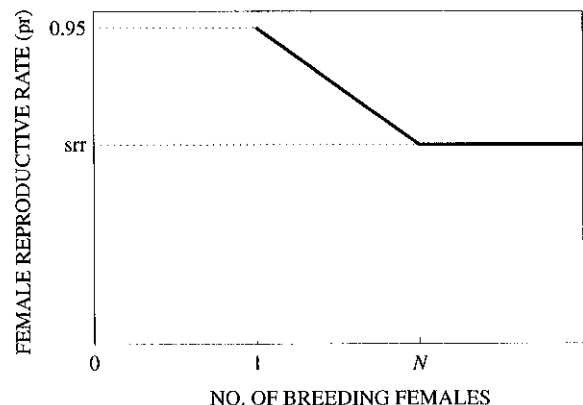


FIG. 3. Density-dependent function for the proportion of females with territory that actually produces some cubs (pr). N = the number of reproductive territories (carrying capacity) of the local population. The designation srr refers to the female reproductive rate in the situation of saturation (as many reproductive females as territories), and its value depends on the local population (see Table 3).

situation (all female breeding territories occupied, $RBAFT \geq 1$; Fig. 3) the value of the reproductive rate will depend on the local population. The annual reproductive rate at saturation (srr, Fig. 3) was estimated as 0.6 (Vera local population) and 0.8 (Matasgordas, where prey abundance is higher) based on 13 and 12 female-years of radio-tracking, respectively (Ferrerás et al. 1997, EBD-Carnivore Group, *unpublished report* and *personal communication*). Using these values as reference, we assigned those corresponding to the remaining local populations (Table 3), taking into account that habitat quality (prey density) of Torrecuadros is high, similar to that at Matasgordas (srr = 0.8) and that prey density at the remaining local populations (Marismillas, Puebla, and Acebuche) is medium, like that at Vera (srr = 0.6).

Litter size

The average litter size was determined to be 2.9 offspring (20, 70, and 10% for 2, 3, and 4 kittens/litter, respectively), according to the composition of nine litters found when a few days old (Aldama 1993, EBD-Carnivore Group, *unpublished report* and *personal communication*). This figure agrees with those reported for some closely related species: 2.7 offspring for bobcats (Anderson 1987); 2.3–2.4 offspring for Canada lynxes (Brand and Keith 1979, Mowat 1993); and 2.9 offspring for Eurasian lynxes (Kvam 1991). A 1:1 average sex ratio within litters was assumed.

Survival rates

We employed the MICROMORT program (Heisey and Fuller 1985, Ferreras et al. 1992) to obtain annual rates of survival for the different age and sex classes. This program is based on calculating daily mortality rates, according to the total number of radio-transmitter days and deaths of radio-tracked animals occurring in the interval covered. As a measure of variation about the means, standard errors of the annual rates estimations were calculated as for binomial distributions (Powell et al. 1996; see Table 3). Survival rates for Vera, Acebuche, and Marismillas were estimated based on our radio-tracking data (Ferrerás et al. 1992, Ferreras 1994) and those from Matasgordas on current studies in that local population since 1993 (EBD-Carnivore Group, *personal communication*). Using these values, those for the remaining local populations (Table 3) were assigned, taking into account their peculiarities, in particular, the potential risks of mortality caused by human factors, such as proximity of roads or illegal trapping and hunting activities in the area.

The most accurately estimated survival rate is that of adults with a territory in Vera and Marismillas local populations. More than 5000 radio-tracking days for each sex allowed us to estimate their annual survival rate as 0.9 (95% confidence intervals: 0.8–1.0 and 0.7–1.0 for males and females, respectively; Ferreras et al. 1992, Ferreras 1994). Despite the fact that no adult

with a territory died during their radio-tracking in the Matasgordas local population between 1993 and 1995 (EBD-Carnivore Group, *personal communication*), we considered this result a consequence of a low sample size (four females and two males radio-tracked during <10 lynx-years [the sum of total radio-tracking time for the different animals involved, expressed in years]), and a survival rate of 0.8, lower than that of Vera and Marismillas, was assumed for Matasgordas. We consider this a realistic value taking into account the greater exposure of Matasgordas to mortality risks associated with its location in the edge of the protected area and close to a human settlement (see Fig. 1). Accurate estimates of annual survival rates for adults with territory in the remaining local populations were precluded by low sample sizes. Only three male lynxes were monitored in Acebuche totaling <2 lynx-years. However, two of them died during that time because of human-related causes (run over on a road and drowned in an irrigation well) and therefore we assigned a survival rate of 0.7, lower than that in Vera, Marismillas, and Matasgordas. Likewise, only two lynxes with territory (one male and one female) were radio-tracked in Torrecuadros during a total of scarcely 4 lynx-years, and that female died because of gunshots. Therefore, we assigned as well an annual survival rate of 0.7 to this local population, reflecting the high human-related risks. Despite our lack of data for the Puebla local population (no territorial lynxes radio-tracked there), a similar rate was applied (0.7).

For the Vera local population, the annual survival rate for cubs was estimated to be 0.5, based on the survival of lynxes firstly captured and radio-tagged as juveniles between 1983 and 1992. From 22 juveniles tracked, coming from 13 different litters, at least 11 (50%) were alive at 1 yr old and at least nine had died by that age. The most pessimistic estimate (assuming juveniles coming from three-cub litters and all the cubs dying except those 11 known to be alive) yields a cub survival of 0.3. The most optimistic estimate (assuming only nine deaths from three-cub litters) gives a value of 0.8. Therefore, we considered 0.5 (11/22) as the most realistic estimate. This value broadly agrees with that estimated from six litters in Matasgordas between 1993 and 1995. We also assigned this value (0.5) to cub survival in the Marismillas local population, since trophic conditions and mortality risks were similar to the Vera, and 0.4 to those more exposed to human activities, and therefore to extra mortality risks (Acebuche, Torrecuadros, and Puebla).

In the stochastic model, we consider that environmental variation affects only the annual survival rate of cubs. This rate was modeled arbitrarily to decrease to 0.2 in adverse years for all the local populations, because of drastic prey decline. Although no direct evidence is available for the Iberian lynx, it is reasonable to suppose that cubs are the first to experience nutritional stress during periods of food scarcity, as has

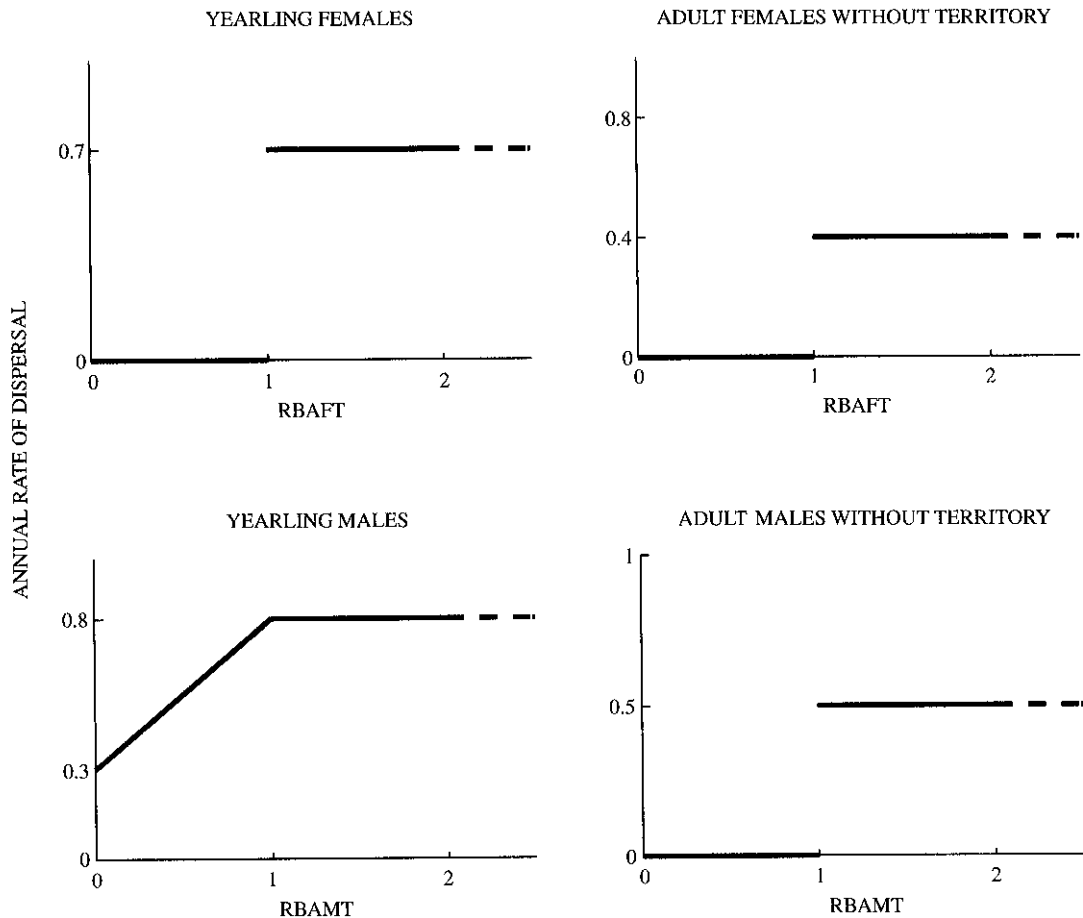


FIG. 4. Density-dependent dispersal functions for the different age-sex classes. Independent variables are the sex-specific ratio of total number of reproductive age adults to number of territories in the patch: RBAFT = ratio of breeding-age adult females to territories; RBAMT = ratio of breeding-age adult males to territories.

been reported for Canada lynxes (Brand and Keith 1979) and lions, *Panthera leo* (Van Orsdol et al. 1985). The frequency of adverse years was simulated as a normal distribution with 10 yr as average based on the duration of climatic cycles in Mediterranean environments (Font Tullot 1983). Variance was set at 0.8 and the distribution was bounded between 7 and 13 yr.

Dispersing individuals can suffer additional mortality as a consequence of the dispersal process (Chepko-Sade and Halpin 1987, Ferreras 1994, Waser et al. 1994). However, no dispersing lynx died when moving between Vera-Marismillas and Vera-Matasgordas, ostensibly because the lynxes travel between these local populations without leaving the protected area. Therefore, no additional mortality other than that corresponding to their sex and age has been considered for dispersing individuals between such local populations. Annual survivals for dispersing males and females out of the protected area were estimated as 0.14 and 0.30, respectively (from 1097 and 301 d of radio-tracking for 12 males and 4 females, respectively; Ferreras et al. 1992). Taking into account the nondispersing annual

survival rates and that the dispersal process has a mean duration of 4 mo (Ferreras 1994) the average composite annual survival rate for a dispersing lynx would be 0.4 and 0.5, respectively, for males and females.

The maximum longevity recorded in the study area was 14 yr (Zapata et al. 1997) and corresponded to an individual who died as consequence of problems associated with old age. Hence, we have considered 13 yr as the maximum life-span for the lynx in our models, assuming individuals would die once reaching that age (Table 3). This age is close to the maximum reported age for wild individuals in populations of closely related species: bobcat 12–13 yr (Crowe 1975); Eurasian lynx 14–16 yr (Breitenmoser, in Nowell and Jackson 1996); Canada lynx 13 yr (Quinn and Thompson 1987) and 14 yr 7 mo (Chubbs and Phillips 1993).

Dispersal rates and direction of the dispersal

Dispersal rates were defined as density-dependent functions (Fig. 4), based in the apparent direct relationship between density and dispersal rates for the lynx in Doñana (Ferreras 1994), also supported by data

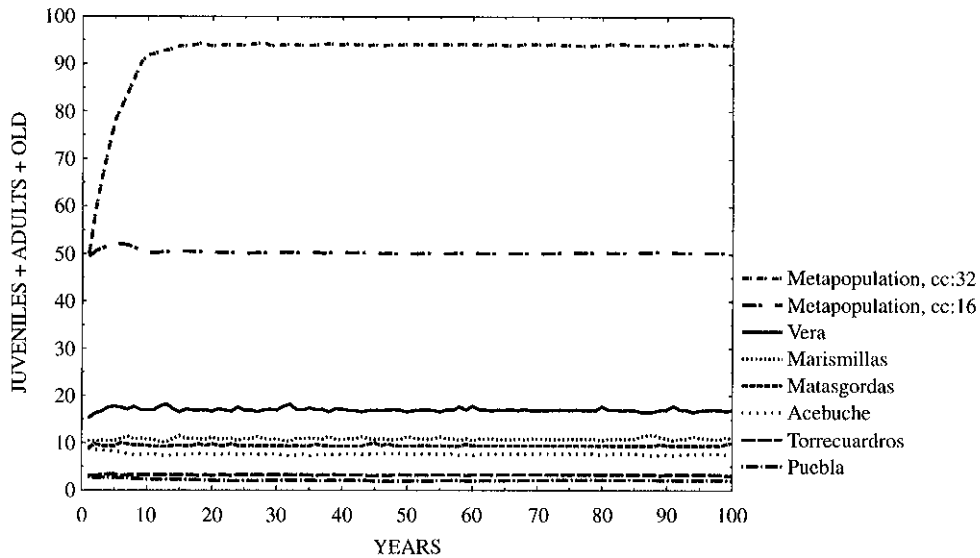


FIG. 5. Projection in time of the Doñana lynx metapopulation with carrying capacity (cc) as estimated in the current situation (Metapopulation, cc: 16) and the contribution of each subpopulation, according to the deterministic version of the model. The projection of a hypothetical metapopulation with doubled carrying capacity (Metapopulation, cc: 32) shows that carrying capacity is the factor limiting its growing ability.

for the bobcat (Griffith and Fendley 1986). In a situation of saturation, annual dispersal rates were estimated for Vera as 0.8 for males and 0.7 for females (Ferreras 1994). We assumed that both males and females older than 2 yr only disperse from their local population when all breeding territories are occupied there ($RBAFT \geq 1$ for females and $RBAMT \geq 1$ for males; Fig. 4). However, a density-independent "intrinsic" dispersal of juvenile males is well documented for mammals (Chepko-Sade and Halpin 1987) and in particular for solitary felids (Maehr et al. 1991, Smith 1993). Therefore, we assumed that yearling males would disperse even when unoccupied territories are available. A value of 0.3 is arbitrarily chosen as the intrinsic rate of juvenile dispersal when all male territories in their local population are empty ($RBAMT = 0$). Dispersal rate lineally increases with $RBAMT$ from that value up to 0.8 at saturation level ($RBAMT \geq 1$; Fig. 4). Functions for dispersal rates are similar for all the local populations.

The proportion of individuals dispersing from one local population to each of the neighbouring ones (Table 3) was estimated from radio-tracking data (Ferreras 1994) as well as taking into account the distances and barriers separating them. The proportion of dispersers traveling to other neighboring local populations from Vera ($n = 6$ individuals) and Matasgordas ($n = 6$) allowed us to define the differential permeability of matrix habitats separating them. In addition to physical distance, it is dependent mainly on habitat quality and human disturbance. In this way, open habitats such as marshes, or those highly transformed by man, such as human settlements, croplands, or high-traffic roads, act as low permeability barriers. Such relative permeabil-

ities of different habitats have been subjectively considered to assign the percentage of dispersers among less known local populations, mainly those occupying the unprotected area (Table 3).

RESULTS

Deterministic model

Simulations of the deterministic model showed the metapopulation converging to a constant size as determined by the carrying capacity (number of territories) of the habitat (Fig. 5). However, in a hypothetical scenario with increased carrying capacity (duplicated in each of the local populations) the metapopulation grows until the new territories are filled (Fig. 5). Therefore, simulations suggest that a hypothetical lynx metapopulation with values of the parameters as those observed in Doñana, without stochasticity and without including genetic considerations, could sustain itself. The deterministic model, for the values of the demographic parameters considered (Table 3), demonstrates that females occupy all their breeding territories (16 females for 16 territories), while males are below carrying capacity (11 males for 16 territories; Fig. 6).

To characterize the different local populations, we simulated isolated local populations in which individuals surviving dispersal would eventually rejoin their local population of origin. The results allow us to define two types of local populations: (a) those that increased, then were limited by carrying capacity (Vera, Marismillas and Matasgordas) and (b) those that decreased (Acebuche, Torrecuadros, and Puebla; Fig. 7). In the context of the metapopulation, therefore, a source-sink structure (Pulliam 1988) can be observed. The sources

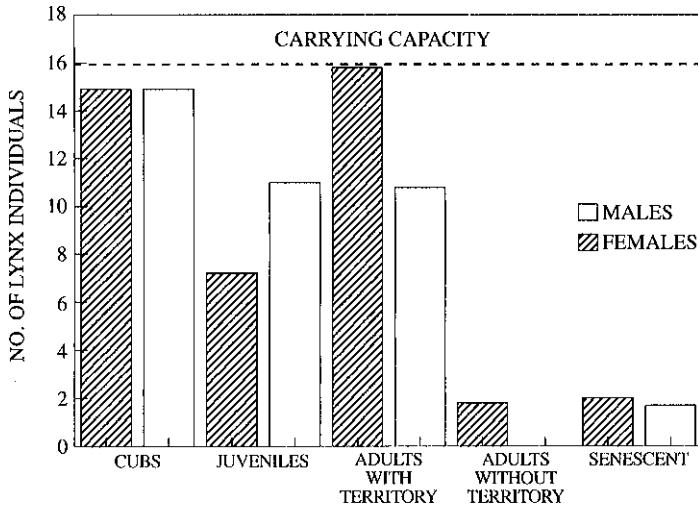


FIG. 6. Age and sex structure of the Doñana lynx metapopulation, according to the deterministic version of the model. Adult females with territory thrive until reaching carrying capacity; meanwhile adult males with territory are far below their carrying capacity.

are responsible for the sustainability of the sinks as well as of the potential growth of the whole metapopulation.

Sensitivity analysis

We used values obtained for the best-studied local populations to estimate the parameters for those with less information. Using the deterministic version of the model, we carried out a sensitivity analysis to calibrate the possible consequences of such extrapolations on the simulation results.

First, we tried to identify those parameters with the greatest effect on the simulation results, as a consequence of their significance in the metapopulation deterministic dynamics. Therefore, we calculated sensi-

tivity coefficients (see *Model description* above) of: (a) the number of adults with territory; (b) the number of adults without territory; (c) the total number of individuals; and (d) the mean annual growth rate of the metapopulation to changes in: (1) the reproductive rate of females; (2) the survival rate of cubs; (3) the survival rate of juveniles; (4) the survival rate of territory-holding adults; (5) the survival rate of adults without territories; (6) the dispersal rates; and (7) the mortality associated with dispersal (expressed as a reduction in survival).

The maximum sensitivity always corresponded to the survival rate of territory-holding adults (Table 5). Therefore, we calculated the sensitivity of the same variables from the first analysis [from (a) above to (d)]

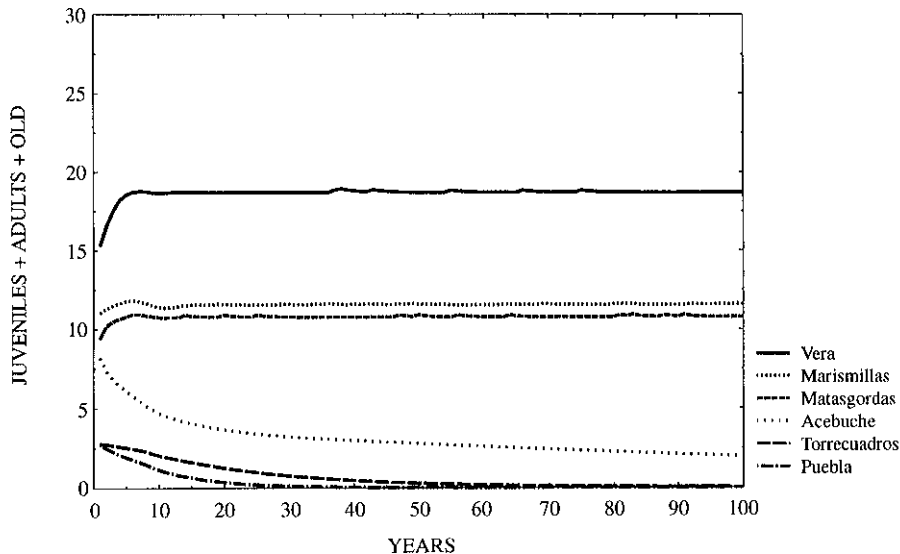


FIG. 7. Projection in time of each of the local populations (deterministic model) under the assumption of isolation among them; lynx surviving the dispersal process would rejoin their original patch. Three local populations (Vera, Marismillas, and Matasgordas) thrive until reaching their carrying capacity, and can be qualified as "sources." The decreasing trend of the three remaining local populations (Acebuche, Torrecuadros, and Puebla) allows us to identify them as sinks.

TABLE 5. Sensitivity of final metapopulation size and rate of increase to model parameters (defined in Table 2). All the analyzed variables show the highest sensitivity to changes in the survival rate of adults with a territory and, especially, in the survival of that age class from the Vera subpopulation. The maximum sensitivity values for each variable are shown in boldface.

Parameter	Sensitivity of the variables			
	Adults with territory	Adults without territory	Total of individuals	Rate of increase
Reproductive rate (srr)	0.3021	0.3881	0.5512	0.4897
Survival (p_m) of:				
Cubs	0.3211	0.3867	0.3801	0.3283
Juveniles	0.4935	0.4125	0.3469	0.3059
Adults with territory	0.7825	0.6440	0.6391	0.5269
Adults without territory	0.0208	0.1437	0.0407	0.0249
Dispersing individuals	0.0856	0.1067	0.0691	0.0627
Dispersal rate (p_m)	0.0208	0.0879	0.0130	0.0310
Survival of adults with territory in the subpopulations				
Vera	0.6724	0.6606	0.6652	0.5915
Marismillas	0.4050	0.4604	0.4162	0.3250
Matagordas	0.3864	0.3414	0.4398	0.3386
Acebuche	0.3544	0.3058	0.2826	0.2083
Torrecuadros	0.1556	0.0755	0.1679	0.1194
Puebla	0.2285	0.0388	0.2486	0.1815

to independent changes in the survival of territory-holding adults in each of the local populations. The results indicate that the dynamics of the metapopulation is most affected by the local population from which more information is available (Vera), and is less affected by the least known and smallest local populations (Torrecuadros and Puebla). Hence, we are confident about the results of the simulations, in spite of potential biases in the parameter estimations for these small local populations.

Stochastic model

Although the deterministic simulation shows that the metapopulation has the capacity to increase (limited by the carrying capacity of the environment), demographic

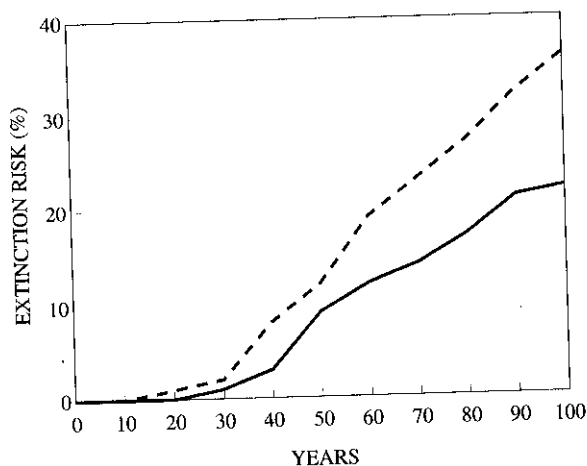


FIG. 8. Extinction probability of the Doñana lynx metapopulation during 100 yr of simulation, according to the models including demographic stochasticity (solid line) and both demographic and environmental stochasticity (dashed line).

stochasticity (related to the small size of the local populations) results in considerable probability of metapopulation extinction (for example, 22% within 100 yr; Fig. 8). This probability increases when environmental stochasticity also is considered (33.8% within 100 yr; Fig. 8).

The model including demographic and environmental stochasticity shows the mean extinction time of the metapopulation to be 60 yr. The average metapopulation size at the end of the simulation (in cases without extinction) was 36 individuals, well below the current population. The sink patches (Acebuche, Torrecuadros, and Puebla) become extinct first, especially those of smallest size (Torrecuadros and Puebla) (Table 6). Acebuche persists longer because of its larger size and a higher level of immigration. This input also is responsible for its high rate of recolonization (4 times during 100 yr, on average) and for its short recolonization time (3 yr, on average) (Table 6).

Vera is the most persistent local population (longest first extinction time; see Table 6), and serves as the primary support of the metapopulation. Only 23.1% of the metapopulation extinctions occurred because of disappearance of females, whereas 69.8% were attributable to the extinction of males. Males, therefore, seem to be a limiting factor in the metapopulation demography.

Simulation scenarios

One of the advantages of modeling is that it allows simulation of hypothetical scenarios that allow evaluation of different situations related to changes in the environment or in the management strategies. We considered different scenarios for both within- and between-patch dynamics, including both a priori negative and positive effects on these dynamics. For within-

TABLE 6. Some results of the simulations (average values from 1000 simulations of 100 yr of duration each).

Population	NL	TE	RE	RC	TRE	TRC	EP	EP*
Metapopulation	36 (1-77)	60 (13-100)	33.8	4.0
Vera	19 (1-38)	87 (9-100)	0.4	0.1	17.2	3.1	32.8	4.0
Marismillas	9 (1-23)	65 (8-100)	1.4	1.0	19.9	4.6	41.3	5.0
Matasgordas	8 (1-23)	45 (4-100)	3.0	2.5	15.5	4.6	48.0	70.0
Acebucho	5 (1-20)	30 (3-100)	4.6	4.1	12.9	3.2	50.0	100
Torrecaudros	2 (1-9)	10 (1-39)	5.0	4.6	5.5	9.9	84.2	100
Puebla	1 (1-5)	7 (1-24)	3.6	2.7	3.8	15.7	94.1	100

Note: NL = number of lynx remaining at the end of the simulation in those cases where the population was not extinct (range between brackets); TE = mean time to first extinction (range between brackets); RE = mean number of extinctions (no males nor females); RC = mean number of recolonizations; TRE = mean time of extinction (time during which the population is occupied) after the first recolonization; TRC = mean time of recolonization (time during which the population is extinct) between successive recolonizations; EP = extinction probability (%) during 100 yr (absence of any of the sex for the metapopulation and absence of both sexes for the subpopulations); EP* = extinction probability (%) during 100 yr under a scenario of isolation of the national park (no dispersal between inside and outside subpopulations).

patch dynamics, we simulated changes in the carrying capacities and the demographic parameters of the local populations. For between-patches dynamics, we simulated reduction in mortality attributable to dispersal and a situation where the national park would be isolated. These scenarios were selected from among many potential ones to help in the understanding of the metapopulation structure and dynamics and to obtain useful information for the conservation of the species.

Within-patch dynamics.—Probabilities of the metapopulation extinction in 100 yr for different levels of carrying capacities in each local population are shown in Figs. 9a-d (no improvements in the smallest populations of Torrecaudros and Puebla were simulated given their reduced spatial possibilities to increase the number of territories; for similar reasons, an increase of one territory only is presumed to be possible in Marismillas).

The effect of summing changes in carrying capacities and improvements in the survival rates in the sinks (equalizing that of their closest sources) is also shown in the abovementioned Fig. 9a-d. In the simulations for Fig. 9a, b, and d, the survival rates in Acebucho were equalized to those for Vera; for Fig. 9c survival rates in Torrecaudros and Puebla were equalized to those for Matasgordas.

Changes in the carrying capacity of Vera, Marismillas, and Matasgordas (sources), both with or without changes of the survival rates in the sinks, significantly affect the viability of the metapopulation (Fig. 9a-c). Changes in the carrying capacity of Acebucho (sink) show the opposite, with no effect on the probability persistence of the metapopulation, unless the survival rates were simultaneously improved (Fig. 9d).

Comparisons of the different scenarios suggest that the most effective strategy would be to improve the carrying capacity of the largest source (Vera). An increase of only two reproductive territories in this local population (Fig. 9a) would reduce the extinction probability of the metapopulation to a level comparable to that obtained by the improvement of survival rates in Acebucho (Fig. 9d).

Between-patch dynamics.—Two scenarios related to between-patches dynamics were considered. In the first, we simulated the effect of reducing mortality associated with dispersal. In the second, we considered a scenario in which the local populations contained within the DNP were isolated from the park's surroundings (dispersal would be possible only among the local populations inside DNP, i.e., the sources).

A 50% reduction in the dispersal mortality only reduces the extinction probability of the metapopulation from 33.8 to 29.9% within 100 yr (Fig. 10). It would be necessary to remove the additional mortality completely during dispersal to lower this probability to 25.2%.

By definition, the sinks would be extinct if isolated from the sources in the DNP. Nevertheless, the consequences of this hypothetical scenario for the sources vary (Table 6). For Vera and Marismillas, the disconnection from the closest sink (Acebucho) has positive consequences, decreasing considerably their extinction risks (from 32.8 to 4% and from 41.3 to 5%, respectively). On the contrary, the extinction risk of the other source (Matasgordas) increases (from 48 to 70%) when the connection with its closest sinks (Torrecaudros and Puebla) is prevented.

DISCUSSION

The situation of the Iberian lynx in the area of Doñana is representative of that of many other endangered species throughout the world (Fig. 11). Their former continuous ranges have been fragmented and their population sizes reduced, as a consequence of external (deterministic) effects linked to human activities (mainly habitat loss and human-induced mortality; Harcourt 1991, Caughley 1994, Thomas 1994). Nonetheless, at present legal protection of species and the creation of sanctuaries (e.g., national parks) try to avoid the extinction of the surviving small populations, which continue to be affected by deterministic factors (although mitigated), but some other internal (often stochastic) effects have been added (Shaffer and Samson 1985, Gilpin and Soulé 1986, Lande 1993). Very often this

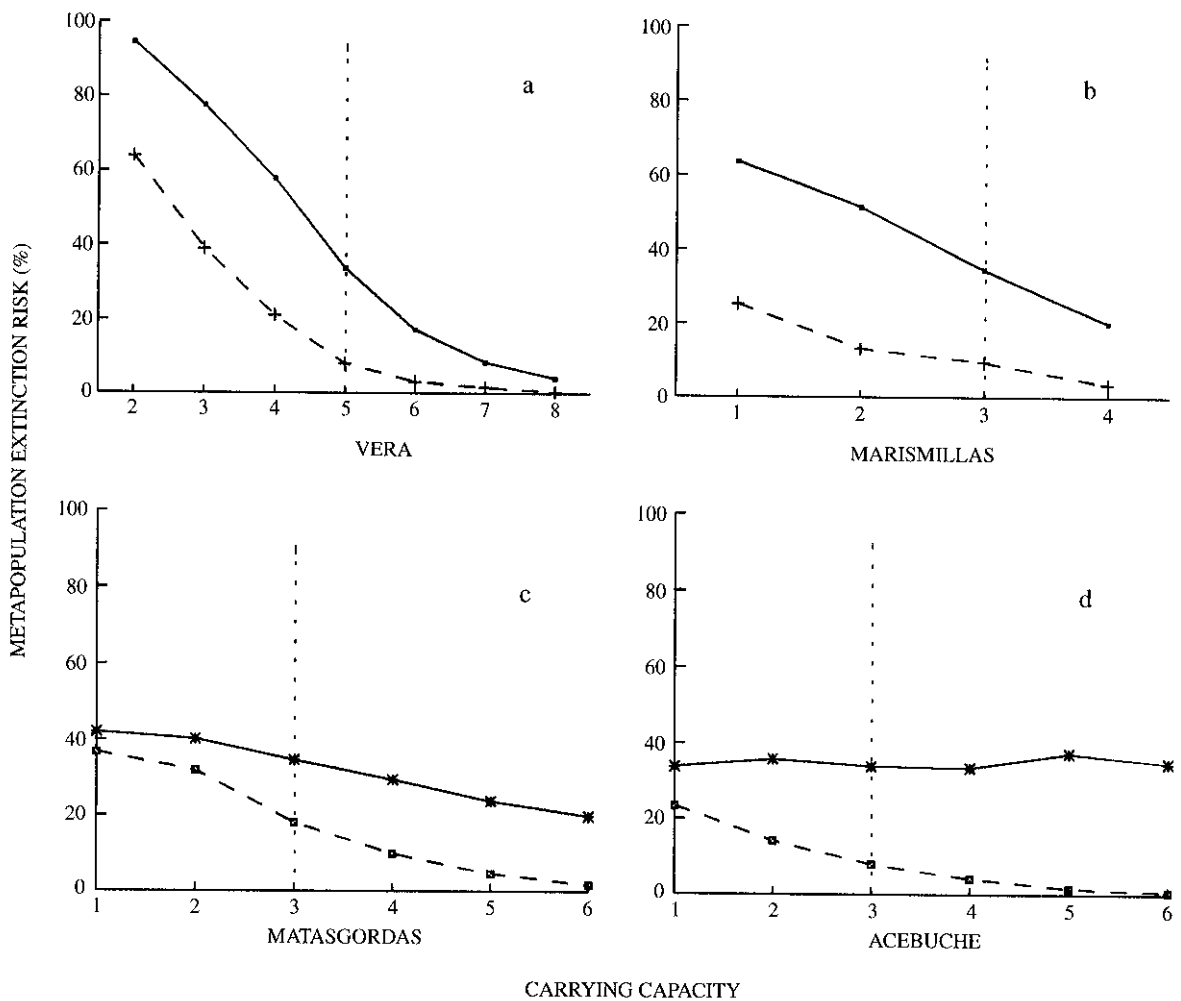


FIG. 9. Effect of changes in carrying capacity (number of female breeding territories) of the sources [(a) Vera, (b) Marismillas, (c) Matasgordas] and the largest sink [(d) Acebuche] on the extinction risk of the whole metapopulation within 100 yr (—). The additional effect of improving lynx survival in the sinks directly connected to each source [Acebuche for Vera and Marismillas in (a), (b), and (d), or Torrecuadros and Puebla for Matasgordas, in (c)], equalizing their survival rates to those at the main source is also represented (---). Current carrying capacity levels are indicated by vertical dotted lines.

situation is not a temporary step, but the only realistic possibility of preserving in the future some endangered species, given that the return to the continuous and large distribution of the past will not be possible. In this sense our approach integrates the small-population and the declining-population paradigms of Caughley (1994) and could be useful to other endangered species (Hedrick et al. 1996).

Most studies on metapopulations have been theoretical (Doak and Mills 1994, Gilpin 1996), but analyzing real natural systems from a metapopulation perspective is a hopeful field for conservation in the next future (McCullough 1996). In spite of the growing number of empirical studies of metapopulations structure and dynamics, the need of adding realism to theoretical models is clear. In addition, the autoecology and behavioral ecology of the target species (McCarthy

et al. 1994, Stacey et al. 1997), socio-economic aspects (Harcourt 1995), and considerations of within-patch and between-patch habitat quality (Thomas and Hanski 1997, Wiens 1997) must be introduced. Intensive field work on the Iberian lynx allowed us to avoid some usual limitations of metapopulation models, such as those resulting from the use of generic computer packages (e.g., VORTEX—Lacy 1993; RAMAS/space—Akçakaya and Ferson 1992; ALEX—Possingham et al. 1992, Possingham and Davies 1995), which necessarily contain a large number of assumptions and model animal behavior rather simplistically (Lindenmayer et al. 1995). In models of metapopulations, frequently similar values of the demographic parameters are assigned to all the local populations (e.g., Lankester et al. 1991, LaHaye et al. 1994, Akçakaya et al. 1995, Lindenmayer and Lacy 1995, Lindenmayer and Possingham 1996),

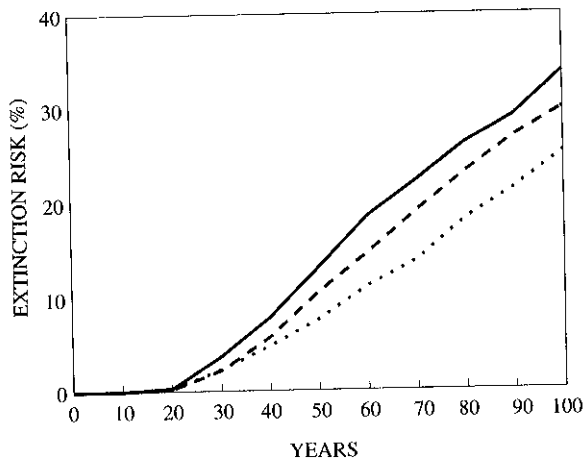


FIG. 10. Effect of reducing additional risks of mortality during dispersal on the extinction risk of the metapopulation within 100 yr. Dashed and dotted lines represent the extinction risks for 50 and 100% reductions in mortality associated with dispersal, respectively. Current risk (no mortality reduction) is represented by the solid line, for comparison.

dispersal rates are considered density independent (Lindenmayer et al. 1993a, Lindenmayer and Lacy 1995) and just a function of the distance between patches and/or their size (Lindenmayer et al. 1993b, Possingham et al. 1994, LaHaye et al. 1994, Akçakaya et al. 1995), or an additional mortality during dispersal is omitted (Lindenmayer et al. 1993a, Lindenmayer and Lacy 1995). All these assumptions can conceal the real structure and dynamics of the modeled population, making it difficult or impossible, for example, to identify source-sink or nonequilibrium (declining) dynamics, whose detection may be indispensable to guide conservation measures (Hanski 1997).

However, our model is not free of assumptions and limitations. Some demographic parameters of the smallest local populations are extrapolations based on our knowledge of the corresponding habitats; nevertheless, the results of the sensitivity analysis (in which the most relevant parameters coincide with those with the best estimates) strengthen our confidence in the results. Also, we have assigned intrinsic rates of dispersal of males starting from scant field data, but these rates could have a strong influence on the metapopulation dynamics. According to some theoretical models there is a threshold for the intrinsic dispersal rate above which the metapopulation could not sustain itself (Howe et al. 1991, Davis and Howe 1992). Eliminating the intrinsic dispersal of juvenile males in our simulation model with stochasticity, the extinction risk of the metapopulation decreases from 33.8 to 10% in 100 yr. Consequently, special attention should be devoted to the rate of intrinsic dispersal when planning new field studies.

Another important limitation of our model could be to forget a possible genetic deterioration of the Doñana lynx population (Frankel and Soulé 1981, O'Brien et

al. 1983, Wildt et al. 1987; but see Caro 1994, Caro and Laurenson 1994). The rate of interpatch migration in our study suggests the whole metapopulation is not genetically structured (Wright 1969). Nevertheless, the small total population size and undoubtedly the even smaller effective population number (Franklin 1980) predict a high rate of genetic variation loss per generation (Falconer 1989). Hence, the population is expected to be highly homozygous (see Beltrán et al. 1996). Although mammalian carnivores could be adapted to small effective population sizes (Chepko-Sade and Shields 1987, Merola 1994; but see Laikre and Ryman 1991, Laikre et al. 1996), this genetic uncertainty should be taken into account in future conservation programs of the Iberian lynx.

The deterministic version of the model suggests that at present time births should exceed deaths in the lynx metapopulation of Doñana, but population growth is limited by the available habitat, particularly for breeding females. This is a common situation in territorial species suffering habitat losses and fragmentation (Wootton and Bell 1992, Lamberson et al. 1994). However, the positive balance when considering only deterministic effects is deeply modified when demographic and environmental stochasticities are included. According to theoretical predictions (Richter-Dyn and Goel 1972, Shaffer and Samsom 1985, Gilpin and Soulé 1986, Soulé 1986, Forney and Gilpin 1989, Boyce 1992), the low number of individuals contained in every local population determines an important extinction risk for the Doñana lynx (demographic stochasticity alone means an extinction risk of 22% in 100 yr). Also, the incorporation of environmental stochasticity means an increase in the probability of extinction (33.8% within 100 yr). Considering that we modeled the environmental stochasticity affecting only the survival of the cubs, its effect is probably underestimated. On the contrary, the consideration of a spatially correlated or "regional stochasticity" (Hanski 1991), based on the proximity of the local populations (distance between those most extreme is 55 km) could overestimate the effect of environmental stochasticity (Goodman 1987, Gilpin 1988, Forney and Gilpin 1989, Harrison and Quinn 1989, Hanski 1991, Burgman et al. 1993). Undoubtedly, more information is needed on this subject.

Catastrophic events, such as diseases (May 1988, Young 1994, Roelke-Parker et al. 1996), are a part of the environmental stochasticity that can sharply decrease population size in a short time, but they are rarely included in population viability analysis (Mangel and Tier 1994). In the case of the Doñana lynx population we think it is useless to simulate the effect of such disease outbreaks, since very probably the entire small population would become extinct. Nevertheless, our simulations of a decreasing carrying capacity of the habitats (Fig. 9) could be regarded as catastrophic events (such as fires, or sharp rabbit declines as consequence of diseases, e.g., viral haemorrhagic disease;

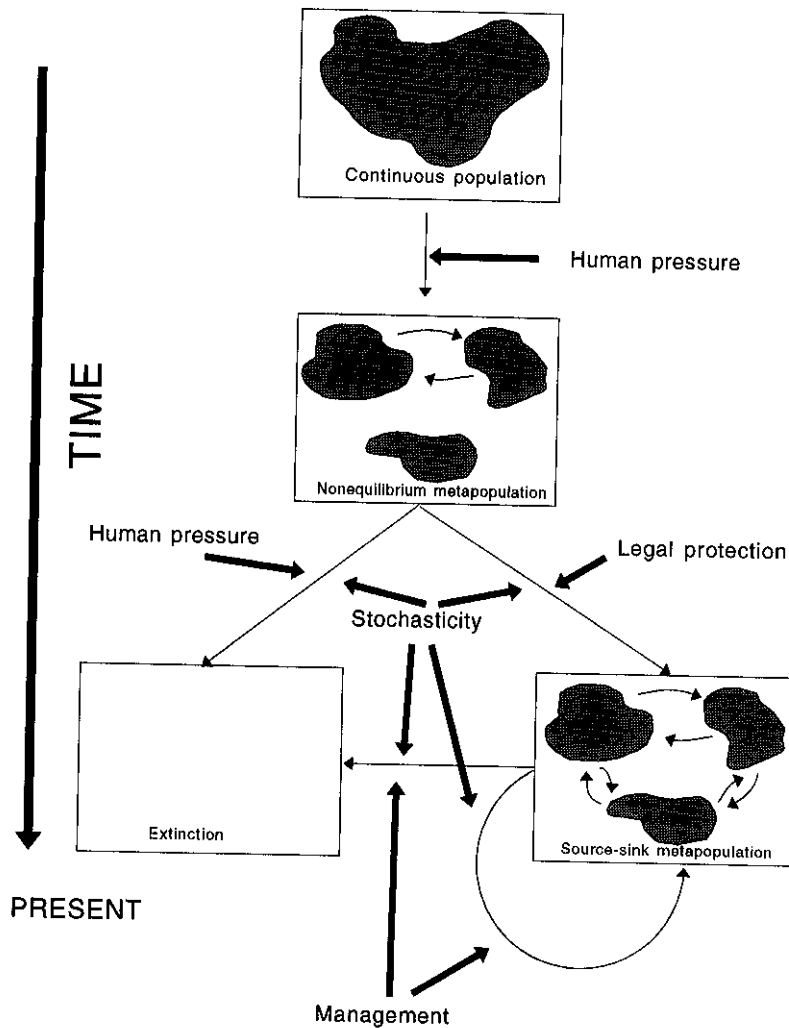


FIG. 11. Schematic representation of the process leading to the present situation of the Iberian lynx population in Doñana, which is common to many other small and fragmented populations of large-size animals. Nowadays the return to the initial state (continuous population) is unrealistic, and the only feasible solution is to manage the fragmented population in order to allow the persistence of the metapopulation.

Villafuerte et al. 1994) affecting, independently, the different local populations. According to our results, catastrophic reductions in the carrying capacity of some patches (sources) will have very negative consequences on the probability of persistence of the metapopulation (Fig. 9).

Although field censuses in 1986–1987 and 1992–1993 (Palomares et al. 1991, EBD-Carnivore Group, *unpublished report*) indicate a stable total population of 50–60 individuals, six years represent scarcely two generations of lynx, and probably this apparent stability is misleading. The high probabilities of extinction and the low average population size after 100 yr in the simulations without extinction (Table 6) suggest the metapopulation is declining. These kinds of nonequilibrium metapopulations are commonly found among species in habitats fragmented by humans (Harrison

and Taylor 1997) and are considered by Hanski (1997) as “living dead.”

The Doñana lynx metapopulation is made of interconnected sources and sinks (Fig. 7). Patches inside the national park yield a positive demography (birth rate exceeds death rate) and are considered sources, while the contrary happens in patches outside the protected area (sinks). Dispersal from source local populations permits sink populations to exist, an idea seldom tested in the field (Harrison and Taylor 1997).

The role of differential mortality between sources and sinks makes a difference between our model and assumptions of most theoretical source–sink dynamics (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996). Usually it is assumed that sources and sinks differ in “natural” habitat quality, so that natality is not enough to compensate for mortality in poor habitat

sink patches. As a result of habitat selection and density-dependent interactions, surplus individuals will migrate from sources to sinks (Holt 1993, Dias et al. 1994). Nonetheless, in our case the negative demographic balance of sinks is due to high "artificial" mortality, a risk factor that the animals are likely unable to detect (Doak 1995). In this case, a habitat selection for sources cannot be expected, as individuals do not recognize sinks as unsuitable habitats.

Harrison and Taylor (1997) suggested that many real metapopulations combine features of different theoretical metapopulation types. The dynamics of the source-sink lynx metapopulation includes characteristics of a mainland-island system (Boorman and Levitt 1973, Hanski and Simberloff 1997), as local extinctions (Table 6) mainly affect the small marginal populations ("islands" outside the park), while the total metapopulation persists as long as do its more persistent local populations ("mainland," or the sum of patches inside the park). Also, recolonization times increase with smallness of patches and their distance to DNP (Table 6), as predicted by mainland-island theory (Schoener 1991). The main difference of the Boorman-Levitt type models with ours is that, in the former, mainlands are assumed to be very large habitat patches (Hanski and Simberloff 1997) and in our case the mainland is not large, but a well-protected area with low human-induced mortality.

In this sense, the Doñana lynx metapopulation can be compared to a predator-prey system in which the prey (lynx) may persist because it has some patches ("refuges," in this case inside DNP; Sih 1987) in which it escapes its "predator" (considering as a predation surrogate all human-related mortality). Harrison and Taylor (1997) underlined the analogy between "refuges" and "sources" and suggested that this kind of predator-prey system could function as single-species metapopulations for the prey when the predator population dynamics is independent of the prey density, as in our case. Simple computer simulations for bobcat populations, a species similar to the Iberian lynx, predicted that size of refuges needed to maintain a harvested population should be large enough to completely enclose 3-5 bobcat territories (Knick 1990), a similar size to the patches included in the DNP in our model. Refuge systems theory implicitly supports some usual management practices for large carnivores, such as the sanctuaries for black bears (*Ursus americanus*) in North Carolina (Powell et al. 1996).

Although the ultimate purpose of our research is to contribute to the conservation of the Iberian lynx, the most vulnerable of all the world felid species (Nowell and Jackson 1996), to provide managers with definite proposals of action is out of the scope of this paper. Nonetheless, some reflections concerning conservation follow naturally from the results above. To begin with, the Doñana lynx metapopulation seems to be declining because of stochastic as well as deterministic factors.

To oppose the decline it is necessary to find ways to increase the population size and range. A high priority issue, but exceeding the studied metapopulation, would be to make corridors to link the Doñana lynxes to the closest breeding territories located 30-50 km away, but with important barriers in between (Rodríguez and Delibes 1992).

Within the current spatial limits of the Doñana population, the simulations of the model indicate that the effect of increasing the number of territories in the sinks (by adding suitable habitat, or decreasing exclusive territories size by improving prey density) would be irrelevant for the fate of the whole metapopulation (Fig. 9). On the contrary, such efforts would have very positive effects if carried out in the sources. Also, it should be difficult and ineffective to reduce the low mortality in the sources, but an improvement of the residents' survival in the largest sink (Acebuche) up to the corresponding values of the largest source (Vera) would reduce the metapopulation extinction risk within 100 yr from 33.8 to 8% (Fig. 9). Hence, management recommendations for the Doñana lynx must be different for sources and sinks, i.e., improving the habitat and thus the carrying capacity in the sources [as previously suggested by Thomas (1994), in general, and by Litvaitis et al. (1996), in relation to the populations of endangered felids] and reducing human-induced mortality in the sinks.

These results emphasize the importance for conservation of identifying sources and sinks (Davis and Howe 1992, Wootton and Bell 1992, Doak and Mills 1994, Dias 1996), but also of recognizing the parameters determining the demographic balance of each local population, and on which of them it is feasible to act (i.e., it may be unprofitable trying to increase natality where it is high or reducing mortality where it is low).

A last aspect to consider concerns the importance for conservation of the small marginal patches. It is usually considered that metapopulation models enhance the role of small sites (Hanski and Simberloff 1997), but it is not clear whether this enhancement can be always applied to source-sink models. While some authors stress the positive features of sinks (Harrison et al. 1988, Wootton and Bell 1992), some others highlight their negative effects (Buechner 1987), even claiming for the isolation of protected areas from their surroundings, considering the negative influence they can receive from external sinks (McKelvey et al. 1993). Our simulations suggest that one of the sinks (Acebuche) has a negative effect on the closest sources (Vera and Marismillas), while two others (Torrecuadros and Puebla) seem to have a positive effect on the nearest source (Matasgordas; Table 6). These results can have direct consequences for the management of the species, and future research must try to identify the factors determining the different effects. This also supports the idea, at least for large and endangered mam-

mals, that any patch of suitable habitat can be relevant for the metapopulation persistence, as suggested by Beier (1993) for the cougar (*Felis concolor*).

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