Animal Conservation (2001) **4**, 265–274 © 2001 The Zoological Society of London Printed in the United Kingdom

Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx

Pablo Ferreras, Pilar Gaona, Francisco Palomares and Miguel Delibes

Department of Applied Biology, Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n, 41013 Sevilla, Spain

(Received 14 August 2000; accepted 27 March 2001)

Abstract

Managers trying to preserve populations of endangered carnivores are often forced to choose between restoring habitat to allow larger breeding populations or reduce risks of mortality to increase survival rates. We modelled the viability of a metapopulation of the Iberian lynx (*Lynx pardinus*) under several scenarios (habitat restoration, anti-poaching, reduction in road kills) in a real landscape to evaluate their relative effects. Increasing carrying capacity was highly effective when performed on the local populations that acted as sources but had no effect when carried out in the sinks. Realistic scenarios consisting of partial removal of the human-related mortality (assuming additive effects of causes) predicted high risk of extinction. When combined, the effects of both management options are highly dependent on where they are carried out. If the sinks are the only targets of carrying capacity enlargement, a complete removal of human-caused mortality is required, whereas increases in the carrying capacity of sources are always effective. The metapopulation risk of extinction decreases dramatically (from 45.5% to 2.1% in 100) if connectivity among source populations can be improved. According to our work, only a detailed knowledge of the spatial and demographic structure of the populations, combined with simulations of realistic situations, can help managers to select the *a priori* optimal strategy, which probably combines different management options.

INTRODUCTION

The main factors driving to the extinction of endangered species populations are contraction and modification of their habitats and increased killing by humans (Caughley & Sinclair, 1994). This is specially true for large and medium-size mammalian carnivores in human-dominated landscapes, as they have important habitat and prey requirements and high risks of mortality of human origin (e.g. Mattson, Blanchard & Knight, 1992; Nowell & Jackson, 1996; Maehr, 1997).

The relative importance of habitat degradation and increased mortality in the decline of specific populations must differ according to each situation. However, Woodroffe & Ginsberg (1998) recently postulated that high mortality in large carnivores inhabiting protected areas counteracts the positive effects of improving habitat, to the point that population size (related to the amount of preserved habitat) is a poor predictor of extinction. According to this hypothesis, conservation efforts that attempt to counter mainly stochastic processes (for instance, by managing habitat to enhance population size) are unlikely to avert extinction. Instead, management of small populations of large carnivores should be focused on reducing mortality.

As funding and current options for conservation are limited, wildlife managers must usually decide between these two broad and non-excluding acting lines: to restore and protect habitats (including prey) or to reduce human interference. Enlarging the suitable habitat should result in more territories of breeding individuals (i.e. increased carrying capacity). Also, improving habitat quality (for instance, by enhancing prey abundance) should reduce the average territory size, thus increasing the number of breeding territories. At the same time, the reproductive success could be improved, although it is constrained by the species-specific life history. On the other hand, knowing the main causes of non-natural mortality should make it possible to increase survival.

Population viability analysis (PVA) has been used as a tool to evaluate *a priori* the relative effectiveness of management alternatives (Heppell, Walters & Crowder, 1994; Bustamante, 1996). The aim of this paper is to analyze the viability of a metapopulation of an

---

All correspondence to: Pablo Ferreras, Instituto de Investigación en Recursos Cinegéticos (CSIC-UCLM), Calle Libertad, 7A, 13004 Ciudad Real, SPAIN. Tel: (+34) 926 225659; Fax: (+34) 926 225184; E-mail: pferreras@irec.uclm.es.

endangered carnivore, the Iberian lynx (*Lynx pardinus*), under different management alternatives that focus on increasing carrying capacity or on increasing survival. The Iberian lynx is considered the most vulnerable of all the Felidae (Nowell & Jackson, 1996) and has similar conservation problems to many other species of carnivores (Delibes, Rodríguez & Ferreras, 2000).

In a previous paper (Gaona, Ferreras & Delibes, 1998) we developed a spatially realistic stochastic model, written specifically to examine some general features of the same population of Iberian lynx. Results suggest that management decisions in this kind of spatially structured population can be complex, as enlarging population carrying capacity will be more effective in some patches, whereas increasing survival will be preferable in others. However, the conclusions of that paper were rather theoretical. In the present paper the old model is updated with new information, adding realism to its spatial structure and its formulation. The improved model is employed to evaluate the effect on the risk of extinction of the Doñana lynx population of several realistic management activities. Particularly we compare the effects of increasing carrying capacity and reducing mortality. Our ultimate purpose is to identify the most efficient conservation tool to improve the chances of survival of this and other source-sink metapopulations of wild carnivores.

THE IBERIAN LYNX AND THE DOÑANA METAPOPULATION

The Iberian lynx is a medium-size felid, patchily distributed in the south-western quarter of the Iberian Peninsula (Rodríguez & Delibes, 1992). The total population was estimated in the 1980s as between 1000 and 1200 individuals, but it could be even lower nowadays, owing to a continuous and generalized decline (Delibes *et al.*, 2000). It is highly specialized on living in

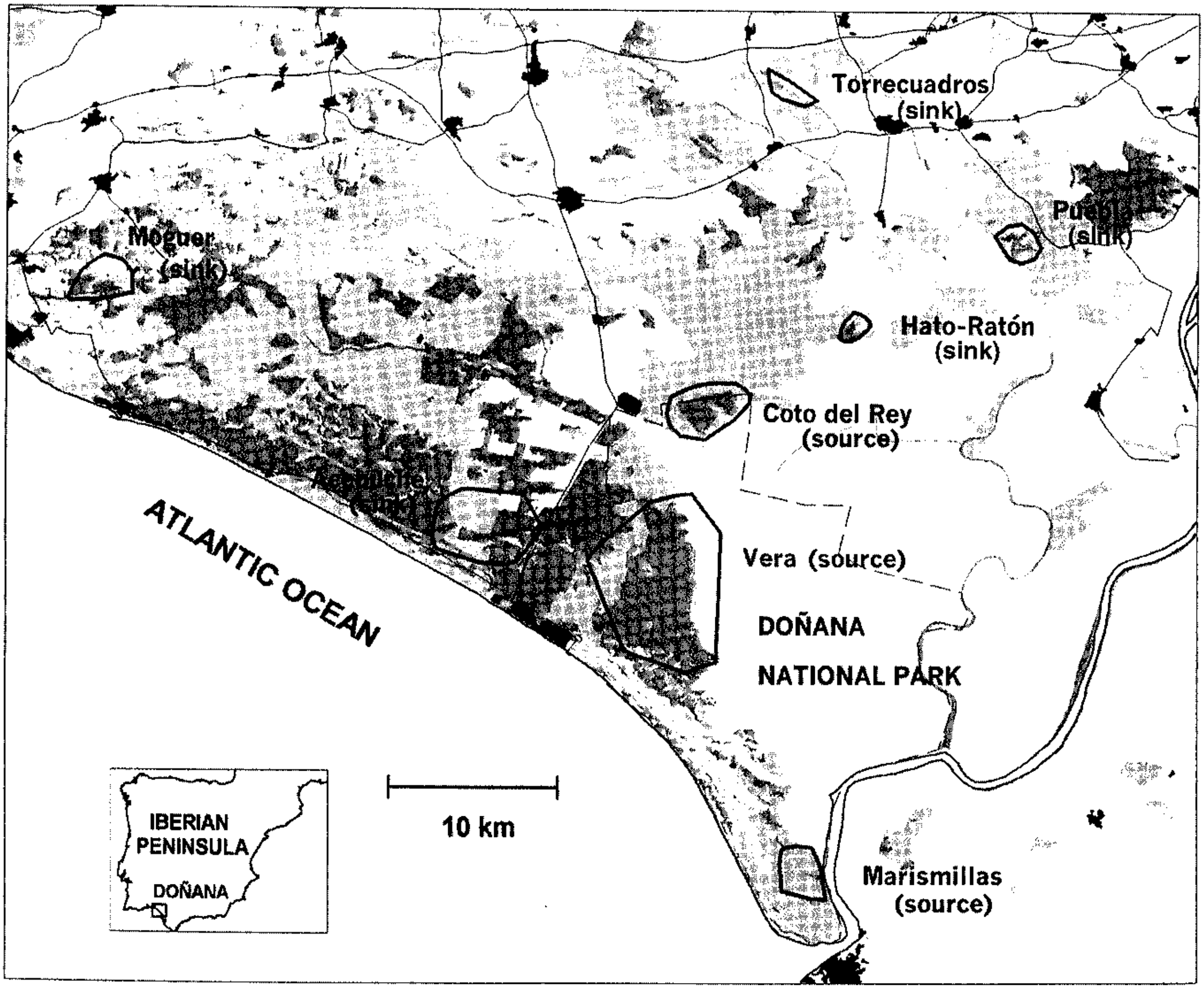

Fig. 1. Study area and spatial distribution of the local populations (thick-line polygons) of Iberian lynx in the Doñana metapopulation. Dark grey areas represent good habitats for lynx settlement (shrubland), light grey areas represent suboptimal habitats (pine and eucalyptus plantations) suitable for habitat management, and white areas represent open habitats (marshes and croplands) unsuitable for lynx. Black areas represent human populations and narrow continuous lines represent roads. The dashed line indicates the boundary of the Doñana National Park.

Mediterranean shrubland and preying upon European rabbits, *Oryctolagus cuniculus* (Delibes, 1980). Since tenure of a territory is required for adults to reproduce, availability of habitat limits the breeding opportunities (Ferreras *et al.*, 1997). Their mating system is polygynic with tendency to monogamy when both sexes are in high density (Ferreras *et al.*, 1997). Females give birth to a maximum of one litter per year of usually three cubs (authors, unpublished data). Iberian lynx suffer high mortality rates, primarily as a result of human-related factors such as poaching and road casualties (Ferreras *et al.*, 1992).

The best-studied population of Iberian lynx, effectively isolated from the remaining populations, has 50–60 individuals patchily distributed within and around the Doñana National Park (henceforth DNP, 37°00'N, 6°30'W), in south-western Spain (Fig. 1; see Rogers & Myers, 1980; Fernández-Delgado, 1997). Field data on the Iberian lynx have been collected there for several decades (e.g. Delibes, 1980; Beltrán & Delibes, 1993; Palomares *et al.*, 2000). Lynxes use for breeding mainly patches of Mediterranean scrub and Mediterranean woodland (mostly within DNP). They also use woodland plantations with little or no undergrowth for dispersal (Palomares *et al.*, 2000). Lynx occupying the discrete patches of breeding habitat constitute local populations, connected among them by dispersers to form a metapopulation (Hanski & Simberloff, 1997). Threats to this metapopulation are common to most of the Iberian lynx populations (Delibes *et al.*, 2000). Breeding opportunities are limited currently to some 12–16 females and males in up to eight local populations (Gaona *et al.*, 1998; authors, unpublished data). Survival of lynxes outside the National Park is highly reduced by human-related causes, specially during dispersal (Ferreras *et al.*, 1992). The outbreak of rabbit viral haemorrhagic disease (VHD), occurring in the Doñana area since 1990, has locally depleted rabbit populations, reducing the environment carrying capacity for lynx (Villafuerte *et al.*, 1994).

A Lynx Recovery Plan (LRP) has been in place in DNP and its surroundings since 1987 (Aymerich, 1990), with the ultimate objective of increasing lynx population in order to improve its viability. Strategies used to achieve this goal include attempts to enlarge the area occupied by lynxes, through regeneration of habitats favourable for rabbits. Pine plantations are cleared and eucalyptus plantations replaced with indigenous tree and shrubland species. Rejuvenation of scrub has been used as a method to increase rabbit densities (Moreno & Villafuerte, 1995). Another aim is to minimize lynx mortality caused by human activities. This is to be attained through surveillance on illegal hunting activities, as well as measures aimed to reduce the number of lynxes killed on roads. Although these management measures were designed on the basis of preliminary data on lynx ecology and mortality risks, no estimation of their expected effectiveness has been previously attempted. The VHD rabbit disease has handicapped the effectiveness of the Plan. As a result, the Park managers are trying to recover rabbit populations through local restocking, although results to date are very limited (Calvete *et al.*, 1997).

According to the objectives and activities of the Management Plan, we modelled the following scenarios:

1. To increase lynx carrying capacity of the area, through two management activities:
    habitat restoration and improvement, that would expand the land suitable for settlement and breeding
    prey (rabbits) enhancement, expected to reduce territory sizes, allowing more lynxes to settle and breed in a given area
2. To reduce mortality, through limiting the effect of human-related risks such as road casualties and poaching.

We also considered other deviations from the current situation, not resulting from management activities. Reductions in the survival rates of all age and sex classes were considered as a likely, undesired alternative scenario resulting from an increase in human pressure throughout the area. To evaluate the effect of a reduction of fragmentation, we also simulated as an alternative scenario the existence of a hypothetical unique population within the protected area.

UPDATE OF THE MODEL

We have improved our previous model of the dynamics of the Doñana lynx population (Gaona *et al.*, 1998) with new information gathered between 1993 and 1997. Both models are spatially realistic and structured, with density-dependent fecundity and migration, and include demographic and environmental stochasticity. The metapopulation is structured in several local populations, each having independent dynamics, and being connected only through dispersing animals. The demographic algorithm in our model was the same for each local population, with differences only due to different values of the parameters (see Gaona *et al.*, 1998 for a detailed description). We have not included the effect of catastrophes since we lack information (frequency, intensity) on occurrence of such events; moreover, probably a catastrophic event would mean the end of such a small population. Also, we have not taken into account the effect of genetic stochasticity, because only preliminary results of Iberian lynx genetics are available (F. Palomares *et al.*, unpublished data), and the effects of the presumably low genetic variability of the studied population on the demographic parameters are unknown.

For the present model, environmental stochasticity, modelled by Gaona *et al.* (1998) as two possible values of cub survival corresponding to adverse/average years, is now modelled as continuous variations in cub survival. Cub survival has a mean of 0.45/0.5 in average/optimum habitat respectively (authors, unpublished data), and its frequencies are simulated through a normal distribution (bounded between 0 and 1) yielding a 10% probability for values over 0.75/0.8 (average-

/optimum habitat) and 10% probability for values smaller than 0.15/0.2 (average/optimum habitat).

In the previous model, no additional mortality was considered for lynxes dispersing between populations within the National Park (Gaona *et al.*, 1998). For the present model all dispersers can suffer additional mortality as a consequence of the dispersal process, because they encounter higher mortality when they leave the protected area, even though their populations of origin and destination are within the National Park. The connectivity between local populations (distribution of dispersers among the local populations) has been estimated on the basis of the distance and habitats separating them (Ferreras, 2001). Also, in the improved model, dispersers can return to the population of origin.

The program was written in TURBO-PASCAL. The population dynamic was simulated 1000 times for 100 years in each of the scenarios. The probability of extinction within specific time intervals (up to 100 yr) for the whole metapopulation under each scenario was obtained. In the context of the metapopulation, the term 'extinction' means absence of at least one sex.

DEMOGRAPHIC DATA

Demographic parameters were estimated using data from 65 lynxes radio-tracked during more than 31,000 radio-days between 1983 and 1997. Below we describe the rationale of changes in the values of parameters with respect to the former model (for details on how the parameters were estimated see Gaona *et al.*, 1998).

In the first model, six local populations were considered, three of them (Vera, Marismillas and Coto del Rey – referred to as 'Matasgordas' in Gaona *et al.*, 1998) within the DNP, the most protected area in the whole Iberian lynx range, and three others (Acebuche, Torrecuadros and Puebla) outside DNP. Two new local populations have been identified recently (Hato-Ratón and Moguer) outside DNP, and subsequently these have been included in the revised model (see Fig. 1). According to the results of Gaona *et al.* (1998), local populations within DNP (Vera, Coto del Rey and Marismillas) have the ability to grow up to their carrying capacity ('sources'), whereas the remaining (Acebuche, Torrecuadros, Puebla, and now also Hato-Ratón and Moguer) tend to decrease ('sinks'). Carrying capacities (CC) are defined as the number of suitable territories we found for males or females (Table 1). Reductions in the CC of Vera (from five to four territories) and Marismillas (from three to two) have been detected since 1993 as a result of decreases in prey abundance. These changes have also been incorporated into the new version of the model. The amount of suitable habitat in the recently identified local populations (Hato-Ratón and Moguer) allows the settlement there of just a couple of breeding lynx (male and female, CC = 1).

Average litter size, estimated in the former model as 2.9 cubs per litter, is now estimated as 3.0 cubs per litter, with two, three and four cubs born in 10%, 80% and 10% of the litters respectively, based on new records of litters in the den (F. Palomares *et al.*, unpublished data). The annual survival rates of some status-and-sex classes are adjusted according to estimates obtained from new radio-tracking data. The changed survival rates are as follows: 0.9 for adults with territory in all local populations within DNP (0.8 in Coto del Rey in the previous model); 0.77 for adults without territory and non-dispersing subadults within DNP (previously 0.6 in Coto del Rey and 0.7 in Vera and Marismillas); and 0.6 for non-dispersing subadults outside DNP (previously 0.5). The remaining survival rates have the same values as in Gaona *et al.* (1998).

Table 1. Demographic parameters estimated in the current situation and expected from some management scenarios: (a) carrying capacities of local populations (maximum number of female–male territories; and (b) annual survival rates for sex-status classes.

(a) CARRYING CAPACITIES

Within DNP	Current situation	Habitat management	Prey enhancement
Vera	4	10	16
Coto del Rey	3	4	4
Marismillas	2	5	6

Outside DNP	Current situation	Habitat management
Acebuche	2	14
Hato-Ratón	1	12
Torrecuadros	1	1
Puebla	1	1
Moguer	1	1

(b) ANNUAL SURVIVAL RATES

	Currently	Without poaching	Without road kills	Without poaching and road kills
Within DNP				
Adult with territory	0.90	0.90	0.90	0.90
Adult without territory and non-dispersing subadult	0.77	0.84	0.80	0.88
Cubs	0.50	0.50	0.50	0.50
Dispersing females	0.56	0.72	0.64	0.78
Dispersing males	0.44	0.66	0.56	0.75
Old	0.60	0.60	0.60	0.60
Outside DNP				
Adult with territory	0.70	0.82	0.77	0.90
Adult without territory and non-dispersing subadult	0.60	0.80	0.70	0.88
Cubs	0.45	0.48	0.46	0.50
Dispersing females	0.48	0.69	0.58	0.78
Dispersing males	0.37	0.64	0.51	0.75
Old	0.50	0.56	0.53	0.60

Current annual survival rates are based on radio-tracking of 65 Iberian lynx between 1983 and 1998. Survival rates in the absence of poaching and road kills are calculated assuming additive effects and that the proportional contribution of both causes to mortality observed in the current situation (deaths due to poaching are twice as many as road kills) is kept for all age classes, except within DNP for adults with territory, cubs and old, which were never found dead from these causes.

MANAGEMENT SCENARIOS

Improvements in carrying capacity of local populations

The main effect of habitat improvement and increased prey populations is the increase in carrying capacity of local populations. Simulated increases of carrying capacities were limited by the habitat characteristics, the area suitable to be improved in the neighbourhood of each local population and the territory sizes of lynx. In a first stage of management, the total area occupied by breeding lynx within DNP could be enlarged, as a result of habitat management. Because territory size is negatively related to prey density (F. Palomares *et al.*, unpublished data), in a second stage of management prey enhancements would allow a higher packing of territories and, as a consequence, a larger number of lynx territories. This is translated in our model into larger carrying capacities within DNP. The next stage in management activities affecting carrying capacity is the enhancement of habitat and prey densities in populations outside DNP. This stage is not necessarily to be attained after the former ones, but we were interested in simulating it separately because management policies are carried out by different public agencies within and outside DNP.

The potential number of territories resulting from each management stage was estimated with a Geographic Information System (Idrisi 2.0; Eastman, 1995). We estimated the land surface of suboptimal habitat (basically pine and eucalyptus plantations) within or adjacent to each local population suitable for being occupied by resident lynx after habitat management. Carrying capacity expected in each local population from this first management stage was estimated by dividing this area by the average size of territories in areas of medium prey density (12.5 km^2; Ferreras *et al.*, 1997). The value expected from the second stage (which also includes prey density improvement) was calculated considering smaller territory sizes (6 km^2) currently found in the area with the highest prey density (Coto del Rey; F. Palomares *et al.*, unpublished data). The effect of increases in carrying capacity on metapopulation persistence was estimated independently for each local population.

Improvement of reproductive rate

As another possible consequence of prey enhancement, we included an increase in the reproductive rate in Vera local population, from the current value (0.6 litters/female/yr) to that found in local populations with higher prey density (0.8 litters/female/yr).

Reduction of human-related risks of mortality

We simulated the effects of mortality reduction due to the main human causes of death (Ferreras *et al.*, 1992). Illegal trapping can be reduced through intense surveillance by wardens. Road kills can be minimized by constructing effective passes under the roads in black spots for lynx, located mainly on the road between Acebuche and Vera, and on the road west of Acebuche (Fig. 1). We considered the effect of these management measures acting either separately or together (Table 1). Survival rates for each sex and social status class were estimated for each scenario, assuming proportional contributions of each cause to the total mortality for each class and additive effect of the causes. According to data from radio-tracking of 65 lynx, poaching contributes to the average annual mortality rate in the population with about twice the importance of road kills (Ferreras *et al.*, 1992; authors, unpublished data). According to this, removal of poaching would increase the annual survival rate by about twice the amount produced by the removal of road kills (Table 1). The effects of simultaneous reduction of mortality in the whole metapopulation and increase in carrying capacities in either the largest source (Vera) or the largest sink (Acebuche) were also evaluated.

OTHER LIKELY SCENARIOS

Reduced survival in a source

We simulated decreases in the survival rates of all individuals in the main local population within DNP (Vera). Mortality increases could result from reductions in warden surveillance or from new causes of mortality such as diseases. For this scenario, survival rates in Vera local population were lowered to the values outside DNP for all age–sex classes. These changes were also simulated in coincidence with increases in the carrying capacity of this source, in order to test whether such increases could counteract the negative effects of increased mortality.

Improvement of connectivity within the National Park

The land separating the local populations within DNP is occupied by natural unsuitable habitat. A marsh 2 km wide separates Coto del Rey and Vera and a system of sand dunes 12 km wide interspersed with small pine pockets occupies the land between Vera and Marismillas (Fig. 1). As a result, connection between these local populations is indirect. Rather, dispersing lynx usually leave the protected area when searching for available territories, even when vacant territories are available in other local population within DNP.

Some management actions focused on modifying the marsh and the dunes separating these local populations could improve the connectivity between them. They could include, for the marsh separating Vera and Coto del Rey, planting small pockets of marsh-tolerant trees on natural or artificial islands, to act as a stepping-stone system for the lynx. For the sand dunes separating Vera and Marismillas, connectivity could be improved through artificially broadening the narrow ecotone between the dunes and the marsh.

We considered the result of such management actions as an alternative hypothetical scenario, despite its probable reduced feasibility. In this scenario the lynx within DNP could work as a continuous population with the sum up of all local carrying capacities. Reproductive rate is set as the average rate of local populations weighted by their carrying capacity. Proportions of dispersers between local populations outside the protected area and local populations within DNP are averaged weighing by their carrying capacity. We simulated the effects of changes in the carrying capacity of this core population, either decreasing, as a consequence of habitat deterioration, or increasing, as a result of successful management. The extinction risk of the metapopulation was compared with that resulting from the current situation (connectivity not improved) with total carrying capacity within DNP similar to that in the hypothetical connected population. For this comparison, increases and reductions of carrying capacity within DNP around the current values were simulated for the local populations with real possibilities of enlargement and/or reduction, and resulting extinction probabilities averaged for each total carrying capacity.

RESULTS

General results of the improved model were rather similar to those of the previous one by Gaona *et al.* (1998). Demographic and environmental stochasticities resulted in higher risk of metapopulation extinction (45.5 % within 100 years) than the value obtained previously (33.8%). This higher extinction risk is mainly due to the reduction in the carrying capacity of two of the sources (Vera and Marismillas). Some other modifications of the model, such as the larger litter size and the higher survival rates for some sex–age classes, tended to reduce the risk of extinction in relation to the previous figure, although their effects were smaller than the effect of the reduction in carrying capacity in the two sources. Vera was still the most persistent local population and served as the primary support to the metapopulation. However, the relative role of Coto del Rey in the metapopulation dynamics was increased in relation to the former model. For instance, the average time to extinction for Vera decreased from 87 to 77 years, whereas it increased for Coto del Rey from 45 to 58 years.

Management and alternative scenarios

Improvements of carrying capacities of local populations

Local populations of Vera, Acebuche and Hato-Ratón had the largest possibilities for enlargement, given the land suitable for improvement within and around them (see Fig. 1). However, increases of only one territory in Coto del Rey and of four territories in Marismillas were possible, owing to landscape limitations. No improvements in the smallest populations of Torrecuadros, Puebla and Moguer were simulated, given the impossibility of spatial enlargement (Table 1). In Vera, Marismillas and Coto del Rey (sources), increased carrying capacities clearly improved the viability of the metapopulation (Fig. 2). However, enlargements of Acebuche and Hato-Ratón (sinks) up to 14 and 12 territories, respectively, had no effect on the persistence probability. The most effective strategy to minimize the risk of extinction of the metapopulation would be to improve the carrying capacity of the largest source (Vera). An increase of only two reproductive territories in this local population would reduce the extinction probability of the metapopulation in 100 years from 45.5% to 11.9% (Fig. 2). The effect of enlargements of Coto del Rey was similar, but only one territory could be gained in this source given its peripheral location within the protected area (see Fig. 1).

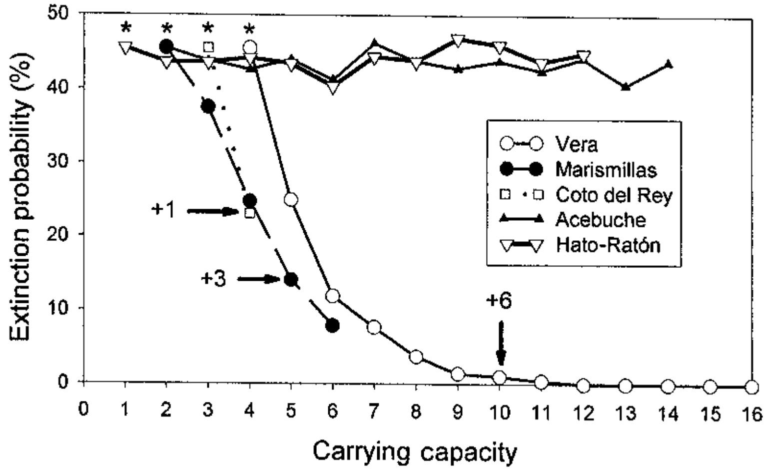

Fig. 2. Effects on metapopulation extinction risk of changes in carrying capacity (measured as number of available territories) of the sources (Vera, Marismillas, Coto del Rey) and the sinks (Acebuche, Hato-Ratón) with possibility of enlargement. Arrows indicate carrying capacities expected to be attained through habitat management alone. Asterisks show current carrying capacities, which are the departure points for management.

Improvement of reproductive rate

Improving the reproductive rate in Vera local population to the value corresponding to areas with high prey density had a large effect on metapopulation viability, reducing its risk of extinction within 100 years from 45.5% to 22%. If accompanied with simultaneous enlargement of Vera carrying capacity, this management would rapidly reduce the extinction probability of the metapopulation (Fig. 3(a)).

Reduction of human-related risks of mortality

If road deaths could be completely avoided in the whole population, the probability of extinction in 100 years would decrease from 45.5% to 22.9% (Fig. 4). This probability would fall to 6.8% if illegal trapping could be eliminated, and it would be negligible (0.2%) if both causes were eliminated. We simulated partial removals of the causes of mortality, as a consequence of limited effectiveness of management actions. The largest effect on the risk of extinction was attainable by acting on poaching: a 50% reduction of the deaths resulting from poaching would reduce the risk of extinction from 45.5% to 18.3% (Fig. 4). However, with a similar reduction (50%) of road kills, the risk of extinction was still 31.5%. Reducing by 50% the deaths due to both poaching and road accidents would mean a 13% risk of extinction in 100 years (Fig. 4). If management could eliminate only 25% of the deaths due to road accidents and illegal trapping, extinction probability would still be as high as 28.7% (Fig. 4).

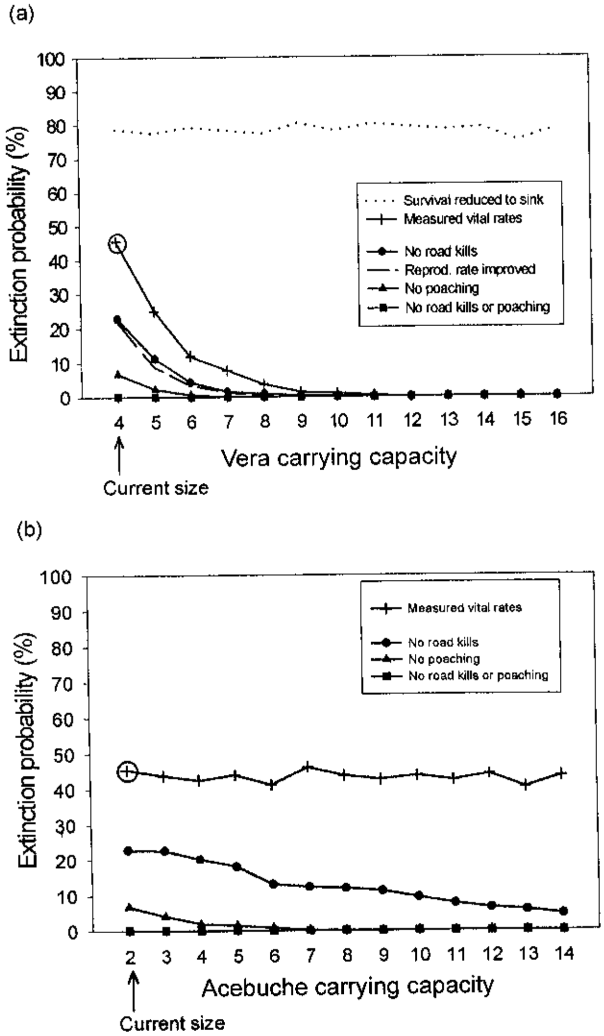

Fig. 3. Effects on the metapopulation extinction risk of increases in the carrying capacity (number of territories) of the largest source (a: Vera) and the largest sink (b: Acebuche), either alone or simultaneous with the elimination of causes of mortality: road kills and poaching. For the source (a) the effect of reduced survival down to the values currently estimated in the sinks (dotted line) and the effect of improving the reproductive rate up to the highest value estimated in Doñana (0.8 litters/female/yr) are also shown. Circles around the points indicate current situation.

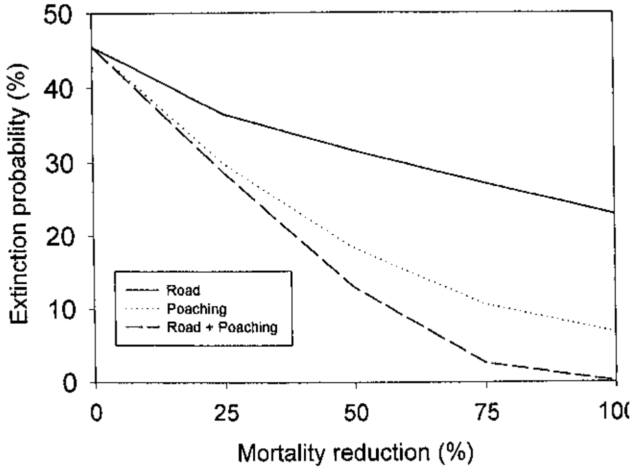

Fig. 4. Effects on metapopulation extinction risk within 100 yr of reductions in the current mortality rates due to road kills and poaching, either separate or combined. Although mortality reductions are simulated simultaneously in the same proportion for all age–sex classes and local populations, the effects are larger in the sinks, where higher mortality occurs (see Table 1).

We evaluated the effect of reducing the risks of mortality and simultaneously increasing the carrying capacity of the largest source (Vera) or the largest sink (Acebuche). A single territory increase in Vera accompanied by the removal of road kills would reduce the probability of extinction to 11.3%. If poaching was eliminated instead, the metapopulation only went extinct in 2.3% of the simulations (Fig. 3(a)). However, the enlargement of the carrying capacity in Acebuche had no effect on the metapopulation extinction risk (Fig. 3(b), upper line), unless it was accompanied by the elimination of any of the causes of mortality. For instance, eliminating road kills reduced the risk of extinction from 22.9% to 13.1% if Acebuche was enlarged from two to six territories. Again, eliminating the deaths due to poaching and simultaneously increasing carrying capacity from two to six territories was more effective, and produced a negligible risk of extinction (0.8%; Fig. 3(b)).

Reduced survival in the sources

The risk of extinction of the metapopulation was highly sensitive to the reductions in the survival rates within the sources. Changing survival rates in the Vera local population down to the values found in its closest sink, Acebuche, increased the extinction risk of the metapopulation to 78.7% (Fig. 3(a)). Enlargements of Vera carrying capacity to 16 territories were not able to counteract the effect of reduced survival. In this hypothetical situation, Vera would become a sink, behaving in a similar way as Acebuche at present (compare upper lines of Figs. 3(a) and 3(b)).

Improvement of connectivity within the National Park

A continuous population within DNP with carrying capacity the sum of the current local populations (nine territories) would go extinct only in 2.1% of the simulations (Fig. 5). Even with a carrying capacity of only five territories, the extinction risk was lower (32.4%) than that estimated for the currently existing metapopulation. Further reductions of the carrying capacity below five caused a dramatic rise of the extinction probability (100% for two territories). With a carrying capacity of 14 territories, such a core population provided a negligible risk of metapopulation extinction (0.1%; Fig. 5). The connectivity enhancement within the protected area reduced the risk of extinction along a broad range of total carrying capacity (Fig. 5). However, for large total carrying capacities (>10) the effect of increasing the connectivity decreased, being negligible above 13 territories (Fig. 5).

DISCUSSION

Limitations of our PVA

Small populations in the wild can suffer increased risks because of inbreeding (Frankham, 1995), as shown by recent empirical studies (Saccheri *et al.*, 1998; Madsen *et al.*, 1999). Therefore, a likely limitation to our model is that it does not include the effects of genetic stochasticity. Some ecological problems, such as a high incidence of disease or a lack of adaptability to changing environmental conditions, could have a genetic origin, as has been shown for the Florida panther (*Felis concolor*; Roelke, Martenson & O'Brien, 1993). If this were a general pattern in the wild, and particularly for the Iberian lynx, our models would underestimate the risks of extinction. Another limitation of our model is that we have ignored the effect of catastrophes. Catastrophic reductions of prey, for example resulting from diseases such as VHD, should affect carrying capacity and/or reproductive rate.

Restore habitat or reduce mortality? The Lynx Recovery Plan in Doñana (LRP)

According to Woodroffe & Ginsberg (1998), population size of carnivores in reserves would be a poor predictor of their viability, because such reserves are often demographic sinks owing to high mortality on their edges. In the case of the Iberian lynx, population size (or carrying capacity) in the sources is an excellent predictor of the persistence of the whole metapopulation, but is not in the sinks (Fig. 2), as previously suggested by Gaona *et al.* (1998). The discussion about the effect of size of protected areas for preserving large carnivores (Woodroffe & Ginsberg, 1998) has its cornerstone in the lack of efficacy of measures for mortality prevention in many such reserves. In some cases, increasing the size of reserves or improving their quality (instead of reducing mortality) would be pointless, since this would produce nothing but larger sinks.

The current focus of the LRP in Doñana is to increase carrying capacity of local populations through vegetation management to obtain optimum habitat areas for rabbits (Aymerich, 1990). According to our results, this should remain an objective for source populations (e.g.

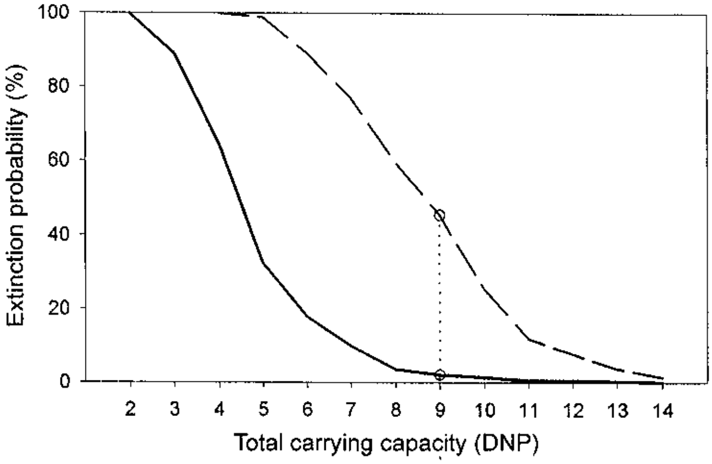

Fig. 5. Effect on the metapopulation probability of extinction of varying the carrying capacity of a hypothetical continuous population within the National Park (continuous line) compared with the current situation with limited connectivity (dashed line) and similar variations in carrying capacity. The dotted line indicates the overall current carrying capacities of local populations inside the protected area.

Vera and Marismillas), but not for sink habitats (e.g. Acebuche). In our case study, the sinks are the results of reduced survival rates of lynx living there. Because of that, a sink such as Acebuche would become a source when any of the anthropogenic causes of mortality is eliminated, and then increases in its carrying capacity would have positive effects on the metapopulation persistence (Fig. 3(b)).

A second aim of the LRP is to reduce lynx mortality resulting from human-related factors throughout the area for both resident and dispersing lynxes. Dispersal between patches seems to be limited by the high mortality associated with the dispersal process rather than by a lack of corridors (Ferreras *et al.*, 1992). Considering specific causes of mortality, the greatest effect could be attained through reducing poaching (Fig. 4). Reducing road accidents seems the easiest measure, since deaths are concentrated in particular black spots on a few roads. Our simulations assume that the effects of the causes of mortality are additive rather than compensatory, as natural mortality inside the protected area does not compensate the lack of human-caused deaths. If mortality due to different human-related causes were, at least partially, compensatory we should expect lower effects on the risk of extinction of partial reductions of a specific cause of death. Therefore, an effective management to preserve the metapopulation should include the simultaneous reduction of all human-related causes of mortality (road+poaching in Fig. 4).

In spite of being in effect since 1987, the LRP has achieved only local increases of rabbit densities throughout DNP (Moreno & Villafuerte, 1995), but no apparent effect on number of reproductive territories for lynx (carrying capacity). The efficacy of the adopted measures may have been counteracted by unexpected negative influences, such as the VHD outbreak in rabbits (Villafuerte *et al.*, 1994) and an apparent depletion of the water table level (reducing pasture availability for rabbits), because of an extended drought and/or overexploitation (Fernández-Delgado, 1997). This reduction in rabbit populations is presumably the cause of the observed carrying capacity decrease in Vera and Marismillas, as taken into account in our updated model.

Some general models postulate that increasing carrying capacity of patches has a stronger effect than increasing patch number and connectivity (Drechsler & Wissel, 1998). This agrees with the results of some specific studies, such as that of Lindenmayer & Lacy (1995). In our situation, improving patch connectivity within the protected area had a stronger effect than increasing the carrying capacity in the sources. However, the effect of increasing connectivity depended on the total carrying capacity, being negligible for large total values (see Fig. 5). Reductions in the carrying capacity of DNP resulted in dramatic increases in the probability of extinction, with either reduced or improved connectivity (Fig. 5). Therefore, carrying capacity within the protected area is probably now at a critical level, such that any reduction would lead to a fast decline of the metapopulation.

Applications to the conservation of wild carnivores

The results of our model stress the usefulness of some well-preserved refuges acting as sources. This need has been previously claimed for the conservation of many wide-ranging carnivores (Powell *et al.*, 1996; Beringer *et al.*, 1998). The size of these refuges (i.e. the carrying capacity) has a large effect on the population persistence, which in our case can be improved by increasing the connectivity among the patches contained within that area (Fig. 5).

Recommendations obtained from models for population conservation are sometimes difficult to implement. For instance, the most effective strategy according to our model, increasing carrying capacities of the sources, could be attained in at least two ways: by enlarging the area suitable for lynx and by improving habitat quality (Litvaitis *et al.*, 1996). The latter is *a priori* the more effective, since prey enhancement can yield not only increases in carrying capacity, but also increase of reproductive rates (Fig. 3(a)). However, this management activity has proved difficult to implement in DNP (Moreno & Villafuerte, 1995). Although large reductions of mortality factors would increase population persistence (Fig. 4), such strategies also have practical difficulties. Whereas reducing road deaths seems possible, an effective action against poaching seems highly difficult in the short term. Our results provide the benefits expected from each management action, but managers should account for the cost and feasibility of each measure and decide which is preferable.

Our paper emphasizes the importance of the spatial structure of the populations to answer the general questions proposed here. When detailed information on demographic parameters allows us to simulate their dynamics and the effects of alternative, realistic management scenarios, it is possible to provide managers with the expected outputs which can help them to select beforehand the best management option. However, this is not usually the case. Therefore, the only way to guarantee the survival of wild carnivores is to provide, at the same time, refuge habitats with high carrying capacity and low mortality.

Acknowledgements

The research was supported by DGICYT (projects 944, PB87-0405, PB90-1018, PB94-0480 and PB97-1163), project LIFE from the European Union, ICONA, CMA of Junta de Andalucía and Rover España S.A. First author was supported by a research contract from the Spanish Ministry of Education and Culture and by an associated teacher contract from the University of Castilla–La Mancha. J. M. Fedriani, J.Calzada, E. Revilla and N. Fernández, among others, provided helpful support for radio-tracked lynxes. Comments from J. Bustamante, S. Harrison, H. Possingham and two anonymous referees improved former versions of the manuscript.

REFERENCES

Aymerich, M. (1990). Management of a lynx population in the Doñana National Park. In *Seminar on the situation, conservation, needs, and reintroduction of lynx in Europe, Neûchatel, Switzerland, 17–19 Oct. 1990, 33–35.* Strasbourg, France: Council of Europe.

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

Beringer, J., Seibert, S. G., Reagan, S., Brody, A. J., Pelton, M. R. & Vangilder, L. D. (1998). The influence of a small sanctuary on survival rates of black bears in North Carolina. *J. Wildl. Mgmt.* **62**: 727–734.

Bustamante, J. (1996). Population viability analysis of captive and released bearded vulture populations. *Conserv. Biol.* **10**: 822–831.

Calvete, C., Villafuerte, R., Lucientes, J. & Osacar, J. J. (1997). Effectiveness of traditional wild rabbit restocking in Spain. *J. Zool. (Lond.)* **241**: 271–277.

Caughley, G. & Sinclair, A. R. E. (1994). *Wildlife ecology and management.* Boston, MA: Blackwell Scientific.

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

Delibes, M., Rodríguez, A. & Ferreras, P. (2000). *Action plan for the conservation of the Iberian lynx (**Lynx pardinus**) in Europe.* Strasbourg: Council of Europe Publishing.

Drechsler, M. & Wissel, C. (1998). Trade-offs between local and regional scale management of metapopulations. *Biol. Conserv.* **83**: 31–41.

Eastman, J. R. (1995). Idrisi *for Windows. User's guide.* Worcester: Clark Labs for Cartographic Technology and Geographical Analysis, Clark University.

Fernández-Delgado, C. (1997). Conservation management of a European Natural Area: Doñana National Park, Spain. In *Principles of conservation biology:* 458–467. Meffe, G. K. & Carroll, C. R. (Eds). Sunderland, MA: Sinauer Associates.

Ferreras, P. (2001). Landscape structure and asymmetrical interpatch connectivity in a metapopulation of the endangered Iberian lynx. *Biol. Conserv.* **100**: 125–136.

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., Beltrán, J. F., Aldama, J. J. & Delibes, M. (1997). Spatial organization and land tenure system in the endangered Iberian lynx (*Lynx pardinus* Temminck, 1824). *J. Zool. (Lond.)* **243**: 163–189.

Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: a review. *Genet. Res.* **66**: 95–107.

Gaona, P., Ferreras, P. & Delibes, M. (1998). Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecol. Monogr.* **68**: 349–370.

Hanski, I. & Simberloff, D. (1997). The metapopulation approach, its history, conceptual domain and application to conservation. In *Metapopulation biology: ecology, genetics, and evolution:* 5–26. Hanski, I. A. & Gilpin, M. E. (Eds). San Diego, CA: Academic Press.

Heppell, S. S., Walters, J. R. & Crowder, L. B. (1994). Evaluating management alternatives for red-cockaded woodpeckers: a modelling approach. *J. Wildl. Mgmt.* **58**: 479–487.

Lindenmayer, D. B. & Lacy, R. C. (1995). Metapopulation viability of Leadbeater's possum, *Gymnobelideus leadbeateri* in fragmented old-growth forests. *Ecol. Applic.* **5**: 164–182.

Litvaitis, J. A., Beltrán, J. F., Delibes, M., Moreno, S. & Villafuerte, R. (1996). Sustaining felid populations in human-dominated landscapes. *J. Wildl. Res.* **1**: 292–296.

Madsen, T., Shine, R., Olsson, M. & Witzzell, H. (1999). Restoration of an inbred adder population. *Nature* **402**: 34–35.

Maehr, D. S. (1997). *The Florida panther: life and death of a vanishing carnivore.* Washington, DC: Island Press.

Mattson, D. J., Blanchard, B. M. & Knight, R. R. (1992). Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *J. Wildl. Mgmt.* **56**: 432–442.

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.

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

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J. & Revilla, E. (2000). Iberian lynx in a fragmented landscape: pre-dispersal, dispersal and post-dispersal habitats. *Conserv. Biol.* **14**: 809–818.

Powell, R. A., Zimmerman, J. W., Seamen, D. E. & Gilliam, J. F. (1996). Demographic analyses of a hunted black bear population with access to a refuge. *Conserv. Biol.* **10**: 224–234.

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

Roelke, M. E., Martenson, J. S. & O'Brien, S. J. (1993). The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Curr. Biol.* **3**: 340–350.

Rogers, P. M. & Myers, K. (1980). Animal distributions, landscape classification and wildlife management, Coto Doñana, Spain. *J. Appl. Ecol.* **17**: 545–565.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**: 491–494.

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

Woodroffe, R. & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**: 2126–2128.