
Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits

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Abstract: *Top predators have often been persecuted because of their supposed negative effects on species of economic concern on which they feed. In some cases, however, they may actually benefit their prey through intraguild predation on other smaller predators that share the prey. In each of two representative situations, in one of which lynx were present and in the other absent, we (1) estimated gross numbers of rabbits taken by lynx and Egyptian mongooses (smaller predators that are themselves preyed upon by lynx); (2) simulated size-structured rabbit populations of different densities, taking into account the reproductive value of the individuals taken by predators; and (3) estimated actual rabbit densities. Numbers of rabbits taken by predators during a year were found to be between 4.8 and 9.5 times greater when lynx were not present. After a year, rabbit population growth for an initial rabbit density of 15/ha was between 12% and 22% lower when lynx were not present. For lower initial rabbit densities, the positive effect of lynx presence on rabbits was greater. Actual rabbit densities in the areas used by lynx were 2–4 times higher than in areas not used by lynx, even though these areas were similar or identical in habitat composition. These results support the suggestion that removal of top predators may sometimes have a negative effect on prey populations of human economic concern.*

Resumen: *Los grandes predadores han sido con frecuencia perseguidos porque se ha supuesto que causan un efecto negativo sobre las especies de presas de interés económico de las que se alimentan. Sin embargo, en algunos casos, podrían afectar positivamente a sus presas si predan sobre otros predadores que también se alimentan de las mismas presas. En cada una de dos situaciones representativas (presencia y ausencia de linces) en Doñana (Suroeste de España), se estimó el consumo bruto de conejos por parte de linces y meloncillos (un predador pequeño que puede ser predado por linces), se simuló una población de conejos con la que también se pudo considerar el valor reproductivo de los individuos capturados por ambos predadores, y se estimó la densidad real de conejos. El número de conejos consumidos en ausencia de linces fue entre 4.8 y 9.5 veces mayor que en su presencia, independientemente del tamaño de los mismos. Las tasas de crecimiento después de un año de la población de conejos simulada fueron entre un 12% y un 22% menores en ausencia de linces. Para densidades menores de conejos el efecto positivo de la presencia del lince fue mayor. Bajo densidades de conejos y predadores poco realistas la presencia del lince no tuvo un efecto positivo sobre las poblaciones de conejos. Las densidades reales de conejos en las áreas usadas por linces fueron de 2–4 veces más elevadas que en las áreas no usadas por linces, a pesar de que las áreas comparadas fueron similares o idénticas en vegetación. Estos resultados apoyan la idea de que la eliminación de los grandes predadores puede tener un efecto negativo sobre las poblaciones de presas que son de interés económico para el hombre.*

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Introduction

Conflict with humans is an important reason for the population decline of many endangered species. Top predators are target species of these confrontations because they can potentially threaten human life and economics (for example, bears, *Ursus arctos*, Maguire & Servheen 1992; wolves, *Canis lupus*, Naess & Myserud 1987) and interfere with game and fisheries (for example, hen harriers, *Circus cyaneus*, Redpath 1991; otters, *Lutra lutra*, Kruuk et al. 1993; lynx, *Lynx lynx*, Capt et al. 1993). Predators have historically been eliminated from large areas as a means of protecting prey species of economic concern to humans, such as small game (see Tapper 1992 as an example in Europe). Although most of these top predators are now legally protected, their conservation is not guaranteed if agencies responsible for wildlife do not present sound and defensible arguments to local people who directly interact with animals. Our aim is to provide an example of how the absence of a top predator probably decreases population density of a small game species due to the increase of smaller predator populations that are normally controlled by top predators (by a process of mesopredator release, sensu Soulé et al. 1988). In this study we examine the relationship among (Fig. 1) Iberian lynx, *Felis pardina* (the top predator), Egyptian mongooses, *Herpestes ichneumon* (the opportunistic predator), and European rabbits, *Oryctolagus cuniculus* (the prey of

economic concern) in the Iberian Mediterranean ecosystem of southwestern Spain.

The Iberian lynx is the top predator of the terrestrial vertebrate community in the ecosystem (Valverde 1960). Its staple prey is rabbits (Delibes 1980), but it also kills smaller opportunistic carnivores such as Egyptian mongooses, red foxes, *Vulpes vulpes*, and European genets, *Genetta genetta* (Valverde 1960; Palomares & Ferreras 1995). Genets are not an important predator of rabbits (Delibes 1974; Palomares & Delibes 1991a), so they were not included in our study. Foxes were also excluded because their spatial relationship with lynx are still unclear; track censusing data suggesting that the number of foxes might not be affected by the presence of lynx (Palomares et al. in press).

The Iberian lynx is the most endangered carnivore in Europe (Mallison 1978) and probably one of the most threatened in the world. It is placed in Annex II of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) and is listed as endangered on the Red List of the International Union for Conservation of Nature and Natural Resources (1986) and the Spanish Red Data Book (Instituto Nacional para la Conservación de la Naturaleza 1992). It is also included in Appendix I of the Convention for the International Trade of Endangered Wild Fauna and Flora Species (Jackson 1990). This felid is restricted to the Iberian Peninsula, where about 1000 individuals survive at present. Although the Iberian lynx is now legally protected, it has been and probably still is hunted because it is considered a vermin species (Rodríguez & Delibes 1992). On the other hand, rabbits are an important species for humans and wildlife in the Mediterranean ecosystem because they constitute the basic game for many hunting areas and the main prey for many endangered predators (Delibes & Hiraldo 1981).

The potential effect that the presence of lynx has on rabbit populations was approached in different stages. (1) We estimated the gross predation by lynx and mongooses on rabbits in each of two adjacent and similar areas that differed in lynx numbers. In one area lynx were uncommon and subjected to human interference; in the other lynx were common and undisturbed. (2) We simulated a size-structured rabbit population and determined what the population sizes would be in each area at the end of complete reproductive cycles, taking into account predation by lynx and mongooses. (3) We determined the actual number of rabbits in different sections of the two adjacent, similar areas that differed in lynx numbers.

Study Area and Methods

We used information gathered since 1986 in Doñana National Park and along its border to the north, (southwestern Spain). In the area of the National Park there are

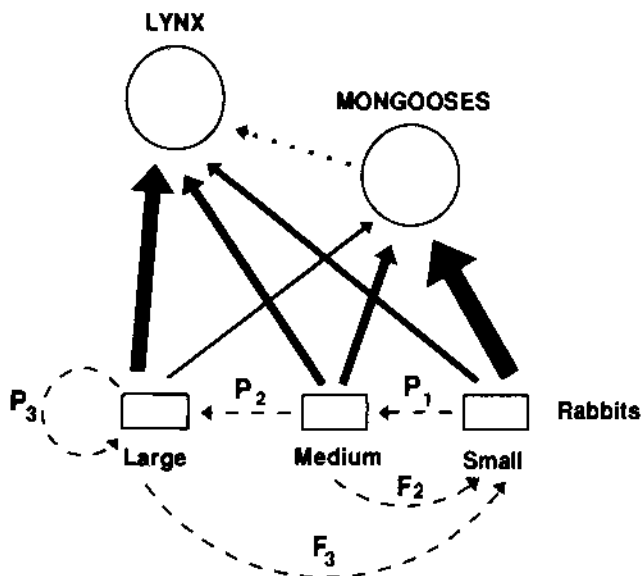


Figure 1: Diagram outlining the interactions between lynx, mongooses, and rabbits in this study. Lynx decrease mongoose density (short-line arrow), while both predators consume rabbits of each size class (continuous-line arrows; line thicknesses show the relative strengths of the interactions). Each class of rabbit size is characterized by different fecundities (F) and mortalities (P).

two patches (about 5 km² and 3 km²) of autochthonous forest of *Quercus suber* trees and *Pistacia lentiscus* shrubs. These patches are both named Matasgordas. Matasgordas is bordered by marsh to the south and east, by pastureland to the west, and by *Pinus pinea* forest to the north. Interspersed in the pine forest are smaller patches of vegetation similar to Matasgordas, except that their overstory, when present, consists of *P. pinea* or *Fraxinus* sp. instead of *Q. suber* (Fig. 2).

The presence of the national park boundary in the study area results in two different levels of human interference. Under full protection is Matasgordas (Fig. 2), where people enter only occasionally and in low numbers. The area outside the national park is subjected to a high level of human interference, mainly from religious pilgrimages, recreational activities, and poaching on ungulates and rabbits. Probably as a consequence of human interference, lynx primarily use Matasgordas and rarely use the rest of the area (Palomares et al. 1991, in press).

Predator Rabbit Consumption

The daily rabbit consumption by predators (PDRC) was estimated as follows:

$$PDRC = \sum (D_i \cdot [\sum NR_{ij} C_{ij}] \cdot PRB_i)$$

where D_i is the predator i density, NR_{ij} is the number of rabbits of the class j taken daily by the predator i , and PRB_i is the daily proportion of rabbit biomass in the diet of the predator i .

Studies on the use of space by lynx and mongooses indicate that Matasgordas and the other, smaller patches of *P. lentiscus* outside Matasgordas are suitable for both species (Palomares & Delibes 1993a; P. Ferreras unpublished data). Lynx mainly use Matasgordas, however, both the two large patches and the patch of *P. lentiscus* with *Fraxinus* sp. in between (to the south of the National Park border; see Fig. 2). Minimum lynx density there is 0.5/km², but mongooses are rare (0.2 ind/km²) due probably to lynx presence (Palomares et al. in press). We also considered an extreme case of 0.75 lynx/km² in our density estimates because lynx can reach in a given year up to 0.7–0.8 ind/km² (Palomares et al. in press). For mongoose density estimates we also considered a decrease of up to 50% within Matasgordas because mongoose density inside Matasgordas was estimated using the information gathered during the year of highest mongoose use of this area.

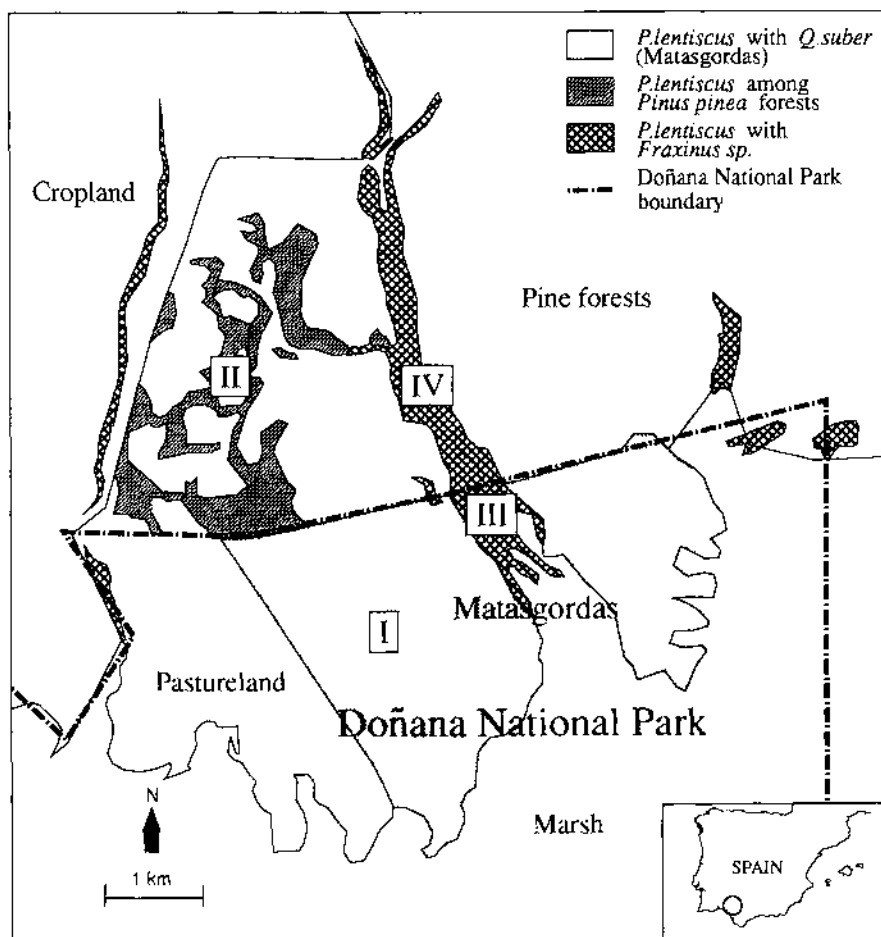


Figure 2. Map of the study area in Southwestern Spain. Rabbit densities were estimated in areas I, II, III, and IV.

Mongoose used patches of *P. lentiscus* outside the national park. Overall minimum mongoose density was 2.0/km² (Palomares & Delibes 1992; Palomares et al. 1995). The overall density estimate does not represent the number of mongooses foraging in *P. lentiscus* patches, where mongooses spent 78% of their activity time (Palomares & Delibes 1993a). Also, taking into account that the suitable patches outside Matagordas represented only 34.6% of the total area where mongoose density was estimated, the corrected minimum mongoose density for these patches was 4.9 ind/km². Mongoose density was estimated using the method proposed by McLellan (1989) consisting of delimiting a trapping area and quantifying the proportional use by each radio-tracked individual over a given time period. Therefore, density estimates largely depended on the actual number of trapped animals, and the figures can report only minimum densities. Thus, mongoose density outside Matagordas might be expected to be higher than 4.9 ind/km². We also considered a maximum increase of up to 25% in mongoose density in spite of the fact that we were confident that we trapped almost every animal living in the area.

We considered annual variations in predator numbers only for mongooses in the area outside Matagordas, where lynx were absent. Palomares & Delibes (1992) estimated a minimum adult density of 1.2 ind/km² in this area (with a corrected minimum adult density of 2.7 ind/km²); the inclusion of young results in a density estimate of 2.0 ind/km² (with a corrected minimum density of 4.9 ind/km²). We considered a mongoose density of 2.7/km² from March to June because young were observed in the area only from July to February (Palomares & Delibes 1993b). We assumed constant densities for lynx because studies of dispersal behavior have shown that subadults leave the natal area a few months after a new lynx is born (P. Ferreras, unpublished data); thus there is no noticeable increase in numbers of lynx preying upon rabbits following reproduc-

tion. We did not consider increased rabbit consumption due to pregnancy and lactation in females for mongooses or lynx.

Hereafter "the most realistic" predator densities will be taken to be 0.5 ind/km² for lynx, 0.2 ind/km² for mongooses in the area used by lynx, and 4.2 ind/km² (the annual mean density) for mongooses in the area where lynx were absent.

Although in general mongooses are opportunistic predators in Doñana, in Coto del Rey they mainly consume rabbits (Palomares 1993). Rabbits represent between 33% and 87% of the biomass consumed by mongooses throughout the year (Table 1). Small rabbits (less than 350 grams and younger than two months) are the most commonly consumed, followed by medium-sized (between 350 and 700 grams and between two and four months), and large (more than 700 grams and older than four months) (Table 1). Daily food intake during a feeding trial carried out with an adult male mongoose (Palomares & Delibes 1990) was 366 grams (SD = 101, range = 213–470, *n* = 7 days), which would be equivalent to 2–3 small rabbits, one medium-sized rabbit, or half of a large rabbit per day. However, field observations made during continuous tracking of mongooses engaged in rabbit capture and consumption indicate that when a mongoose finds a breeding den of rabbits, all the small rabbits available are killed even though some may not be eaten. When medium-sized or large rabbits are captured, usually some rabbit remains are left uneaten (F. Palomares, unpublished data). Therefore, we considered that each mongoose preys on at least one litter in a breeding den (or four small rabbits), a medium-sized rabbit, or a large rabbit. We considered four rabbits to be the number of young per breeding den because it approximates the figure of 3.9 fetuses per female found by Delibes and Calderón (1979) in Doñana.

The lynx basically feeds on subadult and adult rabbits (Delibes & Hiraldo 1981). Rabbits represent between

Table 1. Mongoose density in area not used by lynx, rabbit biomass in lynx and mongoose diet, and rabbit class size eaten by lynx and mongoose.

Time Period	Mongoose Density ^a (ind/km ²)		Rabbit Biomass in Diet (%)		Rabbit Class Size Eaten by Lynx ^d (%)			Rabbit Class Size Eaten by Mongoose ^c (%)		
			Lynx ^b	Mongoose ^c	Small	Medium	Large	Small	Medium	Large
January–February	4.9	6.1	75	87	33	30	37	72	28	0
March–April	2.7	3.4	82	83	0	50	50	88	10	2
May–June	2.7	3.4	88	59	17	58	25	53	40	7
July–August	4.9	6.1	91	33 ^e	17	22	61	20 ^e	20 ^e	60 ^e
September–October	4.9	6.1	95	33	0	27	73	20	20	60
November–December	4.9	6.1	78	48	12	24	64	63	32	5

^a Sources: Palomares & Delibes (1992, 1993a, 1993b).

^b Source: Delibes (1980).

^c Source: Palomares & Delibes (1991b).

^d Source: M. Delibes (unpublished data).

^e Information on biomass in diet and rates of consumption of each rabbit size was not available for this period, so we assumed values similar to September–October.

75% and 95% of the biomass consumed by lynx throughout the year (Table 1). Large rabbits are the most commonly consumed size, followed by the medium and the small sizes (Table 1). We assumed that a lynx daily consumes one large rabbit, two medium-sized rabbits, or four small rabbits, basing our assumption on a study of energy expenditure of free-ranging lynx at Doñana that estimated the daily prey requirements of lynx as the quantity equivalent to a rabbit weighing 800–1000 grams (Aldama et al. 1991).

The percentage of rabbit biomass in the diet and the rabbit size class eaten by mongooses and lynx were taken to be invariable because rabbit consumption was found to be similar in two different years for mongooses (Palomares & Delibes 1991b) and throughout several years for lynx (Beltrán & Delibes 1991).

Rabbit Population Model

We simulated a rabbit population structured in three size classes (small, medium, and large; Fig. 1). These size classes largely correspond with young, subadult, and reproductive individuals in Iberian Mediterranean environments (Soriguer 1981). We elaborated a matrix model where the reproductive and survival characteristics of the rabbit population were summarized. The unit time used in the model was two months, and the simulations were initiated in September–October when all rabbits are expected to be large. The reproductive parameters were obtained from Delibes & Calderon (1979) and Soriguer (1981). The litter size was four and the newborn sex-ratio 1:1. The proportion of reproductive adult females (f = actual number of breeding females/total of females which could breed) changes through the year, so we used the following f values after Soriguer (1981): 0.44 for January–February, 0.68 for March–April, 0.19 for May–June, 0.0 for July–August and September–October, and 0.46 for November–December. Four reproductive periods were considered.

The rabbit population was forced into equilibrium, with survival probabilities close to those estimated by Soriguer (1981) (10% for small, 70% for medium, and 98% for large). Survival probabilities and fertilities were calculated for a birth-flow population, when the births occur continuously over the time interval. The matrix for a such population takes the following form:

$$\begin{bmatrix} 0 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix}$$

where F_i is the size-specific fecundity and P_i is the size-specific survival probability (the subscripts 1, 2 and 3 corresponding to small, medium, and large, respectively). We calculated the matrix coefficients according to Caswell (1989), with the following results:

$$F_2 = 0.3465 \cdot f; F_3 = 1.089 \cdot f; P_1 = 0.1; P_2 = 0.63, \text{ and } P_3 = 0.98.$$

Each rabbit population was then subjected to extraction of rabbits according to the numbers and sizes estimated to be consumed by predators (lynx and mongooses) for each two-month period and for each of the two situations (presence and absence of lynx). Both predators are able to capture some small rabbits from July to October and some medium-sized rabbits from September to December (Table 1). We assumed that an equivalent number of medium-sized rabbits were consumed instead of small ones in July–August, an equivalent number of large rabbits instead of medium-sized and small ones in September–October, and an equivalent number of large rabbits instead of medium-sized ones in November–December because in our simulation we stopped considering rabbit reproduction in July–August and September–October. The full equation follows:

$$\begin{pmatrix} S \\ M \\ L \end{pmatrix}_{t+1} = \left[\begin{pmatrix} 0 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{pmatrix} \cdot \begin{pmatrix} S \\ M \\ L \end{pmatrix}_t \right] - \begin{pmatrix} S_p \\ M_p \\ L_p \end{pmatrix}_t$$

The effect of lynx presence on the rabbit population was obtained by dividing the number of rabbits after one year by the initial number of rabbits—rabbit growth rates after complete rabbit reproductive cycles. According to our simulations, most of the rabbit populations became extinct after a few years—a situation that is not occurring in our study area. Comparing the results after one year, therefore, minimized the effect that time would have on the results if we had selected a greater time interval. Furthermore, empirical data needed to model a rabbit population reaching a stable equilibrium (or only slowly decreasing) after a long time despite predation from lynx and/or mongooses is not available at present.

Rabbit population simulations were used to evaluate the conditions under which the presence or absence of lynx would have no effect on rabbits. Thus we checked if results were sensitive to the parameter values that we used or, on the contrary, if results were tolerant of a broad range of values. The simulation allowed us to determine if lynx presence and absence had no effect on the rabbit population under field conditions. The main factors of concern were initial rabbit density and densities of predators in the areas with or without lynx. Simulations were run with rabbit densities as low as 10/ha and in increments of 5/ha up to 100/ha. Predator densities used were those reported above (namely, 0.5 and 0.75 lynx/km² and 4.2 and 5.2 mongooses/km²) and those others that tended to nullify the differences between lynx presence and absence (in other words, increasing lynx density in the area used by lynx and decreasing mongoose density in the area not used by

lynx). Arbitrarily, we considered that the presence or absence of lynx affected rabbits insignificantly if the effect was less than 5%: $100 \times (\text{rabbit growth rate in the area with lynx} - \text{rabbit growth rate in the area without lynx}) / \text{rabbit growth rate in the area with lynx} < 5\%$. Simulations were run under all possible combinations of initial rabbit density and predator densities. We quantified the sensitivity of the results to these three parameters through a stepwise regression analysis (Rabinovich & Himschoot 1990). The model parameters of concern were the independent variables. The effect of lynx presence on rabbits (percentages) was the dependent variable. For the sensitivity analyses, five values were used for the two predator densities (the most realistic values for both predators, plus values of 5%, 15%, and 25% above and below the most realistic values), and three values were used for initial rabbit density (20 ind/ha and 25% above and below this density). Results of all possible combinations ($5^2 \times 3 = 75$ combinations) were used in the analysis. The standardized partial coefficients of regression were used to determine the relative importance of each independent variable, the parameter having the higher coefficient having the maximum effect on results (see Rabinovich & Himschoot 1990).

Rabbit Density Estimates

We estimated rabbit density using line transect sampling (Burnham et al. 1980) within four sections of the study area. All four sections were dominated by *P. lentiscus* but were differentially used by lynx and mongooses. The areas were Matasgordas, patches of *P. lentiscus* interspersed with pine forest, and two sections of one patch of *P. lentiscus* with *Fraxinus* sp. (areas I, II, III, and IV, respectively, on Fig. 2). Sections II and IV were selected because they were identical in habitat composition (although used differently by lynx and mongooses) and therefore acted as a control for the slight habitat differences in the case of overstory in the other sections compared.

Transects were surveyed on foot in October at dusk (from sunset to about 25 min later), the time of the year with the lowest rabbit density (Soriguer 1981) and the time of day that is the best census time for the study area (Villafuerte et al. 1993). Earlier we carried out three samplings in order to define a truncation distance, a grouping interval of observation distances, and the number of sampling days needed. Observation distances were grouped in 10-minute intervals, with a truncation distance of 50 minutes on each side of the sampling line. Three or four samplings were taken in each section.

During samplings some rabbits may have been resting (for activity patterns in rabbits, see Wallage-Drees 1989), which made them potentially undetectable. Consequently the reported figures probably underestimate

the true rabbit density in the area. This should not matter for the present study because we were interested mainly in detecting differences between sections rather than in accurately estimating rabbit population densities in each section. We also estimated relative rabbit density in each section of the *P. lentiscus* patch with *Fraxinus* sp. (sections III and IV) by fecal pellet counting, because human disturbance in the area outside of the national park might influence the number of rabbits on the surface at the time of sampling. Rabbit fecal pellets were counted in 20 (for section III) and 17 (for section IV) 1.54-m^2 circles set at 50–80-meter intervals. Twenty-one days before counting pellets, old pellets were removed from circles.

Results

Gross Numbers of Rabbits Taken

Using the most realistic density for each predator, we estimated (irrespective of rabbit size) that 393 rabbits per km^2 per year were consumed when lynx were present and 2500 when lynx were absent (Table 2). That is, 6.4 times more rabbits were consumed when lynx were absent than when lynx were present. With other possible combinations of predator densities, between 4.8 and 9.5 times more rabbits per km^2 per year were consumed in like conditions (Table 2).

Simulations of Rabbit Populations

For all possible combinations of predator densities, the growth rate of rabbit populations was lower when lynx were absent than when lynx were present (Table 3). After a year, densities of large rabbits in September–October (using the most realistic predator densities and fixing initial rabbit density at 15 ind/ha) were 16% lower in the absence of lynx than in their presence (Table 3). The lower differences (12%) between presence and absence of lynx were for predator densities of

Table 2. Estimated numbers of rabbits taken by lynx and mongooses in lynx presence and lynx absence using different lynx (LD) and mongoose (MD) densities.

Predator densities	Number of Rabbits Consumed (ind/ km^2 /year)	
	Lynx	Mongoose
Lynx Presence		
LD = 0.50/MD = 0.2	265	128
LD = 0.50/MD = 0.1	265	64
LD = 0.75/MD = 0.2	398	128
LD = 0.75/MD = 0.1	398	64
Lynx Absence		
MD = 4.2*	—	2500
MD = 5.2*	—	3125

* These values refer to mean annual densities; densities vary throughout the year.

Table 3. Growth rates after one year of rabbit populations for different combinations of lynx and mongoose density in the area with lynx presence (LD;MD) and mongoose density in the area with lynx absence (MD).^a

Predator Density Combinations	Population Growth Rate ^b	Increase in Rabbit Population Growth Rate (%) ^c
LD = 0.5; MD = 0.2	0.885	16
MD = 4.2	0.739	
LD = 0.75; MD = 0.2	0.839	12
MD = 4.2	0.739	
LD = 0.5; MD = 0.1	0.892	22
MD = 5.2	0.694	
LD = 0.5; MD = 0.2	0.885	22
MD = 5.2	0.694	

^a Results from MD = 0.1 ind/km² in the area used by lynx were similar to those reported to values of MD = 0.2 ind/km², so they are not included.

^b Initial rabbit density fixed at 15 ind/ha.

^c Increase in rabbit population growth rate = 100 (rabbit growth rate in the area with lynx - rabbit growth rate in the area without lynx)/rabbit growth rate in the area with lynx.

0.75 lynx/km² and 0.2 mongooses/km² in the area used by lynx, and 4.2 mongooses/km² in the area not used by lynx. The higher differences (22%) were for predator densities of 0.5 lynx/km² and 0.2 or 0.1 mongooses/km² in the area used by lynx, and 5.2 mongooses/km² in the area not used by lynx (Table 3).

Increasing rabbit density decreased the effect of lynx presence or absence on the rabbits (Fig. 3). For instance, at the lynx density of 0.75/km² and mongoose density of 4.2/km² where lynx were not present, the effect of lynx presence on rabbits was lower than 5% at rabbit densities of 45/ha (Fig. 3). When mongoose density was 5.2/km² in the area of lynx absence and lynx density was 0.75/km², the effect of lynx presence on rabbits was lower than 5% at rabbit densities of 75/ha (Fig. 3).

When lynx density increased (while mongoose density in the area of lynx absence was fixed at 4.2 or 5.2/km²) the effect of lynx presence on rabbits decreased. Using the lowest rabbit density as reference (10/ha), the effect of lynx presence switched from positive to negative at lynx densities of 1.25 or 1.55/km² for each fixed mongoose density respectively (Fig. 3). Higher densities of lynx would be needed to attain the same effect at higher rabbit densities (Fig. 3). In contrast, mongoose density had to be decreased (while fixing lynx density at 0.5 or 0.75 ind/km²) to levels of nearly 1.7 or 2.5 ind/km² for each fixed lynx density in order to switch the effect of lynx presence on rabbits from positive to negative (Fig. 3). The mongoose density required to switch the effect of lynx presence on rabbit from positive to negative decreased as rabbit density increased (Fig. 3).

The stepwise regression showed that results were

more sensitive to lynx density, followed by mongoose density and initial rabbit density (standardized partial regression coefficients were -0.3232, 0.11, and -0.0074, respectively). The sign (positive or negative) indicates the way each parameter affected results.

Actual Rabbit Densities

Rabbit densities were 2–4 times higher in sections used by lynx (I and III) than in sections not used by lynx (II and IV; Table 4). Differences between sections with lynx presence were not significant. Rabbit densities were similar between the two sections with lynx absence. For the same *P. lentiscus* patch with *Fraxinus* sp., rabbit density was 2.32 times higher in the section used by lynx (III) than in the rest of the patch (IV; section not used by lynx). Fecal pellet counting confirmed this trend because numbers of pellets in the area of lynx presence were 2.27 times higher than in the rest of the patch (Table 4; $t = 4.80$, $df = 35$, $p < 0.0001$; data log-transformed for the test).

Discussion

Our results suggest that the absence of lynx may result in a higher net predator consumption of rabbits, the staple prey of lynx (Delibes 1980) and important for many other predators (Delibes & Hiraldo 1981). Our findings were obtained by considering gross numbers of rabbits taken by predators, the reproductive value of individuals taken (by simulations of size-structured rabbit populations under all combinations of predator densities and rabbits), and finally by collecting data on rabbit densities in different sections of the study area, which appeared to confirm previous findings.

It may have been worthwhile to consider the condition, sex, and social status of the rabbits taken by lynx and mongooses in our model and to consider changes in rabbit reproduction due to different predation pressures and initial rabbit densities (Borrallho et al. 1993; H. Kruuk, personal communication). The dynamics of prey populations might be different if predators differentially take prey in poorer condition, more females than males, or subordinate individuals more often than dominant ones. Nevertheless, there is no evidence to suggest that this is the case for any of the predator species studied here. Also, if females lose young early in the breeding season, further reproduction may be stimulated. Further, at low rabbit densities, litter sizes might increase. At present, however, there is no data to support either of these speculations. In view of the magnitude of the results obtained, the positive effect of lynx presence on rabbit populations would be unlikely to switch to negative due to different overall prey selectivity of each predator or to changes in rabbit reproduction.

Simulations of rabbit populations showed that our re-

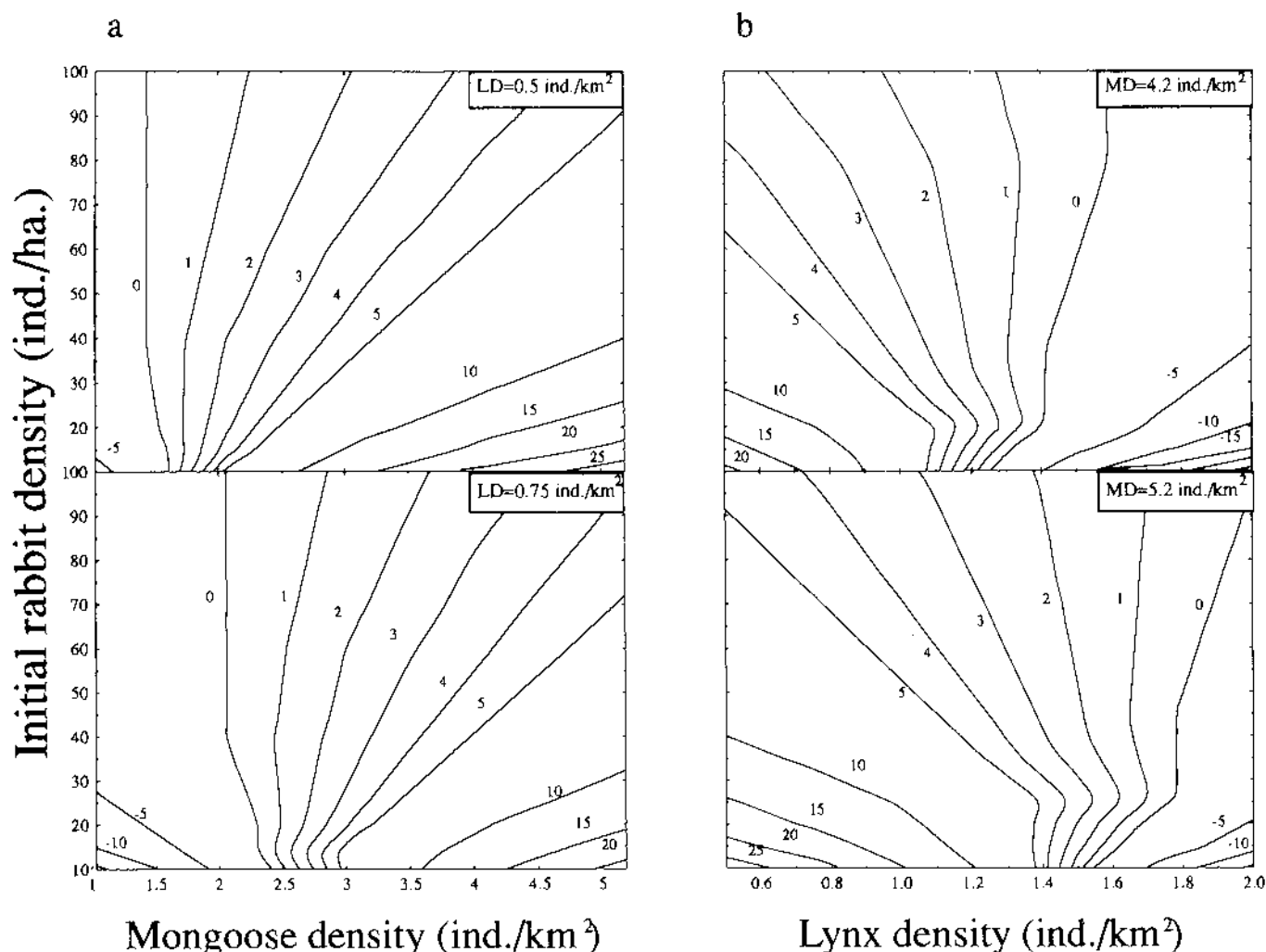


Figure 3: Rabbit population growth rate as affected by lynx presence when (a) varying mongoose density and fixing lynx density (LD) at 0.5 or 0.75/km², and (b) varying lynx density and fixing mongoose density (MD) in the area not used by lynx at 4.2 or 5.2/km². Mongoose density in the area used by lynx was always fixed at 0.2 ind./km² and rabbit density was varied from 10 to 100 ind./ha. Numbers next to isolines indicate the increase or decrease (indicated with -) of rabbit growth rate (%) in the presence of lynx.

sults stood up to great variations in rabbit and predator densities. Values of initial rabbit density, lynx density, and mongoose density (in the area with lynx absence) to which the effect of lynx presence on rabbit would switch from positive to negative were unrealistic or at least difficult to attain in nature. The value for initial rabbit density and the less favorable combination of parameters was 45 rabbits/ha. At present, even though Matagordas is the area with the highest rabbit density in Doñana (R. Villafuerte, personal communication), maximum rabbit density detected in this study was nearer 25/ha (Table 4). At densities of 1.25 lynx/km² there would be no effect on rabbits, when considering the most realistic mongoose density in the area not used by lynx and only 10 rabbits/ha as the initial rabbit density. Matagordas holds the highest lynx density at Doñana—probably the highest density for the complete

range of the species as well (Rodríguez & Delibes 1992). For instance, Rau et al. (1985) estimated 0.16 lynx/km² for another area of Doñana as "good lynx density." Therefore, values of 1.25 lynx/km² are not at all realistic, even less so when this value was obtained by fixing initial rabbit density at only 10/ha. Increasing initial rabbit densities to 15 or 20/ha increases lynx density to 1.4/km² (see Fig. 3). Reducing the number of mongooses to the point that lynx absence has no effect on rabbits is not possible because mongooses are a protected species in Spain (Instituto Nacional para la Conservación de la Naturaleza 1992).

The effect of rabbit density on the results should be considered with caution because some predator response to changes in prey density are to be expected, especially when prey numbers fall below certain levels (Taylor 1984). These levels are unknown for lynx and

Table 4. Mean ($\pm$ SE) rabbit densities and mean ($\pm$ SE) rabbit fecal pellets in different sections of the study area differing in lynx presence and dominated by *P. lentiscus* shrubs.

Lynx's Status	Rabbit Density		Rabbit Fecal Pellets (number/m ² /day)	
	Mean (ind/ha)	95% Confidence Interval	Mean	Range
Present				
<i>P. lentiscus</i> and <i>O. Suber</i> (I)	18.3 ($\pm$ 2.5)	13.4–23.2		
<i>P. lentiscus</i> and <i>Fraxinus</i> sp. (III)	11.5 ($\pm$ 1.4)	8.8–14.2	2.3 ($\pm$ 0.3)	1.0–5.8
Absent				
<i>P. lentiscus</i> in pine forest (II)	3.2 ($\pm$ 0.8)	1.7–4.8		
<i>P. lentiscus</i> and <i>Fraxinus</i> sp. (IV)	5.0 ($\pm$ 1.0)	3.1–6.8	1.0 ($\pm$ 0.1)	0.2–2.1

Roman numbers refer to sections indicated on Fig. 2.

mongooses. If changes in prey density influence lynx numbers, this in turn should influence lynx-mongoose spatial relationships because they might be density-dependent (Delibes et al. 1992). In fact, in other areas of Doñana where rabbits are much scarcer than in Matagordas, lynx and mongooses coexist to a greater extent; but lynx feed on rabbits and occur at low densities, and mongooses feed on several alternative prey species and occur at densities similar to those in Matagordas (Rau et al. 1985; Delibes et al. 1992; Palomares 1993). Our quantification applies only to areas where rabbits are relatively abundant (with densities similar to our study area) and where the staple prey of both predators is mainly rabbits.

The effect of rabbit density on the results suggests that, above a given level of rabbit density, the predators—in both the absence and presence of lynx—are unable to exert any influence on prey populations (for an experimental field study, see Pech et al. 1992). But data also suggest that the level is lower in the presence than in the absence of lynx. Following outbreaks of myxomatosis and viral haemorrhagic pneumonia, rabbit density in some areas is particularly low. This is beyond the scope of our current study, but the presence of lynx in recovering rabbit populations may have important management implications. Comprehensive simulations could be performed to explore this issue.

Actual rabbit densities were higher in sections used by lynx than in those not used by lynx. Nevertheless, differences in rabbit density cannot be considered conclusive without the support of the simulations because factors other than lynx presence may influence rabbit densities (even in sections that are identical in habitat composition). There are at least three other factors that may influence rabbit densities outside and inside Matagordas: (1) unequal densities of other rabbit predators, especially if these are rarely preyed upon by lynx; (2) the effect of people on rabbits; and (3) interspecific competition for food with rabbits. For example, during

nesting kites frequently prey on rabbits (Veiga & Hiraldo 1990), and kite (mainly *Milvus migrans*) nesting is much more abundant in the area used by lynx than within and around the other patches of *P. lentiscus* in the study area (F. Hiraldo, personal communication). Therefore, unequal densities of other predators may decrease rabbit density in the area used by lynx. Rabbit poaching with ferrets occurs more frequently outside Doñana National Park than inside, so people may be decreasing rabbit density in the area not used by lynx. Finally, we observed more deer (*Cervus elaphus* and *Dama dama*) inside the sections used by lynx than in the other sections (11.3 and 0.3 ind/km for the area used and not used by lynx, respectively; F. Palomares, unpublished data). Domestic animals, mainly horses, are also more abundant inside Doñana National Park than outside. Interspecific competition for food with ungulates and domesticated animals may decrease rabbit density in the area used by lynx.

The idea that top predators may be important species for conservation biology is not new. Pimm (1980) discussed the population effects following the loss of a top predator species in food webs, and Terborgh & Winter (1980) suggested that top predators have a disproportionate importance for conservation biology because their extinction can trigger a cascade of unexpected secondary extinctions as a consequence of the disruption of evolved predator-prey relationships. For example, the extinction of some birds nesting on or near the ground in Barro Colorado Island has been repeatedly attributed to the increase of generalist mammals due to the extinction of top predators (Terborgh & Winter 1980; Diamond 1989; Karr 1982), and the decline of songbird populations in North America has been tied to the increase of medium-sized predators (Wilcove 1985; Soulé et al. 1988; Böhning-Gaese et al. 1993).

Our results suggest that intraguild predation and the effect that mesopredator release may have on prey should be considered seriously by managers. Even when

possible, control of medium-sized species such as Egyptian mongooses or red foxes is difficult because they occur in high densities, have high rates of recruitment, and often have great capabilities of dispersal from adjacent unmanaged areas (see Zarnoch et al. 1977; Lloyd 1980). Furthermore, medium-sized predator species can be legally protected, as with Egyptian mongooses in Spain. The results obtained in this study might well have been obtained using other top predators and mesopredators. For instance, Fernández (1991) found a high predation of carnivores by Golden Eagles, and Capt et al. (1993) found that European lynx also frequently prey upon foxes.

Management measures such as direct protection, habitat management, and reintroductions following local extinction, all aimed at maintaining high densities of top predators, may indirectly maintain or improve populations of small game species by limiting the growth of populations of medium-sized predators. Accumulating evidence of the positive effect of endangered top predators on populations of game species may ultimately be an important factor in the conservation of top predators because such evidence could change attitudes toward predator control.

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