

INFLUENCE OF FOOD ABUNDANCE AND QUALITY ON RABBIT
FLUCTUATIONS: CONSERVATION AND MANAGEMENT
IMPLICATIONS IN DOÑANA NATIONAL PARK (SW SPAIN)

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INTRODUCTION

The European rabbit (*Oryctolagus cuniculus* L.) is widely distributed through introduction by human (Flux & Fullagar, 1983). In some places, this species is a serious pest (Gilbert & Myers, 1981), whereas in other regions it is an integral component of the ecosystem (Delibes & Hiraldo, 1981; Moreno & Villafuerte, 1995). In the Iberian Peninsula, rabbits are the most important prey for a number of predators, including several endangered species such as the Spanish Imperial Eagle (*Aquila adalberti*; Collar & Andrew, 1988) and, specially the Iberian lynx (*Lynx pardinus*), listed as the most vulnerable cat in the world (Nowell & Jackson, 1996). In Spain, the persistence of populations of these species will be dependent on reducing human causes of mortality, and availability of rabbits (Ferrer & Calderón, 1990; Litvaitis *et al.*, 1996). Despite the importance of rabbits to the conservation of these predators, very little is known about the factors that influence rabbit populations in this region. Current numbers of rabbits seem to be lower than those reported for previous decades (Valverde, 1967; Delibes, 1978; Rogers & Myers, 1979; Beltrán, 1991; Villafuerte *et al.*, 1995) but no reliable data are available in Spain for comparisons. The incidence of myxomatosis, and more recently rabbit hemorrhagic disease (RHD, Villafuerte *et al.*, 1994; 1995), competition with large herbivores (Soriguer, 1983), high densities of generalist predators (Palomares *et al.*, 1995), and the loss of traditional land management practices (Moreno & Villafuerte, 1995), have been considered as limiting rabbit densities.

The techniques traditionally employed in Spain to restore the rabbit populations have involved the predator control (Villafuerte *et al.* 1997), mainly centered on red foxes (*Vulpes vulpes*), and the restocking of vaccinated rabbits captured in places where rabbits are still abundant (Calvete *et al.*, 1997; Villafuerte *et al.*, 1995). Added to these techniques, in some places have been created artificial warrens (to reduce the effects of flooding and preventing predation by carnivores), control of competitors, and the habitat management. Moreno & Villafuerte (1995) showed that adequate habitat alone produces significant increases, even eight

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times the initial density of rabbits. Calvete *et al.* (1997) considered absolutely inefficient the restocking of rabbits, because rabbits survival rate is under 3%. However, with the exception of these two studies, the effectiveness of these managements has not been assessed.

In this paper, we present data on rabbit abundance at Doñana National Park during a 25-month period, in the middle of which occurred the first RHD outbreak (Villafuerte *et al.*, 1994). We analyse the relationship of rabbit numbers with food abundance and quality, discussing the current management attitudes applied in Doñana to maintain rabbits as an abundant species.

METHODS

STUDY AREA

Our study was conducted in Doñana National Park (37° N, 6° W, Fig. 1) which covers 550 km² of the Guadalquivir estuary. Three main biotopes are

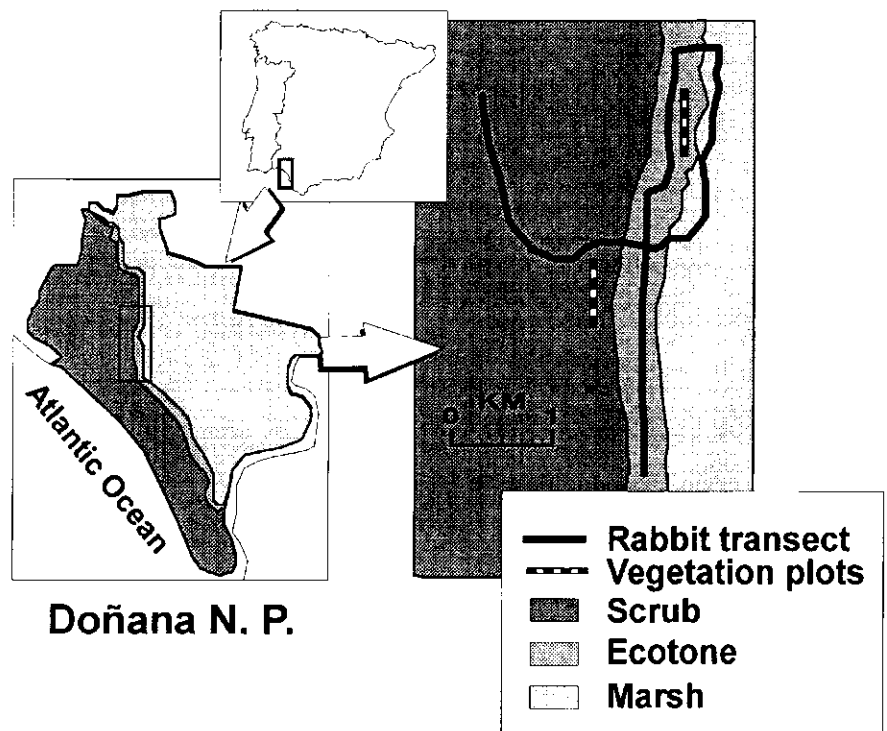


Figure 1. — Location of the Doñana National Park showing the main habitat types, the location of vegetation plots, and the transect route for roadside rabbit counts.

represented within the Park, salt marsh, scrubland, and sand dunes (Rogers & Myers, 1980). An ecotone located between the scrubland and salt marsh is covered by grasslands whose floristic composition depends on both the depth of the ground-water table and the salinity of the soil (Allier & Bresset, 1978). These grasslands and their closest scrub formation (52 % basal cover by shrubs), show the highest densities of mammal herbivores at Doñana, both ungulates (*Cervus elaphus*, *Dama dama*, *Sus scrofa* and livestock) and lagomorphs (Rogers & Myers, 1980). In the winters of rainy years, the ecotone grasslands can be partially flooded. The climate is Mediterranean with typically seasonal temperature and rainfall regimes: hot summers, mild winters, and rainfall concentrated from mid autumn to mid spring (500 to 600 mm per year).

VEGETATION SAMPLING

The abundance and quality of the herbaceous vegetation were assessed monthly in the ecotone grassland (during 1989 and 1990) and in the closest scrub formation (during 1989 and in May 1990). Samples were not obtained when the pastures remained partially flooded from November 1989 to January 1990. Floristic composition was estimated in 50 permanent plots (400 cm²) by using the dry weight rank method (DWR; Marnett & Haydock, 1963). These plots were located along two 500 m transect lines (one in each habitat type, Fig. 1). Samples were obtained from seven 0.2 m² plots per transect. Herbaceous plants were cut to the ground level, and the samples were dried in a hot-air oven at 50 °C until constant weight. Monthly estimates of biomass availability (BA: kg of dry matter [DM] per ha of pasture) were obtained by averaging the dry weights of the samples of each pasture type. An average protein content (PC: the percentage of the total dry weight due to proteins) was estimated using Kjeldahl procedure, analysing a combined sample of each pasture per month. The average value of the total protein availability in the herbaceous layer (PA: kg of protein per ha of pasture) was obtained by multiplying BA and PC. The nomenclature of plant species follows Valdés *et al.* (1987).

RABBIT COUNTS

Rabbit abundance was estimated using roadside counts from January 1989 to January 1991, three times a month on consecutive days. Counts were made at dusk following a permanent route 13 km long that covered both the ecotone pasture and the scrubland formation (Villafuerte *et al.*, 1993, Fig. 1). Perpendicular distances of sighted rabbits from the line transect were estimated. Count data were used to estimate average values of rabbit abundance in each month (RA: rabbits per ha) using the program TRANSECT (Burnham *et al.*, 1980). Data for December 1989, March 1990 and November 1990 were not available.

STATISTICS

Data were analysed using non-parametric methods with a significance level of .05 for all tests. Spearman rank correlations were employed to assess relationships

among variables. Because it was expected a delayed response of rabbit abundance to changes in vegetation parameters, lag-correlogram procedures were used to obtain the best fit between monthly values of the herbaceous layer variables (BA, PC and PA) and rabbit abundance (RA). In comparing two samples, Wilcoxon paired-sample test and Mann-Whitney test were used (Zar, 1984).

RESULTS

VEGETATION CHARACTERISTICS

Annual plant species, both grasses (*Anthoxanthum ovatum*, *Chaetopogon fasciculatus*, *Vulpia* spp.) and forbs (*Anthemis cotula*, *Plantago coronopus*, *Rumex bucephaloforus*, *Trifolium* spp.) predominated in the ecotone grassland and in the herbaceous layer of the scrubland (>80 % of the dry biomass in May estimated through DWR, in both pasture types). Because most of these plants are consumed by rabbits in Doñana (Soriguer, 1983), BA and PC are reliable indexes to assess the total availability of food. Most of these plants became dry in June, increasing the relative importance of perennial grasses (*Cynodon dactylon* and *Panicum repens*) during summer and autumn to 40 % of the dry biomass. The values of maximum standing crops were very similar within each year for both pasture types (1989: $2\,032 \pm 297$ kg DM ha⁻¹ in the scrubland, $2\,269 \pm 183$ kg DM ha⁻¹ in the ecotone grassland; 1990: $1\,353 \pm 170$ kg DM ha⁻¹ in the scrubland, $1\,159 \pm 401$ kg DM ha⁻¹ in the ecotone grassland). The monthly estimated values obtained from the two grassland types for the three vegetation variables were positively correlated (BA: $r_s = .883$; PC: $r_s = .817$; PA: $r_s = .700$; $n = 9$, $p < .05$ for the three coefficients). Because of these correlations, the lack of data on the scrubland's herbaceous layer in 1990, and the known similitude in rabbit trends in scrubland and ecotone areas (Beltrán, 1991), the values for the ecotone grassland were considered to be descriptive of the whole area covered by rabbit censuses.

The dry biomass of herbaceous plants increased from winter (the lowest annual values) to early summer, and then showed a rapid decrease (Fig. 2a). The average protein content was higher during winter and early spring and minimum at the end of the summer (Fig. 2a). The combined variation of both BA and PC made maximized the total availability of protein in the herbaceous layer during the spring and early summer months (Fig. 2b). Intense rainfalls in November and December 1989 (564 mm, 45 % of total precipitation during the study period) partially flooded the ecotone grassland (53 % of its area in December), affected the growth of the plants in the flooded areas, and may have been responsible for the lower levels of plant biomass in 1990 as compared with 1989.

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The rabbit abundance (RA) fluctuated during the study period. The maximum values (near 8 individuals per ha) were observed in May and June 1989 (Fig. 3), after a rapid increase from a winter value of approximately 1 rabbit per ha. RA

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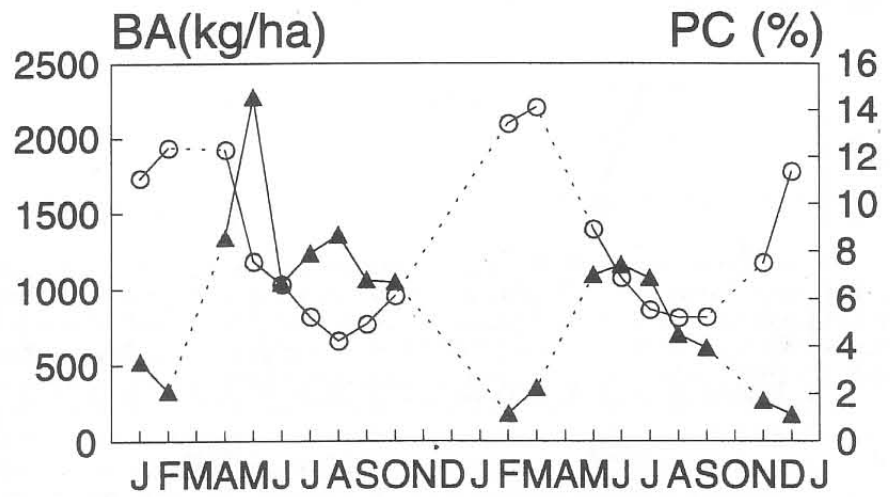
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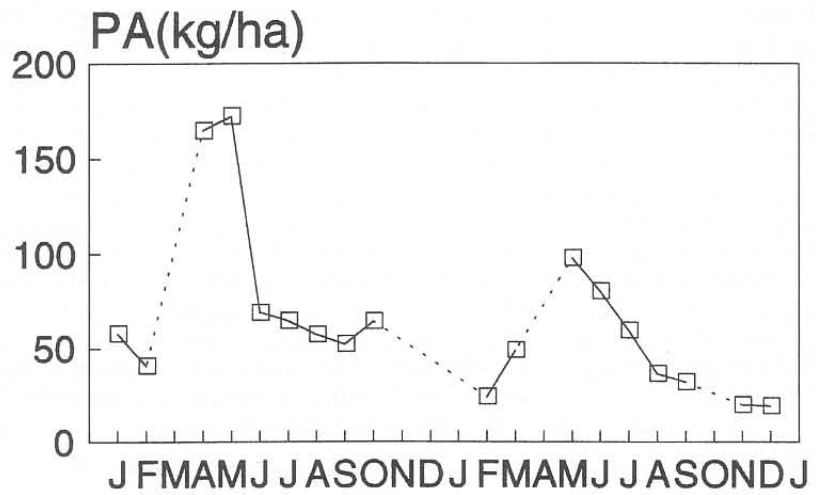


Figure 2. — Average values of dry plant biomass (BA; triangles in fig. a), protein content (PC; circles in fig. a) and total available protein (PA; squares in fig. b) in the herbaceous layer of the ecotone grassland.

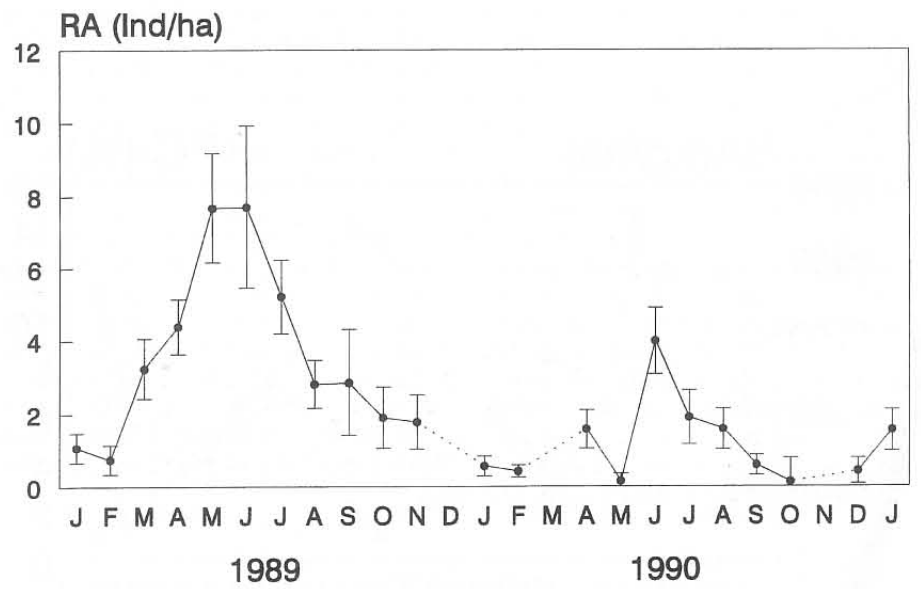


Figure 3. — Monthly abundance \pm S.E. of rabbits (RA) in the study area.

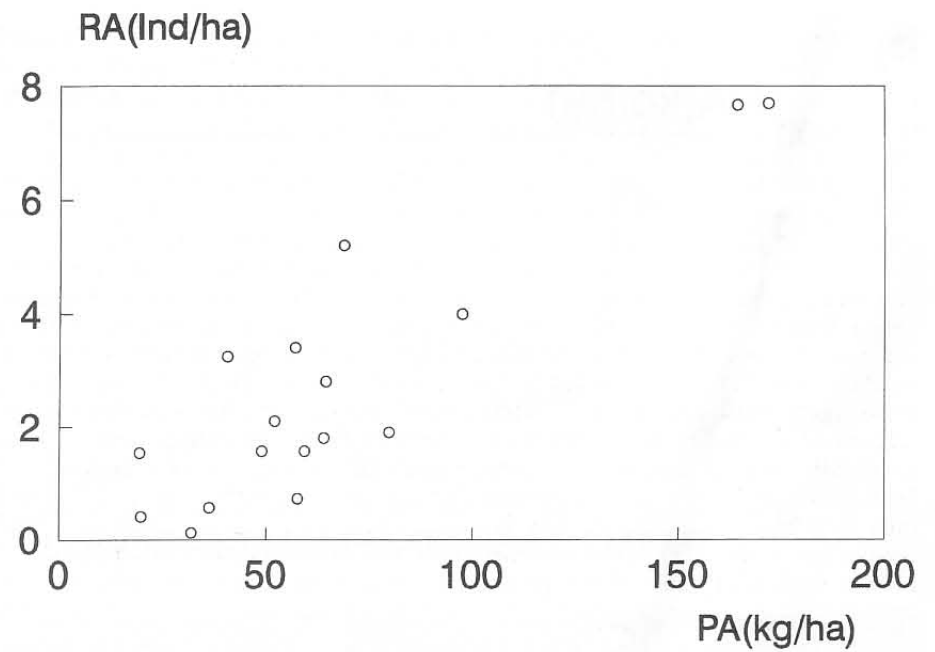


Figure 4. — Plot of rabbit abundance (RA) versus total protein availability in the ecotone grassland during the previous month (PA). Values corresponding to the whole study period.

declined from the maximum value to low levels in the winter 1989-90, but during 1990 did not reach the monthly values of 1989 (Wilcoxon test: $T(9) = 0$, $p = .005$, two tailed). Rabbit abundance was positively correlated with biomass availability in the ecotone grassland if a lag of one month was applied to data, ($r_s = .688$, $n = 17$, $p < .01$), but was not correlated with the protein content of the herbaceous vegetation ($r_s = .146$, $n = 17$, $p = .559$). The fit between rabbit abundance and a vegetation variable was improved when the total availability of protein was used rather than the biomass availability ($r_s = .777$, $n = 17$, $p < .005$; Fig. 4).

The floods in the winter of 1989 affected both the length of the reproductive period of rabbits and the total number of animals breeding (unpublished data). In March and April 1990, the incidence of the first spread of RHD caused a high mortality rate, around 55 %, affecting only adult animals (Villafuerte *et al.*, 1994). As a result of the incidence of both factors, floods and disease, on rabbit reproduction, the monthly ratios between the number of rabbits and the total protein availability in the post-reproductive period were lower in 1990 than in 1989 (comparison of the June-October period by the Mann-Whitney test: $U[5,5] = 24$, $p = .01$, one tailed), i.e., in 1990 the incidence of rabbit reproduction was lower than expected by food availability.

DISCUSSION

FOOD SUPPLY AND NUMBER OF RABBITS

Monthly fluctuations of rabbit abundance in Doñana during the study period were similar to those reported by Soriguer & Rogers (1981) in an area 90 km north of Doñana and by Beltrán (1991) in our same study area. In Mediterranean environments, the onset of rabbit reproduction is determined by the eruption of the annual vegetation, usually in late autumn, and the extent of the breeding period by the length of the growing period of the herbaceous plants (Delibes & Calderón, 1979; Rogers, 1981; Vandewalle, 1989). This generates fluctuations in rabbit numbers closely related to the phenology of the herbaceous vegetation.

The diet of the rabbits in Doñana is dominated by annual plants that are consumed more than expected from their availability in the sward (Soriguer, 1988). During the winter and spring, the growing periods of annuals, these plants can satisfy most of the requirements of high quality food that rabbits need for reproduction (Cooke 1981; 1982; Cheeke, 1981). Our results do not show a continuous relationship between rabbit abundance and the quality of these plants (estimated as their protein content) but between rabbit abundance and the total availability of protein in the herbaceous vegetation. This agrees with the results of Wallage-Drees (1983), who suggested that the onset of rabbit reproduction, and thus its influence on rabbit density, is not merely related with an increase in food quality but with a rise in the availability of high quality food. The incidence of protein availability on rabbit reproduction could explain also the differences in maximum levels of rabbit abundance between our two study years. Lower levels of total protein availability in the swards during 1990 than during 1989 were associated with lower values of rabbit density, suggesting that the abundance of high quality food during the breeding period is a factor influencing the maximum abundance of rabbits in Doñana.

The autumn rainfall influences the germination and growth of the annual plants directly (Espigares & Peco, 1993) and, indirectly, the onset and duration of the breeding season of rabbits in Doñana (Delibes & Calderón, 1979). However, if rainfall is very intense it can have the opposite effect. In November and December of 1989 intense rainfall flooded partially the ecotone zone for several weeks, inhibited plant germination and growth, and inundated warrens delaying the onset of the reproductive period. In Camargue, floods usually limit food availability for rabbits during the winter and thus constrain the length of the reproductive period (Vandewalle, 1989). In Doñana much of the feeding areas and breeding places for rabbits are located in areas in which floods are frequent, intense rainfall in autumn and winter can therefore seriously affect the annual pattern of rabbit abundance.

In Doñana, the presence of large herbivores is greatest in the ecotone zone (reaching near 75 animals per km², all species included; unpublished data). Despite this, the role of competition for food between rabbits and large herbivores seems limited. There is no evidence of starvation of rabbits, even when the food supply is at its minimum in autumn, contrary to that observed in populations in which either food shortage or competition with other herbivores are important factors in rabbit mortality (Gibb, 1977; 1981; Wallage-Drees & Michielsen, 1989). Furthermore, the cessation of reproduction and the decline in rabbit abundance seem not to be associated with a reduction in food supply due to overgrazing but to the death of most annual plants at the end of the spring, and thus rabbits become more selective in their feeding (Rogers, 1981). Energy expenditures in obtaining food may increase, and loss of body condition may then inhibit reproduction (Boyd & Myhill, 1987).

OTHER FACTORS LIMITING RABBIT NUMBERS: DISEASES AND PREDATION

Rabbit hemorrhagic disease was directly responsible for a low rabbit densities in Doñana after its irruption in 1990 (Villafuerte *et al.*, 1994). Our data suggested that this low density seemed to be lower than expected by the levels of food availability. An analogous case has been reported by Peiró & Seva (1993) in eastern Spain.

The importance of the other important rabbit disease, myxomatosis, as a factor constraining population densities has been widely discussed (see Ross & Tittensor, 1986). In Doñana this disease causes indirectly the death of 30-40 % of the young animals every year by raising greatly their susceptibility to predation (unpublished data). The effect of the disease is centered mainly in the post-reproductive period, and therefore does not bear upon the maximum levels of rabbit abundance in each year. However the disease can diminish the total number of adult animals entering reproduction in the next year. Soriguer & Rogers (1981) found that the incidence of myxomatosis was a factor explaining variations in maximum rabbit density between two consecutive years, but Ross & Tittensor (1986) considered that the disease may not have any long-term regulatory effect on rabbit populations. We have no evidence of a different incidence of myxomatosis in both years of our study period.

The magnitude of predation on rabbits and its effects on the fluctuations of rabbit numbers in Doñana is linked to the incidence of diseases. In the Iberian

Peninsula, most of the predators are opportunistic species that capture young rabbits and adults handicapped by myxomatosis (Delibes & Hiraldo, 1981; Viñuela *et al.*, 1994; Villafuerte, 1994). This means that predation principally influences the decline of rabbit density after reproduction. In fact, Villafuerte (1994) detected in Doñana a greater mortality due to predation during autumn and winter than during spring or summer (mean mortalities 0.7 and 0.3 respectively). It has been argued that predation may play a more important role than food availability in the regulation of rabbit abundance (Gibb, 1981; Wallage-Drees & Michielsen, 1989). However, our results suggest that the rabbit population of Doñana fluctuates accordingly with food supply and quality, a situation not expected under a predator regulation of low density populations of rabbits (Trout & Tittensor, 1989; Pech *et al.*, 1992).

IMPLICATIONS FOR CONSERVATION

According to our results, the factors causing fluctuations in rabbit abundance at Doñana National Park fall into two groups. One affects mainly the onset and duration of reproduction (i.e. the productivity of the population), these factors include: the availability of high quality food in winter and spring, the incidence of the RHD, the occurrence of floods in the breeding and feeding places. The other group affects mainly the decline in rabbit density after the peak of maximum abundance, and includes the incidence of myxomatosis and predation.

The first goal of rabbit conservation in Doñana is the maintenance of a stable and dense population as the main food source for endangered species of predators (i.e. Litvaitis *et al.*, 1996). Therefore, it is necessary to reduce the incidence of those factors affecting the reproductive period and the maximum levels of rabbit density achievable each year. Low levels of reproduction in consecutive years, could cause the rabbit population to be maintained at low densities by predation, making difficult the recovery of high levels of rabbit abundance (Trout & Tittensor, 1989; Newsome *et al.*, 1989).

However, the current management plans at Doñana emphasize the reduction of large herbivores, and the habitat management (Moreno & Villafuerte, 1995). Because massive vaccinations makes necessary the capture of a great proportion of rabbits (usually impracticable), this technique has not been used in Doñana, although recently some vaccinated rabbits have been restocked.

Our results suggest that the control of generalist predators (a measure that might alter the structure of the animal communities in the Park), and the reduction in the density of large herbivores, may be considered only as secondary measures in order to conserve high density populations of rabbits in Doñana.

Therefore, measures related to habitat management (the conservation of pastures, as well as the increment of the total surface covered by annuals plants), and the increase of the number of safe places for the location of artificial warrens to diminish the risks of floods on reproduction, surely will be associated with higher densities of rabbits.

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SUMMARY

European rabbits (*Oryctolagus cuniculus*) are the major prey in Spain for several endangered carnivores and raptors. In recent years, many different efforts have been directed at increasing rabbit populations, and thus enhancing the survival of these endangered predators. The aim of this work was to improve our understanding of the factors that influence the natural variation in rabbit populations, specially those regarding on the food abundance and quality, and to discuss the efforts actually used to manage rabbit populations. Estimates of rabbit abundance were obtained monthly from roadside counts during a 25 month period developed at Doñana National Park. Simultaneously, samples of the herbaceous layer were obtained from the area covered by censuses. Fluctuations in rabbit abundance were compared with changes in biomass and quality of the herbaceous plants. Rabbit abundance showed the best fit with the total protein availability in the herbaceous layer. Variations in the precipitation pattern between years, which affected both food availability and rabbit reproduction, and the incidence of the first epizootic of the rabbit hemorrhagic disease, caused the observed differences between maximum values of rabbit abundance in two consecutive years. The relative importance of other factors influencing rabbit numbers in Doñana including myxomatosis, predation, and competition for food with large herbivores is discussed.

RÉSUMÉ

Le lapin de garenne (*Oryctolagus cuniculus*) constitue la proie principale de plusieurs carnivores et rapaces menacés. Ces dernières années, une variété d'efforts a été déployée afin d'accroître les populations de lapins et ainsi augmenter la survie de ces prédateurs en danger de disparition. L'objet du présent travail était d'améliorer notre compréhension des facteurs qui jouent sur la variation naturelle des populations de lapins, en particulier ceux relatifs à l'abondance et à la qualité de la nourriture, et de discuter les efforts actuels en matière de gestion des populations de lapins. Des estimations de l'abondance des lapins furent obtenues chaque mois à partir de comptages routiers et ce durant une période de 25 mois dans le Parc National de Doñana. Simultanément, des échantillons de la strate herbacée étaient recueillis sur la zone des recensements. Les fluctuations d'abondance des lapins furent comparées aux changements en biomasse et qualité des plantes herbacées. L'abondance des lapins s'est avérée être le mieux corrélée avec la disponibilité totale en protéines dans la strate herbacée. Les différences observées entre les valeurs maximales de l'abondance des lapins durant deux années consécutives furent dues à l'incidence de la première épizootie de virus hémorragique, couplée aux variations d'une année sur l'autre de la pluviométrie, ce qui affecta à la fois la disponibilité de la nourriture et la reproduction des lapins. L'importance relative des autres facteurs influençant les effectifs de lapins à Doñana, incluant la myxomatose, la prédation et la compétition alimentaire avec les grands herbivores, est discutée.

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