available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

Rabbits as a keystone species in southern Europe

Miguel Delibes-Mateos[a,*], *Steve M. Redpath*[a,b], *Elena Angulo*[c,d], *Pablo Ferreras*[a], *Rafael Villafuerte*[a]

[a]*Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, 13005 Ciudad Real, Spain*
[b]*CEH Banchory, Hill of Brathens, Banchory, Aberdeenshire, Scotland AB31 4BW, United Kingdom*
[c]*University Paris-Sud XI, Laboratorie Ecologie Systematique et Evolution, Batiment 362, F-91405 Orsay Cedex, France*
[d]*Estación Biológica de Doñana (CSIC), Apdo 1056 E, 41013 Sevilla, Spain*

ARTICLE INFO

Article history:
Received 13 July 2006
Received in revised form
11 January 2007
Accepted 31 January 2007

Keywords:
Aquila adalberti
Hunting
Oryctolagus cuniculus
Raptor conservation
Spain
Spanish imperial eagle

ABSTRACT

A keystone species is one that is crucial in maintaining the organization and diversity of their ecological communities. We tested the idea that rabbits act as a keystone species in southern Europe by exploring relationships between rabbit abundance and the abundance and diversity of raptor species. At 20 sites in southern Spain we assessed rabbit abundance through counts of animals along transects and assessed the number of raptor individuals and species through watches from vantage points. In a further 120 locations we also derived an index of rabbit abundance, from pellets and compared this to the presence or absence of the critically endangered Spanish imperial eagle. Rabbit abundance was positively associated with the number of observations of raptors, the number of raptor species and the number of species of conservation concern. Sites with the most rabbits had higher conservation value. Moreover, the presence of Spanish imperial eagle was strongly associated with sites where rabbits were at high density. We conclude that rabbits do act as a keystone species and we suggest that conservation efforts should focus on improving the status of this small-game species in southern Europe.

1. Introduction

The concept of keystone species has been widely employed in community ecology and conservation biology (Simberloff, 1998). Keystone species are those considered exceptional, relative to the rest of the community, in maintaining the organization and diversity of their ecological communities (Paine, 1969; Holt, 1984; Mills et al., 1993). In this paper, we explore the idea that the European Rabbit *Oryctolagus cuniculus* acts as a keystone species in Mediterranean ecosystems. We test our ideas by comparing the abundance and diversity of avian predators in relation to the abundance of rabbits across southern Spain, the area where the rabbit was thought to have originated (Monnerot et al., 1994).

The Iberian Peninsula is home to 33 species of birds of prey, representing more than 60% of the total number of raptor species of Europe (i.e. Bruun and Singer, 1980). Many of these species are of conservation concern, being threatened by a variety of factors including changing land use and illegal killing (Villafuerte et al., 1998; Madroño et al., 2004). Of particular concern to raptor conservation in southern Europe is the decline in the populations of the European rabbit. According with Delibes and Hiraldo (1981), at least 29 different predators in this region, including 17 raptors and 9 carnivores capture rabbits

* *Corresponding author:* Tel.: +34 926 29 54 50; fax: +34 926 29 54 51.
E-mail addresses: Miguel.Delibes@uclm.es (M. Delibes-Mateos), s.redpath@ceh.ac.uk (S.M. Redpath), elena.angulo@ese.u-psud.fr (E. Angulo), Pablo.Ferreras@uclm.es (P. Ferreras), Rafael.Villafuerte@uclm.es (R. Villafuerte).
0006-3207/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2007.01.024

with variable frequency. Yet, despite the dependency of many raptor species on rabbits (Jaksic and Soriguer, 1981; Jaksic and Delibes, 1987), relationships between rabbit and raptor abundance in southern Europe have not been quantified.

Over the last 50 years, rabbit populations have undergone a sharp decline in the Iberian peninsula, mainly as a result of the arrival of two viral diseases, Myxomatosis in the 1950s (Ratcliffe et al., 1952) and Rabbit Haemorrhagic Disease (RHD) at the end of the 1980s (Villafuerte et al., 1995). The additive effect of both diseases has reduced rabbit numbers in most of its historical range, especially in ecologically less-favorable areas (Villafuerte et al., 1995). In Spain, where more than 30,000 private hunting estates cover more than 70% of the country (Villafuerte et al., 1998), rabbits are an important resource, and the decline in rabbit abundance is reflected in the number shot, from 10 million in the late 1980s to four million during recent years (INE, 2006). This decline poses potentially profound consequences for the Mediterranean predator community with repercussions for the associated ecosystems. Indeed, some rabbit-specialist predators such as the Iberian Lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*) are now considered as the most endangered cat and raptor of the world and Europe, respectively (Nowell and Jackson, 1996; Ferrer and Negro, 2004). It has been argued that declines in these species are, at least in part, due to declines in rabbit abundance (Moreno et al., 2004). Many other predators are also reported to have suffered because of the rabbit decline (Fernández, 1993; Real and Mañosa, 1997).

A further potential consequence of disease outbreaks and declining rabbit populations is that many of the generalist predators that fed largely on rabbits may have switched to feeding on red-legged partridges (*Alectoris rufa*) once rabbits became scarce (Ontiveros et al., 2005). This in turn may have contributed to the conflict between hunters and the conservation of predators in Spain. For instance, illegal killing of red kites, *Milvus milvus,* increased after the appearance of RHD and the species' range was reduced, particularly in high rabbit density areas (Villafuerte et al., 1998).

In this paper, we evaluate the application of the concept of keystone species to rabbits. For this purpose, we explore the relationships between rabbit abundance and birds of prey at two distinct levels. First, we evaluate relationships at a predator community level. We hypothesized that higher rabbit densities would be associated with higher predator numbers and species diversity. Second, we investigated the relationship between rabbit numbers and the critically endangered Spanish imperial eagle. Again, we expected to find a higher likelihood of eagle presence in areas of high rabbit abundances. We finally discuss the importance of rabbits for the conservation of birds of prey in this biodiversity hotspot (Myers et al., 2000).

2. Methods

2.1. Community level

Data were collected from 20 hunting estates in southern Spain during 1997 and 1998 (Fig. 1). To estimate rabbit abundance on each study area, a driven-transect (min. 8.6 km; max. 18 km) was selected to count rabbits at dusk each month from April 1997 to October 1998. From this transect we derived the number of rabbits seen per kilometre (Crawford, 1991). All avian predators were counted monthly for approximately two consecutive hours 2 h after dawn from May 1997 to June 1998, by one observer from an elevated vantage point over the area where rabbit abundance was estimated (Bibby et al., 2000). The average size of area watched was 212 ± 10.45 ha (mean ± SE).

Raptor data were analysed as the number of species seen and the total number of individuals counted per unit area. We considered all species of diurnal raptor, owl and *Corvidae* as predator species. Using information from Cramp and Simmons (1980), Delibes and Hiraldo (1981), and Jaksic and Soriguer (1981), we divided these predators into three broad groups: species that regularly killed rabbits, species that principally scavenged on dead or dying rabbits and other species that rarely fed on rabbits (Table 1). In total, six categories of avian predator abundance were estimated: the number of species of rabbit killers, scavengers and others, and the number of observations of predators in these three categories.

Finally, we estimated an index of conservation value using information from the Spanish red data list (Madroño et al., 2004). Each species was scored according to the following categories: in critically endangered (5), endangered (4), vulnerable, (3) near threatened (2) and not threatened (1). For each site we estimated the number of species of conservation interest (categories 2+) and a conservation index by summing the indices for those species observed in each site over the study period.

2.2. Single species level

To examine the relationship between Spanish imperial eagle and rabbits we used data from 120 surveys, completed during the summers of 2002 and 2003 in central southern Spain (Fig. 1). These survey sites were selected according to previous studies on rabbit abundances. Thus, most of these sites (80) had been part of a more comprehensive survey performed in 1993, when over 300 sites were surveyed throughout the entire country (Villafuerte et al., 1995, 1998). The remaining 40 sites had been part of two rabbit studies in Andalucia and Castilla la Mancha regions (Angulo, 2003; M. Delibes-Mateos, unpublished data). Along each transect, two observers walked 4 km counting the number of rabbit pellets within a 0.47 m^2 circular plot at 100 m intervals, avoiding counts on or near a latrine (Palomares, 2001). The number of pellets counted in the 40 plots along each transect provide a pellet abundance index (pellets/m^2; PAI).

The range and abundance of imperial eagles is well-known (Ferrer, 2001; Madroño et al., 2004). However, to corroborate eagle presence or absence on each study site, we also asked members of the "Spanish imperial eagle working group", a group consisting of researchers, Non Governmental Organisations (NGO), regional governments and hunting managers.

2.3. Statistical methods

We were interested in whether more raptors were seen on those sites where rabbits were more abundant. For each site we had information on raptors and rabbits from repeat sam-

Fig. 1 – Localities in which the relationship between rabbits and avian predators was surveyed (Black triangles represent study plots at the community level and grey dots at the single species level; see Section 2 for details).

ples collected during 14 and 18 consecutive months, respectively. We used Generalised Linear Mixed Models (GLIMMIX) in Littell et al. (1996) with a log link function and Poisson error structure to analyse these data. Denominator degrees of freedom were calculated using Satterthwaite's formula (Littell et al., 1996). Over dispersion was corrected for by dividing the deviance by the residual degrees of freedom. In these models we used a count of observations of avian predators as the response variable with an offset of the area and time watched. The explanatory variable was average rabbit abundance for each site, estimated as the mean value of the number seen (+1) per km of transect. As months represented an annual cycle we converted to radians by converting to four variables using sine (month), sine (month * 2), cosine (month) and cosine (month * 2). Month, year and site were included in all models as random effects and the subsequent influence of rabbit abundance on raptor numbers estimated. When comparing the total number of species seen and the index of

Table 1 – List of predator species and number seen during 512 h of observation on 20 sites in Andalucia

Species	Rabbit predators	Scavengers	Other spp.	Conservation status	No sites	Total no observations
Accipiter nisus			*	1	2	2
Aegypius monachus		*		3	4	44
Aquila adalberti	*			4	3	14
Aquila chrysaetos	*			2	11	40
Bubo bubo	*			1	1	6
Buteo buteo	*			1	14	113
Circaetus gallicus	*			1	10	186
Circus aeruginosus	*			1	5	50
Circus cyaneus	*			1	4	21
Circus pygargus	*			2	1	1
Corvus corone		*		1	14	223
Corvus monedula			*	1	13	2374
Cyanopica cyanus			*	1	10	384
Elanus caeruleus			*	2	3	4
Falco columbarius			*	1	1	1
Falco peregrinus			*	1	2	2
Falco tinnunculus			*	1	5	12
Garrulus glandarius			*	1	8	36
Gyps fulvus		*		1	11	657
Hieraaetus fasciatus	*			4	4	16
Hieraaetus pennatus	*			1	10	65
Milvus migrans		*		3	9	669
Milvus milvus		*		2	7	129
Neophon percnopterus		*		4	1	4
Pernis apivorus			*	1	1	1
Pica pica		*		1	10	320
Pyrrhocorax pyrrhocorax			*	2	2	19
Total identified						5393
Unidentified raptor spp.						189
Total observations						5582

Predators were placed into one of three categories, based on whether they were considered mainly rabbit predators, scavengers or species that rarely ate rabbits (i.e. Cramp and Simmons, 1980; Delibes and Hiraldo, 1981; Jaksic and Soriguer, 1981). Each species was allocated a conservation index, based on its inclusion in the red data list (Madroño et al., 2004).

conservation value for each site, we controlled for area watched and used Spearman Rank in Proc Corr in SAS to compare with average rabbit abundance.

To evaluate the relationship between rabbit abundance in 2002 (PAI) and the occurrence of Spanish imperial eagle, we employed a Generalised Linear Model (GLIMMIX) in Littell et al. (1996) with a logit link function and a binomial distribution. Site and year were included in the model as random effects.

All tests are 2-tailed and average values are given ±1SE.

3. Results

3.1. *Community level*

In total, 512 h were spent censusing raptors, with an average of 25.6 ± 3.0 h per site. Overall, 5582 observations of 27 species of avian predator were made (Table 1). There was considerable variation between sites in rabbit abundance (range of average values: 0.0–26.1 km^{-1}) and the number of raptor species seen (range 1–15 species). The number of species of both rabbit predators and scavengers seen on each site was positively correlated with average rabbit abundance (Fig. 2a). Similarly, the number of observations of these two predator types was highest on sites where rabbits were most abundant (Fig. 2b). Relationships between other predator species and rabbit abundance were also positive, but not significant (Fig. 2).

There was also a positive relationship between rabbit abundance and both the number of species of conservation concern and the index of conservation value. According to our criteria, sites with the most rabbits were of higher conservation value (Fig. 3).

3.2. *Single species level*

In the wider sample of sites, rabbit abundance (PAI) ranged from 0 to 302 pellets/m^2 (Fig. 4). The Spanish imperial eagle was present in approximately 25% (n = 31) of the localities where rabbit abundance was surveyed. Eagles were more likely to occur in sites with high rabbit abundance (Fig. 4). PAI average of those localities with imperial eagles averaged 101.33 pellets/m^2 (range = 2.97–302.87; SE = 14.88), compared to 13.96 pellets/m^2 in sites without eagles (range = 0–108.88; SE = 2.04).

4. Discussion

The correlative evidence presented in this study strongly suggests that rabbits are critically important to the conservation of the predator community in the Mediterranean. Of the 17 raptor species we saw during our surveys that are known to

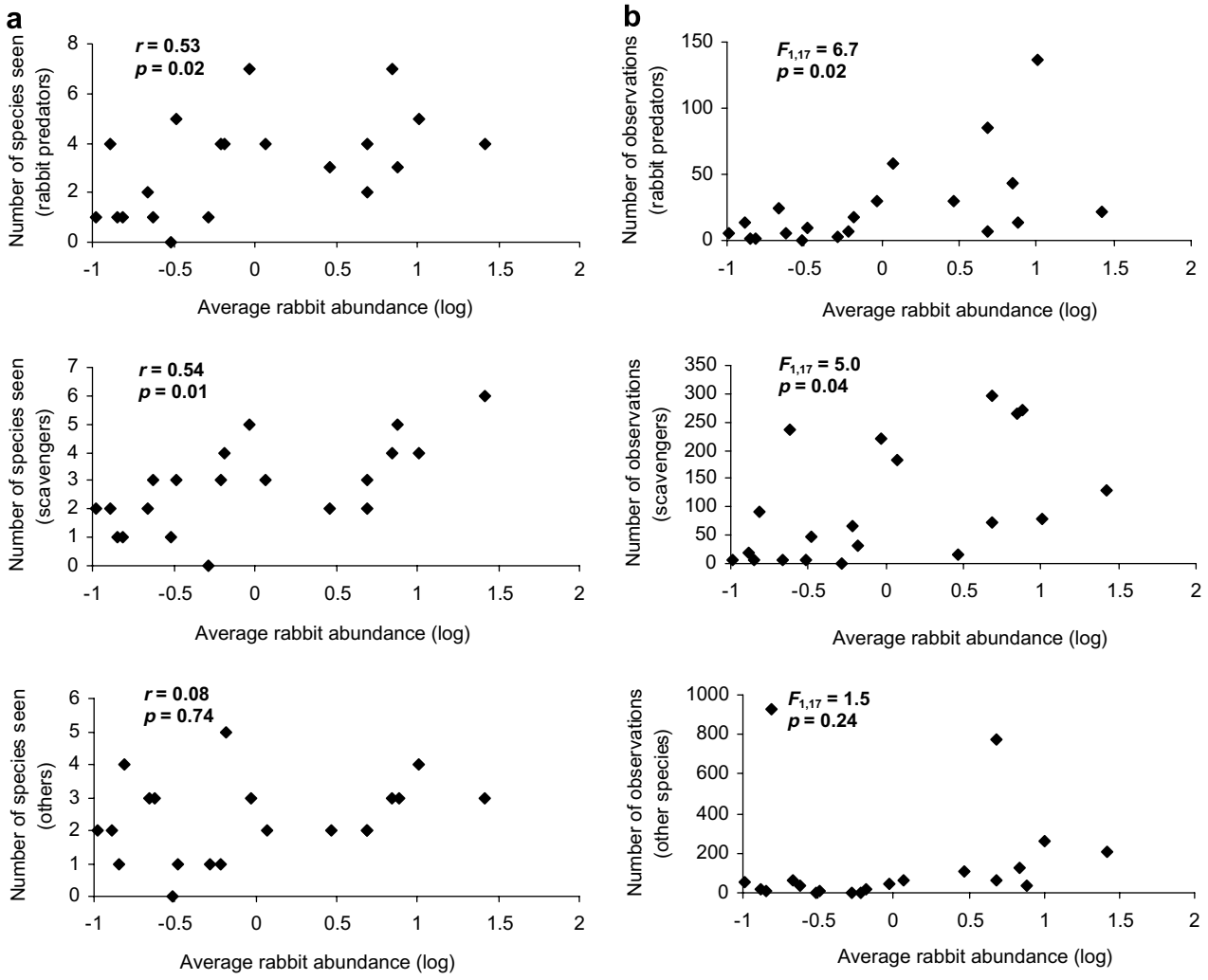

Fig. 2 – Relationships between predator numbers and rabbit abundance. Figures shown for the number of species seen at each site (a), and the number of observations of avian predators (b). Predators divided into rabbit predators, scavengers and others. Statistics given in (a) are Spearman Rank correlations between species per unit area and rabbit abundance, and in (b) are *F* values from Mixed Models controlling for year, site and month.

kill rabbits or scavenge on rabbit carcasses, both the number of species and the number of individuals seen were correlated with rabbit abundance. Moreover, those species of highest conservation concern, including the critically endangered Spanish imperial eagle, were more likely to be seen in areas with more rabbits.

There are two hallmarks of keystone species; their presence is crucial in maintaining the organization and diversity of their ecological communities and second, it is implicit that these species are exceptional, relative to the rest of the community, in their importance (Paine, 1969; Holt, 1984; Mills et al., 1993). Our analysis is the first to show the relationship between rabbit abundance and raptor diversity and supports the idea that rabbits are indeed a keystone species in the Iberian ecosystem, as suggested by Valverde (1967). Rabbits are able to maintain their abundance in the face of predation, via a high reproductive rate (Gibb, 1990) and therefore they can affect community structure by sustaining the density of predators and scavengers (Fig. 2). Removing rabbits would decrease overall species diversity in the predator community (Mills et al., 1993). A similar role of keystone species has been observed in other lagomorphs such as plateau pikas (*Ochotona curzoniae*; Lai and Smith, 2003).

The Spanish imperial eagle was mainly present in areas with high rabbit density (Fig. 4). There are, however, some exceptions where birds occur despite the fact that rabbits are scarce. For instance, in Doñana National Park rabbit numbers are very low (15.64 pellets/m^2), but a recent estimate suggests that seven pairs still remained there at the turn of the century (Ferrer et al., 2003). This may be because there are many other prey species there that can support the birds at least temporarily (Delibes, 1978). However, given the importance of rabbits to these eagles we suspect that ultimately these birds will decline unless rabbit populations recover (Ferrer et al., 2003). In several other areas with low rabbit density, the NGO WWW/ADENA supplies rabbits to feed endangered predators, and this may be sufficient to support imperial eagles (González et al., 2006).

After the outbreak of RHD, the conflict between hunters and predators increased in Spain (Villafuerte et al., 1998).

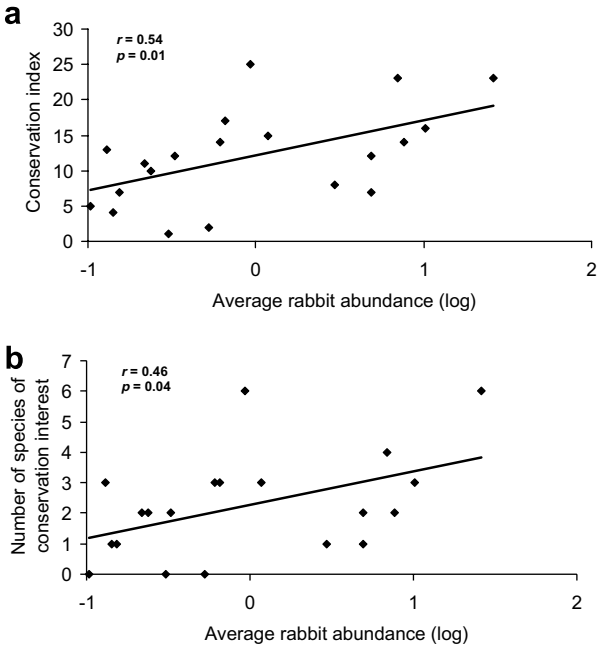

Fig. 3 – Relationships between the conservation index per site and the average rabbit abundance (a), and the number of species of conservation concern and rabbit abundance (b). The analyses control for area watched.

Virgós and Travaini (2005) observed that carnivore species richness in central Spain was significantly lower in hunting estates (where rabbits are abundant) than in non-hunting areas. In contrast, we have found higher raptor species richness in areas where rabbits are abundant (Fig. 2). On hunting estates, many techniques such as traps, snares or burying poisoned bait are frequently used to control terrestrial predators, so carnivores could be more affected by predator control than the avian predator community. Reduced predation by carnivores may benefit raptors in some areas, leading to higher than expected numbers. In contrast, in other areas, illegal management techniques affect raptors (Villafuerte et al., 1998). It seems plausible that these factors may in part explain some of the remaining variation around our relationships between rabbits and raptor abundance.

Keystone species typically function as predators, prey, mutualists or habitat modifiers (Mills et al., 1993). Rabbits differ from most conventional keystone species because they fulfil more than one action. In this paper, we have focused only on the relationship between rabbits and raptors. However, rabbits also exert a strong influence on the habitats of other species through consumption of vegetation, dispersal of seeds, scattering latrines and burrowing. For instance, Gómez-Sal et al. (1999) demonstrated the essential role of rabbits in maintaining a savanna-like pattern in Mediterranean *Retama sphaerocarpa* scrubland. Rabbits can also disperse the seeds of at least 58 plant species in the Mediterranean region (M. Delibes-Mateos, unpublished data). Moreover, rabbit latrines have a demonstrable effect on soil chemical fertility and plant growth (Willot et al., 2000) and also provide feeding areas to a number of invertebrates (Galante and Cartagena, 1999). On the other hand, rabbit warrens provide refuge areas for many other Mediterranean species such as the Montpellier snake *Malpolon monspessulanus,* the Eurasian badger *Meles meles* (Blázquez and Villafuerte, 1990; Revilla et al., 2001, respectively), or even the Iberian Lynx (P. Ferreras pers. comm.).

The role of rabbits as a keystone species in southern Europe is akin to the role of functionally similar prairie dogs (*Cynomys* spp.) in prairie systems of the United States, since both are social species and can occur at high densities. Similarly to rabbits in the Mediterranean region, prairie dogs can alter prairie landscapes and provide foraging, shelter and nesting habitat for a diverse array of species (reviewed in Kotliar et al., 1999). Additionally, owing to their size and ability to reach high abundance, both rabbits and prairie dogs serve as prey for a number of predators, including highly endangered predators. For instance, the black-footed ferret (*Mustella nigripes*) is apparently so specialized on prairie dogs that it does not persist where prairie dogs are eliminated (Kotliar et al., 1999). This situation resembles the results obtained in this paper regarding the distribution of the Spanish imperial eagle (Fig. 4).

In this study, we have recorded higher conservation index values in areas where rabbits reach high densities (Fig. 3).

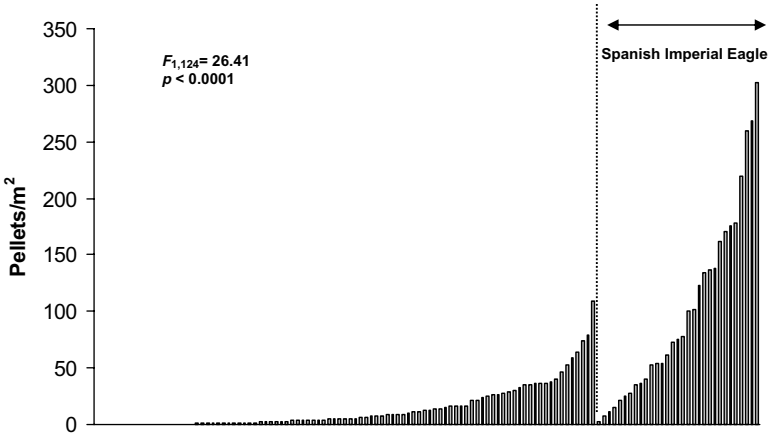

Fig. 4 – Rabbit abundance as the Pellet Abundance Index (PAI) in the 126 localities where the occurrence of the Spanish imperial eagle was surveyed. The dotted line separates areas occupied by the eagle from those in which it does not appear. Statistic given is *F* value from Mixed Model controlling for site and year.

Although it is impossible to determine causality from our results, they strongly suggest that rabbit conservation confers protection to a large number of naturally co-occurring species. Consequently, preserving viable populations of rabbits could protect other members of the natural community (Bifolchi and Lodé, 2005), including several predator species of valuable conservation concern.

The number of endemic or endangered species has usually been taken into account to select priority areas for conservation in the Iberian peninsula (Filipe et al., 2004), although there is no biological justification for using them (Possingham et al., 2002). In contrast, rabbits have not traditionally been considered when designing areas of special conservation interest in Spain (M. Delibes-Mateos, unpublished data). Only in recent years has rabbit recovery has been included as a strategy in several recovery plans for the restoration of rabbit specialist predators. For instance, the recovery and maintenance of viable populations of rabbits is among the main objectives of the Iberian Lynx LIFE project in Andalusian region (http://www.juntadeandalucia.es/medioambiente/LIFE_-lince/infogeneral/introduccion.html).

To summarise, we have observed that rabbits act as a keystone species in the Iberian ecosystem. Based on our results, we suggest that rabbit abundance provides a valuable measure for conservationists to pinpoint areas of current or future interest for conservation. The relationship between rabbits and conservation is, however, complicated by the fact that rabbits are more abundant on hunting estates, and hunters have been implicated in the decline of some predators (e.g. Villafuerte et al., 1998). Clearly, it is in the interests of nature conservation for conservationists to find ways of working together with hunters to improve rabbit numbers whilst conserving rare and protected predator species.

Acknowledgements

M.D.-M. was supported by a I3P grant funded by the European Social Fund through the "Consejo Superior de Investigaciones Científicas" (CSIC). Funding was provided by the Projects CGL 2005-02340/BOS by the Spanish Ministry of Education and Science and PAI06-170 by the regional government of Castilla-la Mancha. We specially thank to Dr. J. Viñuela who provided valuable information about the distribution of the Spanish imperial eagle. D. Elston provided statistical assistance. Special thanks go to P. Ayala, G. Calabuig, J. Castillo, P. Castro, A. Finque, A. Linares, S. Luna, J. Martínez, L. Mínguez, M. Reglero, O. Rodríguez, C. Rouco, J. Viñuela and E. Virgós for field assistance during rabbit surveys. Two anonymous reviewers notably improved the manuscript.

REFERENCES

Angulo, E., 2003. Factores que afectan a la distribución y abundancia del conejo en Andalucía. Ph.D. Thesis, University Complutense of Madrid.

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. Bird Census Techniques. Academic Press, London.

Bifolchi, A., Lodé, T., 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. Biological Conservation 126, 523–527.

Blázquez, M.C., Villafuerte, R., 1990. Nesting of the Montpellier snake (*Malpolon monspessulanus*) inside rabbit warrens at Doñana National Park (SW Spain): phenology and a probable case of communal nesting. Journal of Zoology 222, 692–693.

Bruun, B., Singer, A., 1980. Guía de las aves de España y Europa. Omega, Barcelona.

Cramp, S., Simmons, K.E.L., 1980. The Birds of the Western Palearctic, vol. 2. Oxford University Press, Oxford.

Crawford, T.J., 1991. The calculation of index numbers from wildlife monitoring data. In: Goldsmith, B. (Ed.), Monitoring for Conservation and Ecology. Chapman and Hall, London (Chapter 12).

Delibes, M., 1978. Ecología alimenticia del Águila Imperial Ibérica *Aquila adalberti* durante la crianza de los pollos en el Coto de Doñana. Doñana Acta Vertebrata 5, 35–60.

Delibes, M., Hiraldo, F., 1981. The rabbit as prey in the Iberian Mediterranean ecosystem. In: Myers, K., MacInnes, C.D. (Eds.), Proceedings of the I World Lagomorph Conference. University of Guelph, Ontario, pp. 614–622.

Fernández, C., 1993. Effect of the viral haemorrhagic pneumonia of the wild rabbit on the diet and breeding success of the golden eagle *Aquila chrysaetos* (L.). Terre et Vie 48, 323–329.

Ferrer, M., 2001. The Spanish Imperial Eagle. Lynx editions., Barcelona.

Ferrer, M., Negro, J.J., 2004. The near extinction of two large European predators: super specialists pay a price. Conservation Biology 18, 344–349.

Ferrer, M., Penteriani, V., Balbontin, J., Pandolfi, M., 2003. The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish imperial eagle in Donana. Biological Conservation 114, 463–466.

Filipe, A.F., Marques, T.A., Seabra, S., Tiago, P., Ribeiro, F., Moreira da Costa, L., Cowx, I.G., Collares-Pereira, J., 2004. Selection of priority areas for fish conservation in Guadiana River Basin, Iberian peninsula. Conservation Biology 18, 189–200.

Galante, E., Cartagena, M.C., 1999. Comparison of Mediterranean dung bettles (Coleoptera: Scarabaeoidea) in cattle and rabbit dung. Environmental Entomology 28, 420–424.

Gibb, J.A., 1990. The European rabbit, *Oryctolagus cuniculus*, in: Chapman, J.A., Flux, J.E.C. (Eds.), Rabbit, Hares and Pikas: Status Survey and Conservation Action Plan. IUCN/SCC Lagomorph Specialist Group, Information Press, Oxford, pp. 116–120.

Gómez-Sal, A., Rey-Benayas, J.M., López-Pintor, A., Rebollo, S., 1999. Role of disturbance in maintaining a savanna-like pattern in Mediterranean Retama *Retama sphaeorcarpa* shrubland. Journal of Vegetation Science 10, 365–370.

González, L.M., Margalida, A., Sánchez, R., Oria, J., 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). Biological Conservation 129, 477–486.

Holt, R.D., 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. The American Naturalist 124, 377–406.

INE, 2006. Instituto Nacional de Estadística, Madrid. <http://www.ine.es/inebase/cgi/um?M=%2Ft01%2Fa098%2Fa1998&O=pcaxis&N=&L=0> (Accessed 18.01.2006).

Jaksic, F.M., Delibes, M., 1987. A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: causes, correlations, and consequences. Oecologia 71, 461–472.

Jaksic, F.M., Soriguer, R.C., 1981. Predation upon the European rabbit (*Oryctolagus cuniculus*) in Mediterranean habitats of

Chile and Spain: a comparative analysis. Journal of Animal Ecology 50, 269–281.
Kotliar, N., Baker, B.W., Whicker, A.D., Plumb, G., 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24, 177–192.
Lai, C.H., Smith, A.T., 2003. Keystone status of plateau pikas (*Ochotona curzoniae*): effect of control on biodiversity of native birds. Biodiversity and Conservation 12, 1901–1912.
Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Inst. Inc., Cary, NC.
Madroño, A., González, C., Atienza, J.C., 2004. Libro rojo de las aves de España. Ministerio de Medio Ambiente, SEO Birdlife, Madrid.
Mills, S., Soule, M.E., Doak, D.F., 1993. The keystone-species concept in ecology and conservation. BioScience 43, 219–226.
Monnerot, M., Vigne, J.D., Biju-Duval, C., Casane, D., Callou, C., Hardy, C., Mougel, F., Soriguer, R.C., Dennebouy, N., Mounolou, J.C., 1994. Rabbit and man: genetic and historic approach. Genetics Selection Evolution 26, 167–182.
Moreno, S., Villafuerte, R., Cabezas, S., Lombardi, L., 2004. Wild rabbit restocking for predator conservation in Spain. Biological Conservation 118, 183–193.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
Nowell, K., Jackson, P., 1996. Wildcats: Status Survey and Conservation Action Plan. World Conservation Union, Gland.
Ontiveros, D., Pleguezuelos, J.M., Caro, J., 2005. Prey density, prey detectability and food habits: the case of Bonelli's eagle and the conservation measures. Biological Conservation 123, 19–25.
Palomares, F., 2001. Comparison of 3 methods to estimate rabbit abundance in Mediterranean environment. Wildlife Society Bulletin 29, 578–585.
Paine, R.T., 1969. A note on trophic complexity and community stability. The American Naturalist 103, 91–93.
Possingham, H.P., Andelman, S.J., Burgman, M.A., Medellín, R.A., Master, L.L., Keith, D.A., 2002. Limits to the use of threatened species lists. Trends in Ecology and Evolution 17, 503–507.
Ratcliffe, F.N., Myers, K., Fennessy, B.V., Calaby, J.H., 1952. Myxomatosis in Australia. A step forwards the biological control of the rabbit. Nature 170, 1–13.
Real, J., Mañosa, S., 1997. Demography and conservation of Western European Bonelli's Eagle (*Hieraaetus fasciatus*) populations. Biological Conservation 79, 59–66.
Revilla, E., Palomares, F., Fernández, N., 2001. Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area. Journal of Zoology 255, 291–299.
Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? Biological Conservation 83, 247–257.
Valverde, J.A., 1967. Estructura de una comunidad de vertebrados terrestres. Monografías de la Estación Biológica de Doñana. CSIC, Madrid.
Villafuerte, R., Calvete, C., Blanco, J.C., Lucientes, J., 1995. Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. Mammalia 59, 651–659.
Villafuerte, R., Viñuela, J., Blanco, J.C., 1998. Extensive predator persecution caused by population crash in a game species: The case of red kites and rabbits in Spain. Biological Conservation 84, 181–188.
Virgós, E., Travaini, A., 2005. Relationships between small-game hunting and carnivore diversity in central Spain. Biodiversity and Conservation 14, 3475–3486.
Willot, S.J., Miller, A.J., Incoll, L.D., Compton, S.G., 2000. The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. Biology and Fertility of Soils 31, 379–384.