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ORIGINAL ARTICLE

Can widespread generalist predators affect keystone prey? A case study with red foxes and European rabbits in their native range

Javier Fernandez-de-Simon[1,2,5] · **Francisco Díaz-Ruiz**[1,4] · **Manuel Rodríguez-de la Cruz**[1] · **Miguel Delibes-Mateos**[1,3,4] · **Rafael Villafuerte**[1,3] · **Pablo Ferreras**[1]

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Abstract Widespread generalist predators may affect declining keystone prey populations. However, this phenomenon is not well understood. In this paper, we assessed whether the abundance and population growth of European rabbits *Oryctolagus cuniculus*, a keystone prey species in Mediterranean Iberia, was related to the abundance and diet of red foxes, *Vulpes vulpes*, a widespread generalist predator. In a locality in central Spain, where rabbit population abundance declined, we estimated rabbit abundance during almost 3 years and determined fox abundance and diet during two concurrent years. We calculated a fox predation index (percentage of consumed rabbit biomass × fox abundance) to assess the importance of rabbits to foxes. We employed a multi–model approach to explain rabbit abundance and population growth. Foxes consumed between 60 and 99 % rabbit biomass in their diets, and this was independent of rabbit abundance. Periods of higher fox predation index coincided with lower rabbit density and vice versa. Two models best explained rabbit abundance and four rabbit population growth. They included the fox predation index and its interaction with rabbit abundance during the previous month. Altogether, fox predation, intraspecific density dependence, and their interaction partly explained rabbit population dynamics. We conclude that in order to propel the recovery of the rabbit in Iberia, it is essential to better understand the role of these factors in driving the abundance of the species.

Keywords Diet · Intraspecific density dependence · *Oryctolagus cuniculus* · Predator control · Prey limitation · *Vulpes vulpes*

Introduction

The European rabbit (*Oryctolagus cuniculus* L.), a lagomorph native to the Iberian Peninsula, is the most preferred prey of foxes (*Vulpes vulpes* L.) in central–southern Iberia (Díaz-Ruiz et al. 2013). Rabbits are the main prey item for foxes and other predators because of its considerable size and usual high abundance (Delibes and Hiraldo 1981; Ferrer and Negro 2004; Delibes-Mateos et al. 2008a). Rabbits in this part of the world are thus considered a keystone species i.e., a species that maintains the structure and integrity of the community, and is therefore a species of high conservation concern (Delibes-Mateos et al. 2007; Wagner 2012). Rabbits create open areas, promote soil fertility and increase plant growth and diversity (Gómez-Sal et al. 1999; Willot et al. 2000). In addition, rabbit latrines provide food for many invertebrates (Verdú and Galante 2004) and rabbit burrows provide nest sites and shelter for vertebrates and invertebrates (Gálvez et al.

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✉ Javier Fernandez-de-Simon
jafdsr@yahoo.es

[1] Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), Ronda de Toledo n° 12, 13071 Ciudad Real, Spain

[2] Laboratoire Chrono–Environnement, UMR UFC/CNRS 6249, Université Bourgogne Franche-Comté, F-25000 Besançon, France

[3] Instituto de Estudios Sociales Avanzados, IESA (CSIC), C/Campo Santo de los Mártires, 7, 14004 Córdoba, Spain

[4] CIBIO/InBIO, Universidade do Porto, Campus de Vairão, 4485-661 Vairão, Portugal

[5] Calatrava 20, 3°-C, Ciudad Real, Spain

2009). The rabbit is also of high economic importance in Iberia since it is one of the most hunted small game species in Spain and Portugal (Delibes-Mateos et al. 2008a).

In recent decades, most Iberian rabbit populations have decreased drastically due to the impact of viral diseases such as myxomatosis and rabbit hemorrhagic disease (hereafter RHD), alongside with habitat loss and over-hunting (Delibes-Mateos et al. 2009). Because of these declines, the rabbit is now classified as a “Vulnerable” species in the Spanish Red List (Villafuerte and Delibes-Mateos 2007). Understanding which factors may hinder the recovery of the rabbit in the Iberian Peninsula, is crucial to propose mitigating actions (Delibes-Mateos et al. 2009, 2014a, b). In particular, assessing the role of predators on rabbit populations is fundamental given that predation is one of the main processes structuring animal communities (Sinclair and Krebs 2002).

Predation effects on a prey species are often difficult to quantify (Valkama et al. 2005), and predation consequences on ecosystem functioning are often not well understood. However, baseline information on predator abundance and prey consumption can be used to quantify predation intensity (Korpimäki et al. 1991), and the relationship between predation intensity, prey abundance and its population growth employed to estimate the effects of predation on a prey (Sinclair et al. 1998, 2006). Here, we assessed whether predation by the main predator of the rabbit in Iberia, the red fox, was related to the abundance and population growth of the rabbit populations in a locality in central Spain.

The red fox is considered to be one of the most widespread generalist vertebrate predators in the world (Macdonald and Reynolds 2004). Red foxes are known to limit prey abundance, especially when prey populations are already declining or at low densities (Saunders et al. 2010). Studies demonstrating fox effects on rabbit abundance were mostly from Australia where rabbits were introduced and are considered pests (Pech et al. 1992; Banks 2000). In Iberia, however, foxes are often assumed to affect the abundance and population growth of rabbit populations (Villafuerte et al. 1996; Calzada 2000; Delibes-Mateos et al. 2008b), though there is no empirical data to adequately demonstrate this. In central Spain, most small game hunters argue that foxes negatively impact rabbits and partridges; hence foxes are often controlled in hunting estates (Delibes-Mateos et al. 2013). But, the effects of fox predation on Iberian rabbit population dynamics are not well understood (Norbury and Jones 2015), with no evidence that rabbit populations increase with fox control (Díaz-Ruiz and Ferreras 2013).

In this paper, we first examine rabbit consumption by foxes and estimate fox abundance changes in a locality where an overall decline in rabbit abundance had been recorded for a three–year period. We also employed a smaller concurrent two–year dataset, to analyse and discuss the potential role of fox predation on the rabbit population. Finally, we discuss how our results can be utilised to better understand predator–prey relationships in a context of biodiversity conservation.

Materials and methods

Study area

We carried out our fieldwork in a property located in the Albacete province (central Spain, Fig. 1). The climate is Mediterranean, characterized by mild wet winters and warm dry summers. The landscape is typical of most rural Mediterranean areas (Blondel and Aronson 1999), occupied by Mediterranean scrubland (e.g., with rosemary *Rosmarinus officinalis* L., kermes oaks *Quercus coccifera* L., thyme *Thymus* sp.), pastures (mainly grasses), ‘dehesas’ (savanna–like formations combining pasture with intermittent cereal cultivation in park–like woodlands of mainly oaks *Quercus ilex* ssp. *rotundifolia* Lam., Blondel and Aronson 1999), and croplands (mainly cereals and vineyards *Vitis vinifera* L.). Besides agriculture, other sources of income included horse breeding and hunting of small game, such as rabbits. During the study, a gamekeeper, who was responsible for regulating hunting and controlling predators, was employed in the property during the study except for the last two months. Predator control is generally undertaken in a non–systematic way in small game hunting estates (Delibes-Mateos et al. 2013) and unfortunately, for our study site no data on the intensity of fox control was available.

Because our study locality contained gentle slopes and ecotones between Mediterranean scrubland areas and pastures or cropland, it was highly favorable for rabbits and foxes (Lombardi et al. 2003; Macdonald and Reynolds 2004). Highest rabbit densities were usually found along the ecotones between open scrub and cereal crops; areas of softer soil of greater ease for building rabbit warrens. Rabbit densities in the study area ranged from low to high densities for Iberia (Fernandez-de-Simon et al. 2011a; Delibes-Mateos et al. 2014b). Fox abundance was considered as very low to intermediate for this region (see Results; Sobrino et al. 2009; Fernandez-de-Simon 2013).

Rabbit and fox abundance estimation

To estimate rabbit abundance we conducted cleared–plot pellet counts during a period of three years (summer 2006–summer 2009). Cleared–plot pellet counts is a cost–efficient method that is widely used in rabbit studies; it provides one of the most reliable estimates of rabbit

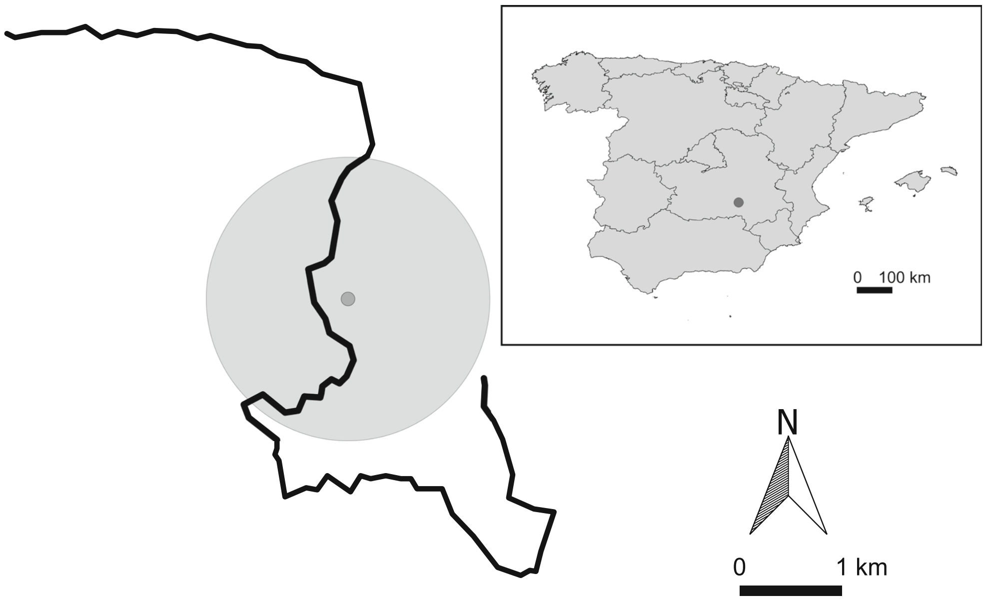


Fig. 1 Location of the study area in central Spain. The transect for spotlight fox counts is depicted as a *black thick line* within this study area. The location of the sampling grid for cleared–plot rabbit pellet counts is shown as a *dark grey* point. The *circle* in *light grey colour* shows the area where red fox scats were collected during transects on foot

abundance (Fernandez-de-Simon et al. 2011a, b; Ferreira et al. 2014). Within a 40 × 70 m grid, we set 40 circular (0.5 m^2) plots distributed regularly in the area with the highest rabbit abundance that was accessible to foxes living in the surroundings (see below, Fig. 1). Every month, we obtained a pellet count index corrected for pellet persistence (hereafter N, pellets m^{-2} day^{-1}; see Fernandez-de-Simon et al. 2011a, b). We also calculated the monthly rabbit population growth by using N from consecutive months (Sinclair et al. 2006) as follows:

$$NPG_t = (\log_e(N_t/N_{t-1})/T) \times 30.42$$

where T is the number of days between visits and 30.42 is the average length of a calendar month in days.

To estimate fox abundance, we conducted spotlight counts along a 15–km–transect driven at night, starting at least one hour after sunset. Surveys were undertaken for three consecutive nights, unless prevented by meteorological conditions or logistic constraints. Our fox transect was as close as 300 m from the rabbit abundance sampling grid (Fig. 1) to allow us to detect changes in fox abundance that may prey upon our monitored rabbit population. To account for seasonal changes in fox abundance (Reynolds and Tapper 1995), we conducted spotlight count surveys twice a year: in winter–spring (March–May), and in summer (July) during 2007–2009. We used the mean number of individual red foxes seen per km and night in each period as a red fox abundance index (hereafter RF, Pech et al. 1992; Sobrino et al. 2009).

Fox diet assessment

We examined changes in fox diet during a two–year period (March 2007–June 2009) from scats collected along transects (2.4–9.0 km long) walked every month (Fig. 1). Transects, though not standardised, traversed land features (e.g., tracks, paved roads, water streams, fences, rabbit warrens, etc.; Webbon et al. 2004) where foxes regularly deposited scats during territory marking. Fox scats were identified by their scent, size, shape, thickness and by the presence of fox hairs, which appear in scats because of grooming (Delibes-Mateos et al. 2008c and references therein). We analyzed a total of 342 fox scats. In April 2007, December 2007 and March 2009 no scats were collected due to logistic constraints. In our analyses we excluded May 2009, since fewer than 5 scats were available for that month. For the remaining months, at least 5 scats were available for analysis (Fig. S1 in Electronic Supplementary Material (ESM)); this sample size was considered adequate since only a small number of food items were consumed (mainly rabbits, see below, Table 1).

Scats were dried at 60 °C for a period of 48 h and then weighted to the nearest 0.001 g using a digital scale. The scats were then soaked overnight in water, after which we teased them apart over a 0.5 mm sieve (Reynolds and Aebischer 1991). We classified remains found in each scat into 10 food classes: (a) rabbit, (b) hare, (c) undetermined lagomorph, (d) small mammals, (e) carrion (wild ungulates, livestock and mammalian carnivores), (f) birds and

Table 1 Red fox diet (percentage of dry weight and percentage of biomass) estimated in a study locality monitored monthly in central Spain between March 2007 and June 2009 by means of the analysis of 342 scats

Food class	Percentage of dry weight	Percentage of biomass	Coefficients of digestibility
European rabbit	85.63	83.24	16.00
Iberian hare	1.69	2.02	19.70
Undetermined lagomorph	0.05	0.05	17.85[a]
Small mammals	2.06	2.08	16.60
Carrion	<0.01	<0.01	37.20
Birds/eggs	5.35	6.58	20.25
Reptiles/amphibians	0.25	0.49	32.10[b]
Arthropods	3.31	2.49	12.40[c]
Fruits/seeds	1.65	2.99	29.80
Others	0.02	0.03	23.74[d]

The coefficients of digestibility (fresh ingested food/dry weight of the scats produced), used to obtain biomass consumption estimates from scat analyses are also shown. These coefficients were estimated from feeding tests with captive foxes, except those with a superscript for which bibliographic values were employed. See text for further details

[a] Average from European rabbits and Iberian hare coefficients of digestibility, from authors' data

[b] Average from Sarmento (1996) "lizards" and "snakes" coefficients of digestibility

[c] From Reynolds and Tapper (1995)

[d] Average from the coefficients of digestibility of undetermined lagomorph, small mammals, carrion, birds/eggs, reptiles/amphibians, arthropods, and fruits/seeds

eggs, (g) reptiles and amphibians, (h) arthropods, (i) fruits and seeds, and (j) others (rare items or impossible to determine). The dry weight of the remains of each food class in each scat was estimated as the product of the percent volume of each prey item and the scat's dry weight (Delibes-Mateos et al. 2008c). We calculated the consumed biomass of each item by multiplying the dry weight of the item in the scats by the coefficient of digestibility specific to the food class. The latter is the ratio of the fresh ingested food/dry weight of the scats produced (Reynolds and Aebischer 1991), obtained from 10–day food trials using two captive red foxes (one male, one female) at the IREC–UCLM experimental facility (Table 1; Fernandez-de-Simon 2013). For arthropods, and reptiles/amphibians, we used the coefficients of digestibility reported by Reynolds and Tapper (1995) and Sarmento (1996), respectively. To assess the contribution made by rabbit to fox diet during each month, we estimated the percentage of rabbit biomass consumed. We also calculated a monthly red fox predation index (hereafter *RFI*) as the product of monthly rabbit consumption (percentage of consumed rabbit biomass) and the fox abundance index (*RF*, see also Korpimäki et al. 1991). We derived a winter *RF* for the period December–May, and summer *RF* for the period June–November.

Data analyses

To understand the feeding ecology of the fox in our study locality, we first investigated the relationship between the percentage of rabbit biomass consumed and rabbit abundance. We then assessed the relationship between the predation index, RFI_t (see above) and rabbit abundance index (N_t) and rabbit population growth (NPG_t). Given the time series for rabbit abundance spanned from August 2006 to June 2009, but data of *RF* (and thus *RFI*) was collected between April 2007 and May 2009, our analyses only refer to the overlap period of two years. We developed general linear models for (a) N_t and (b) NPG_t as dependent variables. We considered (i) RFI_t, (ii) month, (iii) year, and (iv) the interaction $N_{t-1} \times RFI_t$ as independent variables. All models included N_{t-1} to correct potential temporal autocorrelation. We also run a model with N_{t-1} only to test whether previous abundance of rabbits alone could also explain rabbit abundance and population growth. In addition, we compared the performance of these models with a null model (intercept only) as an indicator of overall model performance (Burnham and Anderson 2002). In total, 17 models were generated with all possible variable combinations. Models were fitted with a normal error distribution and an identity link function. For model selection we inspected mainly the AIC_c (Akaike Information Criterion corrected for small sample size), but also D^2 (explained deviance). Given the large number of models tested, we only show those models within $\Delta_i < 2$ (Δ_i = difference in AIC_c with the most parsimonious model). We tested normality, linearity and homocedasticity of model residuals and variables used (Zuur et al. 2007). To meet model assumptions, we transformed, when necessary, either the dependent and/or independent variables with the decimal logarithm transformation (see Zuur et al. 2007). We also tested temporal autocorrelation by a linear model of the

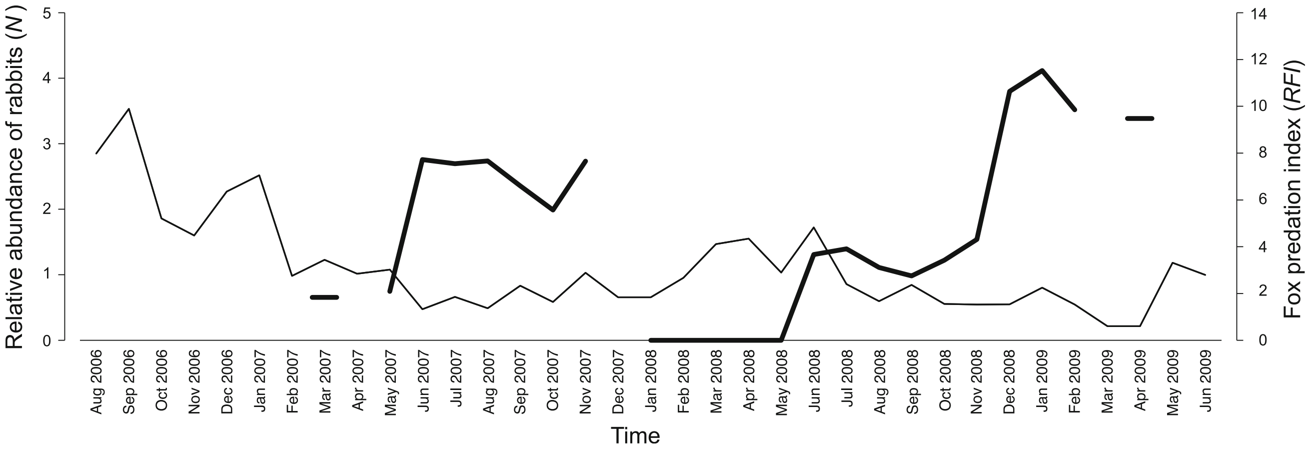


Fig. 2 Relative abundance of rabbits (N, pellets m^{-2} day^{-1}, *thin line*) and fox predation index (RFI, percentage of rabbit biomass × foxes km^{-1}, *thick line*) in the study locality

consecutive residuals against each other (Breusch–Godfrey test for autocorrelation, Godfrey 1978; Breusch 1979). However, we did not find evidence of temporal autocorrelation. Parameters and probability values of individual variables in the best models are shown. We were more interested in inference than in hypothesis testing so we preferred not to use a critical probability threshold. In this way, models with non–significant variables ($P > 0.05$) are taken into account and included for inference purposes (see also Burnham and Anderson 2002). We performed these analyses using R version 3.0.1 (R Development Core Team 2013).

Results

Rabbit abundance decreased along three years with maximum in September 2006 ($N = 3.53$ pellets m^{-2} day^{-1}) and minimum in March and April 2009 ($N = 0.22$ pellets m^{-2} day^{-1}, Fig. 2).

Rabbits were the main prey item consumed by foxes in our study area (Table 1). Monthly rabbit consumption by foxes ranged between 60 and 99 % in biomass terms, and varied independently of rabbit abundance (Fig. 3).

Fox abundance also varied across time, with a minimum in winter–spring 2008, with no foxes observed, to a maximum in winter–spring 2009 ($RF = 0.13$ foxes km^{-1}, Fig. 4). Predation Index was lowest during winter–spring 2008 ($RFI = 0.00$ percentage of rabbit biomass × foxes km^{-1}), and highest in winter–spring 2009 ($RFI = 11.53$ percentage of rabbit biomass × foxes km^{-1}). Predation index was inversely related to rabbit abundance for the overlap period (Fig. 2, see below).

Two models explaining rabbit abundance (log N_t) had $\Delta_i < 2$; these included RFI_t (Fig. 5) and the interaction log $N_{t-1} \times RFI_t$ (Tables 2 and 3). Four rabbit population growth models also had $\Delta_i < 2$, that included the variable N_{t-1} (log–transformed, Fig. 6), RFI_t and the interaction log $N_{t-1} \times RFI_t$ (Tables 2 and 3).

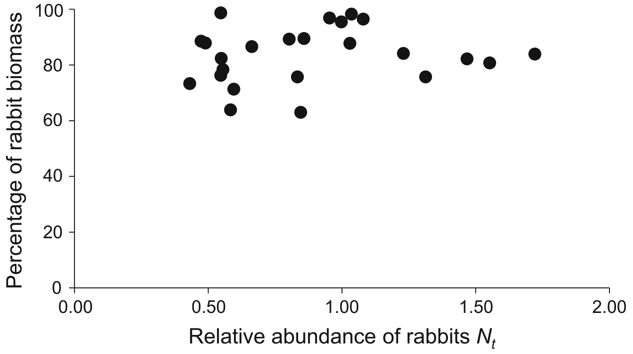
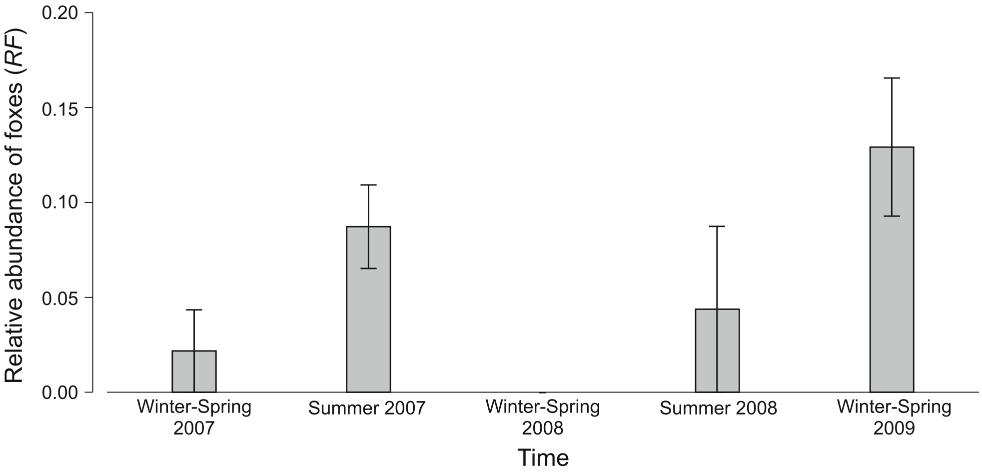


Fig. 3 Percentage of rabbit biomass consumed by foxes at different relative abundance of rabbits (N_t, pellets m^{-2} day^{-1}) in the study locality

Discussion

Fox predation was related to the decline in rabbit abundance along the two years we were able to obtain simultaneous data on foxes and rabbits. This is in agreement with previous studies conducted in Australia (Pech et al. 1992; Banks 2000), which showed the fox predation had a severe impact on dwindling rabbit populations. In Iberia, Calzada (2000) suggested that foxes could limit and regulate rabbit numbers at low densities within Doñana National Park (SW Spain). In central–southern Spain, Delibes–Mateos et al. (2008b) showed that the removal of foxes was the main management practice that positively contributed to rabbit population change (but see Díaz-Ruiz and Ferreras 2013; Norbury and Jones 2015). Our work

Fig. 4 Temporal variation of the relative abundance of foxes (*RF*, foxes km^{-1}) during the spotlighting periods in the study locality. Standard errors are shown as *bars*



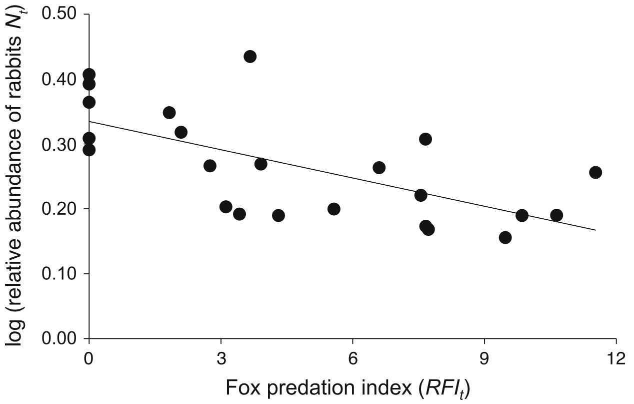


Fig. 5 Graphical representation to explain the logarithm of relative abundance of rabbits (N_t, pellets m^{-2} day^{-1}) which includes the fox predation index (RFI_t, percentage of rabbit biomass × foxes km^{-1}). See Tables 2 and 3 and text for further details

here suggests, more specifically, a close relationship between rabbit population trends and fox predation. To our knowledge, this is the first study conducted in the rabbit's native range that takes into account fox abundance and this species' diet to measure the impact of fox predation on rabbit abundance and population growth. Although our study was conducted at only one location, this site is potentially representative of many areas in central Iberian Peninsula (e.g., hunting estates of low–to–high rabbit densities, where predator control is carried out, and with other economic activities like agriculture, small game hunting or animal production).

Our findings indicate that, despite the fact that foxes are considered generalist predators capable of consuming a wide range of food items (Macdonald and Reynolds 2004), they may also specialize on more abundant prey items. This has been demonstrated for other parts of the Iberian Peninsula where rabbits are moderately abundant (Díaz-Ruiz et al. 2013). In our study, we showed that high rabbit consumption by foxes occurred independently of rabbit abundance; thus the observed lack of variation in rabbit consumption in our study may indicate that, under the estimated rabbit abundance, foxes specialize on rabbits (Delibes-Mateos et al. 2008c).

We showed that rabbit population growth was negatively related to the previous month's rabbit abundance. This suggests that rabbit populations may be limited by intraspecific density dependence (Ruiz-Azpurua et al. 2014). The growth of rabbit populations observed at low rabbit densities (Fig. 6) could be explained by a lower intraspecific competition (Ruiz-Azpurua et al. 2014), which favours exploitation of the resources available in

Table 2 Models explaining rabbit abundance (log N_t) and rabbit monthly population growth (NPG_t) in the study locality. RFI_t is the red fox predation index and log N_{t-1} is the previous month rabbit abundance

Dependent variable	Model and independent variables	K	AIC$_c$	Δ_i	D^2
log N_t	(1) log N_{t-1} + log N_{t-1} × RFI_t	4	−54.71	0.00	0.47
	(2) log N_{t-1} + RFI_t	4	−53.01	1.70	0.43
NPG_t	(3) log N_{t-1}	3	25.82	0.00	0.33
	(4) log N_{t-1} + log N_{t-1} × RFI_t	4	25.94	0.12	0.40
	(5) log N_{t-1} + RFI_t + log N_{t-1} × RFI_t	5	26.91	1.09	0.46
	(6) log N_{t-1} + RFI_t	4	27.41	1.59	0.36

The models with $\Delta_i < 2$ are shown and labelled with numbers between parentheses (1–6, see Table 3). See also text for further details

Table 3 Parameters of models explaining rabbit abundance (log N_t) and rabbit monthly population growth (NPG_t) in the study locality

Model	Coefficient	SE	*T*	*P*
Model (1)				
log N_t				
Intercept	0.25	0.06	3.98	<0.001
log N_{t-1}	0.27	0.19	1.42	0.170
log $N_{t-1} \times RFI_t$	−0.06	0.02	−3.02	0.007
Model (2)				
log N_t				
Intercept	0.31	0.08	3.66	0.002
log N_{t-1}	0.08	0.24	0.35	0.731
RFI_t	−0.01	0.01	−2.65	0.015
Model (3)				
NPG_t				
Intercept	0.86	0.27	3.17	0.005
log N_{t-1}	−3.11	0.98	−3.19	0.004
Model (4)				
NPG_t				
Intercept	1.21	0.34	3.57	0.002
log N_{t-1}	−3.75	1.02	−3.68	0.002
log $N_{t-1} \times RFI_t$	−0.17	0.10	−1.62	0.121
Model (5)				
NPG_t				
Intercept	0.54	0.57	0.94	0.361
log N_{t-1}	−1.68	1.75	−0.96	0.350
RFI_t	0.13	0.09	1.43	0.170
log $N_{t-1} \times RFI_t$	−0.64	0.34	−1.85	0.080
Model (6)				
NPG_t				
Intercept	1.25	0.45	2.80	0.011
log N_{t-1}	−4.03	1.28	−3.15	0.005
RFI_t	−0.03	0.03	−1.11	0.281

RFI_t is the red fox predation index and log N_{t-1} is the previous month rabbit abundance. Models with $\Delta_i < 2$ are shown. These models are labelled with numbers between parentheses corresponding to models shown in Table 2. See text for further details

these situations (Sinclair and Krebs 2002; Sinclair et al. 2006). In addition, the interaction between fox predation index and previous month rabbit abundance was included in the models that best explained rabbit population growth. Fox predation at lower rabbit abundance may produce a higher proportional loss in the rabbit population and potentially regulate it, in contrast to what has been observed at higher densities (Pech et al. 1992; Norbury and Jones 2015).

Other factors could also explain the observed rabbit population trends (e.g., diseases, food scarcity or absence of refuges; Moreno et al. 2007; Delibes-Mateos et al. 2014a; Ferreira et al. 2014). For instance, rabbit hunting was carried out in our study site and, apart from the rabbit mortality imposed by hunters and effects on rabbit population trends (Williams et al. 2007; but see Delibes-Mateos et al. 2008b), this practice may also force rabbits to become more nocturnal (J. Fernandez-de-Simon et al., unpublished data). As a consequence, it may also allow higher rabbit availability at night, and thus may attract nocturnal predators like foxes (Reynolds and Tapper 1995), potentially with an increase in fox abundance and pressure. Other studies could further assert our findings for other parts of the rabbit's range (see e.g., experimental approaches in Pech et al. 1992; Tapper et al. 1996; Allen and Leung 2014; Allen et al. 2014).

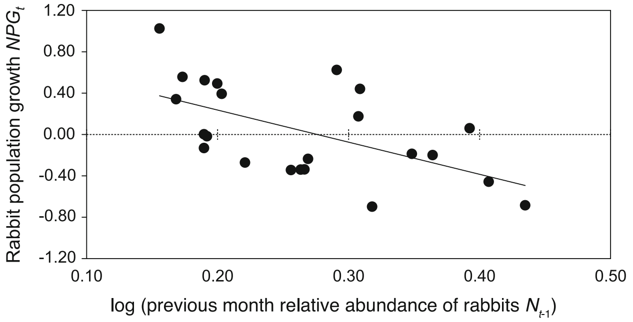


Fig. 6 Graphical representation to explain rabbit monthly population growth (NPG_t) which includes the logarithm of the previous month relative abundance of rabbits (N_{t-1}, pellets m^{-2} day^{-1}). See Tables 2 and 3 and text for further details

In conclusion, we have shown the potential role of fox predation on rabbit abundance and population growth in the Iberian portion of the Mediterranean hotspot. It is essential to increase the understanding of this and other factors driving the abundance of European wild rabbit populations in Iberia, as recovering this keystone species is among the most challenging ecological problems for biodiversity conservation in this region.

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