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The landscape in southern Iberia has, over the last four decades, altered as a result of the land abandonment, while the abundance of wild boar *Sus scrofa* and red deer *Cervus elaphus* has simultaneously increased, and some key prey species such as the European rabbit *Oryctolagus cuniculus* have declined. In this work we explore: 1) the relationships between big game species (red deer and wild boar) and rabbit abundance, and 2) whether these relationships could have effects on food quality (total nitrogen available in the pasture and percentage of leguminosae) and food availability of (herbaceous cover). We therefore selected nine big game estates with a range of abundance as regards ungulates and similar Mediterranean habitat. Wild boar abundance was statistically negative in relation to rabbit abundance, while no significant statistical relationships between rabbit abundance and habitat structure and forage quality were evidenced. However, wild boar abundance, but not that of red deer, was negatively associated with leguminosae cover, and the percentage of surface rooted by wild boar was negatively associated with the percentage of herbaceous cover. Overall, our results suggest that the abundance of wild boar is negatively related to that of rabbits, and could have a negative effects on rabbit abundances by food competition as a result of: 1) a decrease in herbaceous coverage and leguminosae in the pasture and 2) an increase in the total percentage of soil disturbed as a result of rooting.

In southern Spain, the fact that traditional agriculture and cattle management in forested areas has been abandoned over the last four decades has contributed to an increase in the total area covered by bushes (Fernández-Alés et al. 1992), which may favour some species whilst others are displaced (Sirami et al. 2008). Changes in land uses drove changes in landscape, since marginal agricultural lands and extensive livestock pasture have been replaced by big game hunting estates, particularly those devoted to wild boar *Sus scrofa* and red deer *Cervus elaphus* hunting (Bugalho et al. 2011). However, prey species such as the European rabbit *Oryctolagus cuniculus* and red legged partridges *Alectoris rufa* have undergone a considerable decline in these areas (Delibes-Mateos et al. 2009a).

The European wild rabbit is an essential keystone element as regards both maintaining the high biodiversity of Iberian Mediterranean ecosystems and its role in hunting, which is an important economic activity in Iberia (Delibes-Mateos et al. 2008a). However, rabbit populations have undergone a sharp decline in recent decades, principally as a consequence of optimal-habitat loss (Ward 2005) and the outbreak of two viral diseases: mixomatosis in the 1950s and the rabbit haemorrhagic disease (RHD) at the end of 1980s (Villafuerte et al. 1995). After this decline, the recovery of the rabbit populations has been spatially uneven (Delibes-Mateos et al. 2008b). In some areas, local rabbit populations have recovered and reached high densities to the point that they are considered as an emerging pest (Barrio et al. 2012), while in many other areas their populations remain at low densities or are even extinct (Virgós et al. 2007).

Many areas in which rabbit recovery projects take place (Guerrero-Casado et al. 2013) overlap with areas in which high densities or even 'overabundance' of big game species occurs as a result of intensive management that favors high densities. In southern Spain, the current local abundances of red deer and wild boar are probably the highest recorded in Europe, reaching densities higher than 50 deer km^{-2} and 90 wild boar km^{-2} in intensively managed hunting areas (Acevedo et al. 2008, Bosch et al. 2012). According to Caughley and Grigg (1981), a particular wildlife species can be considered as "overabundant" if, among other things, it causes dysfunctions in the ecosystem (the consequences of "overabundance" are dealt by Côté et al. 2004). Previous studies have highlighted the negative effects of over-foraging by ungulates on vertebrate or invertebrate wildlife, vegetation and soil dynamics (Mohr et al. 2005,

Häsler and Senn 2012, Macci et al. 2012). High densities of ungulates may affect other species as a result of habitat modification and the degradation of certain resources that are critical for other species (Côté et al. 2004). What is more, ungulates can act as ecosystem engineers through the great impact that they have on general features of habitat, and may strongly modify the structure of vegetation (Putman et al. 2011). The high density of red deer and wild boar may also have a negative effect on other herbivores as a result of direct food competition (Côté et al. 2004), while wild boar may negatively affect rabbits (Abáigar 1993, Briedermann 2009) and other fauna species by direct predation (Focardi et al. 2000), and the alteration of grassland by rooting activity (Bueno et al. 2010). Although previous works have shown a negative effect of wild ungulates on rabbits (Lozano et al. 2007, Cabezas-Díaz et al. 2011), the effect of current wild ungulate abundance on rabbit abundance has received little attention. In this scenario, the high density of ungulates may act as an additional harmful factor that is limiting the recovery of wild rabbit populations (Cabezas-Díaz et al. 2011), and what is more, these high densities may jeopardise the predators' populations by reducing the amount of prey that is available (Lozano et al. 2007). This could be a major concern in bush and forested areas where their endangered predators, such as the Iberian lynx *Lynx pardinus* or the Spanish imperial eagle *Aquila adalberti*, still inhabit (Delibes-Mateos et al. 2009b) and in which wild ungulates attain high densities.

Our general goal was therefore 1) to study the statistical relationships between big game species (red deer and wild boar) and rabbit abundances. Since grass quality is known to affect rabbit abundance (Ferreira and Alves 2009), we 2) also aimed to test whether ungulate effects could be mediated by their impact on forage quality (total nitrogen available in the pasture, Arnold and Dudzinski 1967, and percentage of leguminosae, Ritchie et al. 1998) and availability (herbaceous cover). Finally, 3) we addressed the relationships between abundances and forage quality faecal nitrogen in herbivores (rabbit and red deer), which is an indicator of pasture quality (Leslie and Starkey 1987).

Material and methods

Study area

Data were collected from nine different hunting estates with a high range of ungulate abundance (as commonly occurs in the study area), which were located in southern Spain in the province of Cordoba. The altitude ranges from 400 to 800 m a.s.l., and the dominant Mediterranean vegetation includes tree species such as holm oak *Quercus ilex* and cork oak *Q. suber*, together with pine plantations, *Pinus pinea* and *P. pinaster*, accompanied by Mediterranean scrubland dominated by *Cystus* spp., *Erica* spp., *Pistacia* spp., *Phyllirea* spp. and *Rosmarinus* spp. with scattered pastures and small areas of crops. These savannah-like landscape units are called 'dehesas'. The study sites are mainly devoted to the recreational hunting of wild boar and red deer.

Estimating red deer density

Deer density was estimated on each hunting estate, and these estates were considered as discrete management units. We performed two spotlights census carried out on the same transect in August and September 2011 by driving at 10–15 km h^{-1}. Each transect was an average of 20.3 km $\pm$ 2.34 (SE) in length. The distance from the observer to the deer or to the centre of a deer group was measured, and compass bearings were taken to determine the angle between deer, or deer groups, and the transect line. The distance between the observer and the animal was measured using a telemeter (range 15–1100 m; precision ± 1 m $\pm 0.1\%$). Red deer density was estimated using distance sampling (Buckland et al. 2004, Distance 5.0 software). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term were based on Akaike's information criterion (AIC).

Estimating wild boar abundance

We estimated the wild boar abundance index following the protocol described by Acevedo et al. (2007). The counts took place in two transects of 4 km per estate in September and October 2011. Each transect count consisted of 40 segments of 100 m in length and 1 m in width, divided into 10 sectors of 10 m in length. Sign frequency was defined as the average number of 10-m sectors containing droppings per 100-m transect (Acevedo et al. 2007), and a single average value of wild boar abundance was calculated per estate.

Estimation of rabbit and carnivore abundance index and wild boar rooting intensity

We designed two to four transects of 4 km in length per estate between July–September 2011 (n = 24), where we recorded the number of carnivore's scats and rabbit latrines per km (Calvete et al. 2006). A latrine was defined as an accumulation of 20 or more pellets on a surface of 200 $\times$ 300 mm (Virgós et al. 2003). Latrine abundance and rabbit density estimated by direct observations have been shown to have a high correlation in the study area (Mediterranean scrubland in Sierra Morena; Gil-Sánchez et al. 2011). The percentage of soil rooting by wild boar in these transects was also calculated, in which a fixed bandwidth of 1 m was established and the length of each rooting was scored within this band (Bueno et al. 2010). This allowed us to obtain a percentage of rooted soil (Cuevas et al. 2010).

Faecal and diet nitrogen

In this study, faecal nitrogen and nitrogen content in the pasture were used as an indicator of diet quality (Hamel et al. 2009). In spring 2011, 16 samples of deer droppings (10 stools/sample), rabbit and pasture samples were collected on each estate, thus a total of 144 samples was obtained for each group (deer, rabbit and pasture). The concentration of

nitrogen was estimated using an elemental analyzer, which determines the quantitative carbon, nitrogen, hydrogen and sulphur content of the samples. This technique is based on the Dumas method (Simonne et al. 1997), which in this case consisted of the complete thermal oxidation of 1 to 2 mg of the sample by combustion in an oxygen enriched atmosphere at a temperature of 1020°C. The combustion gases are transported by a carrier gas (He) to a chromatography column where they are then separated and detected using a thermal conductivity detector. We thus obtain the percentage content of each element in the sample, in this case nitrogen-analyzed with regard to weight (Acevedo et al. 2011).

Habitat structure and composition

Habitat composition per estate was determined using GIS tools and land use maps from Andalusia (Mapa de usos y coberturas del suelo de Andalucía 1/25000, Junta de Andalucía 2007). For this purpose, 10 stratified transects per estate were performed in two different habitats: 1) open lands, composed of 'dehesa' habitat and pastures, and 2) woodlands, composed of Mediterranean scrubs and forests. Pine plantations (where almost no pasture grows) were removed from the study design and sampling. The transects were of 50 m in length and were performed in May (spring production), August–September (low production) and November (autumn production) (San Miguel et al. 1996) 2011 to estimate shrub, woodland and pasture cover, and the percentage of bare soil. The maximum height of the grass in each transect was also recorded by using a ruler as an indirect measure of pasture availability (Lazo et al. 1992). In the spring transects the percentage of cover occupied by herbaceous leguminosae was also calculated (area occupied by leguminosae/ area occupied by all herbaceous matter × 100) (Ritchie et al. 1998).

Statistical analyses

In all cases the analysis were performed at rabbit level transect (n = 24) using InfoStat software. In order to evidence the relationships between the explanatory variables (Table 1) and the dependent variable 'abundance of rabbits'

Table 1. Variables initially included in the study and used in statistical step 1, indicating which were significantly associated with rabbit abundance[a], percent of herbaceous cover in spring[c], leguminosae cover[b], rabbit fecal nitrogen[d] and red deer fecal nitrogen[e].

Species abundances. Wild boar dropping frequency abundance index[a,b,d,e], deer density[d] (deer/ha[−1]), carnivore abundance[a] (scats km^{−1}), rabbit abundance[b] (latrines km^{−1}).
Fecal and diet nitrogen. Nitrogen in deer droppings (n = 144), nitrogen in rabbit pellets (n = 144) and nitrogen in pasture (n = 144).
Habitat availability. Percentage of scrubland, woodland and pasture, and edge distance (m).
Grass cover and height. Maximum height[a] and herbaceous stratum cover in spring[b], maximum height and herbaceous stratum cover in summer[e], maximum height and herbaceous stratum cover in autumn[c], percentage of leguminosae cover in spring[a,c], and percentage of rooted soil[c].

(latrines km^{−1}) we performed a two step statistical analysis (similar to Acevedo et al. 2005). In the first step, we discarded a number of variables that had no statistical relationship with the dependent variable (the cut off p-value was set a $p < 0.05$). In step 2, the variables selected in step 1 were included in a linear mixed model (model 1, step 2) (LMM) with a normal error distribution and an identity link function. This model included rabbit abundance (latrines km^{-1}) as the dependent variable and the estate (ninelevels) as a random factor, such that the transect was nested in the estate.

Following the same two-step procedure as in the previous model, a Pearson matrix (step 1) was used to select those variables that were significantly associated with the percentage of leguminosae, the percent of herbaceous cover in spring, rabbit faecal nitrogen and red deer faecal nitrogen. These variables were included in four LMMs (model 2, 3, 4 and 5) with the same characteristics as above (step 2), where percentages of leguminosae and of herbaceous cover, and the rabbit and red deer faecal nitrogen were the response variables respectively. The explanatory variables were not collinear in any model (Pearson correlation $r_p < 0.8$).

A backward procedure based on Akaike's information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002) was used to perform model selection, and the model with the lowest AICc was considered the best one. We also reported the ΔAICc value in order to compare the difference between each model and the best model. As a rule, differences in AICc (ΔAICc) higher than 2 between a given model and the model with the lowest AICc indicate low or no empirical support for that model (Burnham and Anderson 2002). The assumptions of normality, homogeneity and independence in the residuals were fulfilled in all cases (Zuur et al. 2009).

Results

The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score. The average red deer density, expressed as the number of deer per 100 ha, ranged from 25 to 68. The coefficients of variation of distance-sampling estimates ranged from 2.95% to 38.86%. The wild boar frequency index ranged from 0.04 to 0.47 (mean ± SE 0.26 ± 0.15), and rabbit abundance ranged from 1.9 to 14.08 latrines km^{−1} (mean ± SE 6.19 ± 4.36).

In the first Pearson correlation matrix (step 1, Table 1), the wild boar abundance index, the carnivore abundance index, the percentage of leguminosae and the maximum height of grass in spring were significantly correlated with the abundance of rabbits. Hence, the model using rabbit abundance as a dependent variable was constructed with these four variables (step 2), and two best models were selected by following the AICc criteria (ΔAICc = 0.48, Table 2). In both models, the variable 'wild boar abundance' was statistically negatively related to rabbit abundance, whereas carnivore abundance was positively associated with it.

With regard to the factors related to leguminosae cover (model 2), only wild boar and rabbit abundances and the

Table 2. β-coefficients, p- and F-values of the most parsimonious LMMs (step 2, n = 24 transects in nine locations, which were included as random factors) to explain rabbit abundance per transect (model 1a and 1b), the percentage of leguminosae (model 2), the percentage of herbaceous cover in spring (model 3), rabbit fecal nitrogen (model 4) and red deer fecal nitrogen (model 5). Significant p-values are highlighted in bold type.

Rabbit abundance per transect (model 1a, ΔAICc = 5.63)			
	F	p	β
Wild boar abundance	9.83	**<0.01**	−17.58
Carnivore abundance	5.44	**0.03**	0.49
Leguminosae cover	0.75	0.4	−0.19
Rabbit abundance per transect (model 1b, ΔAICc = 0.48)			
Wild boar abundance	9.78	**<0.01**	−15.91
Carnivore abundance	6.07	**0.02**	0.36
Percentage of leguminosae (model 2, ΔAICc = 0)			
Percentage of herbaceous cover in spring	12.98	**<0.01**	0.13
Wild boar abundance	2.55	0.15	−12.98
Rabbit abundance	1.36	0.26	0.26
Percentage of herbaceous cover in spring (model 3, ΔAICc = 2.41)			
% Leguminosae	7.59	**0.01**	1.86
Percentage of surface rooted by wild boar	13.83	**<0.01**	−2.63
Rabbit fecal nitrogen (model 4, ΔAICc = 0)			
Wild boar abundance	2.51	0.16	−0.45
Red deer abundance	0.22	0.64	−0.25
Red deer fecal nitrogen (model 5, ΔAICc = 0)			
Wild boar abundance	4.24	**<0.01**	0.7
Percentage of herbaceous cover in summer	3.92	**<0.01**	0.01

ΔAICc indicates the improvement in model fit of the final model compared with the next best model. ΔAICc equals zero when the final model is the same as the full model.

percentage of herbaceous cover in spring were retained after step 1 (Table 1). In the final model (step 2) wild boar abundance was negatively associated with leguminosae cover, whereas the percentage of herbaceous cover was positively correlated with it (Table 2).

As regards the factors related to the percentage of herbaceous cover in spring (model 3), the percentage of leguminosae, percentage of rooting and percentage of herbaceous in autumn were retained after step 1 (Table 1). In the final model (step 2) the percentage of surface rooted by wild boar was statistically negatively associated with the percentage of herbaceous cover, while the percentage of legumes had a positive effect (Table 2).

Finally, with regard to the factors related to rabbit faecal nitrogen (model 4), wild boar and red deer abundance were retained after step 1 (Table 1), but they were not significant in the final model. Regarding to red deer faecal nitrogen (model 5), wild boar and the percentage of herbaceous cover in summer were retained after step 1 (Table 1), and both variables were statistically positively correlated with the red deer faecal nitrogen (step 2, Table 2).

Discussion

Despite the increase in the abundance and distribution of ungulates in many regions of southern Spain, there are no studies on either the relationship between rabbit abundance and big game or the factors related to rabbit abundance and performance (measured as fecal nitrogen), particularly in the context of high ungulate abundance, which are predominant in large forestry areas in Spain. In our study area, rabbit abundance was negatively correlated to wild boar abundance, which is consistent with previous studies carried out in other areas in Iberia (Lozano et al. 2007, Cabezas-Díaz et al. 2011). These works suggest that wild ungulates induce a 'competitor pit effect' that may hinder the recovery of wild rabbit populations. However, to our knowledge the causes of the negative relationship between the abundances of wild boar and rabbit remain unexplored. In our experiment, this negative relationship was analyzed by measuring the coverage of leguminosae, since its high nitrogen content (protein) and low values of structural carbohydrates make it an indispensable component in rabbits' diet (Ferreira and Alves 2009) and essential for reproduction (Villafuerte et al. 1997). Indeed, wild boar abundance (but not that of red deer), was negatively associated with leguminosae cover; and the percentage of surface rooted by wild boar was statistically negatively associated with the percentage of herbaceous cover. Overall, our results suggest that wild boar could have a negative effects on rabbit abundances mediated by: 1) a decrease in herbaceous coverage and leguminosae proportion in the pasture and 2) an increase in the total percentage of soil disturbed as a result of rooting.

Wild boars have the potential to exert a large and varied number of effects on the environment (Barrios-Garcia and Ballari 2012). For instance, rooting behaviour removes understory vegetation from large areas, thus modifying soil composition, the pH and the decomposition process, which implies changes in vegetation diversity and structure (Mohr et al. 2005, Bueno et al. 2010). The areas with the highest percentage of leguminosae could attract greater amounts of wild boar (Bugalho and Milne 2003), which use them as a source of protein (Ritchie et al. 1998) and can harm the rabbit by direct competition through the consumption of leguminosae (Côté et al. 2004), since habitat alteration by rooting can affect hundreds of hectares (Bueno et al. 2011).

Nonetheless, the direct predation of rabbits by wild boar, particularly in dens, might also explain part of the negative relationship between both species. Although no empirical studies have been conducted to test the effect of wild boar predation on rabbit, it is known that wild boar prey on young and sick rabbits (Abáigar 1993, Briedermann 2009), which could also affect wild rabbit populations. Contrary to what we expected, we did not detect any effect of deer density on rabbits within the rank of deer abundances studied, which may be owing to the fact that all the areas had high densities (>20 ind/100 ha, Acevedo et al. 2008), and the effect of deer was therefore always above a given threshold of overgrazing. Further research, including lower deer density areas, is therefore needed. Wild boar, meanwhile, covered a wide range from scarce to a very high abundance index (Acevedo et al. 2007), which could condition the existence of relationships with rabbit abundance, while the case of red deer is less contrasted.

Interestingly, carnivores had a positive relationship, possibly owing to the attraction effect of rabbits on predators, which concentrate their foraging efforts on higher rabbit abundance areas (Viñuela et al. 1994). This highlights the key role of rabbits as prey and their importance as regards supporting richer predators communities in areas now devoted to big game hunting (Virgós and Travaini 2005).

Management implications

The results obtained show that wild boar may have a negative impact on wild rabbit populations in typical big game estates in southern–central Spain. The fact that traditional agriculture have been abandoned and intense hunting management has favoured the proliferation of ungulates, without considering the possible effects that these species may have on small game species, and therefore on the availability of these prey for predators. Overall, this study supports the possibility that rabbit abundance may have been affected by a decrease in the availability and quality of food as a consequence of high density populations of wild boar. We therefore argue in favour of the scientifically based management and control of ungulate populations in Mediterranean conditions in order to conserve key prey species, specifically in those areas in which endangered predator species still coexist and rabbit populations remain at low densities.

References

Abáigar, T. 1993. Régimen alimentario del jabalí (*Sus scrofa*, L. 1758) en el sureste ibérico, Doñana. – Acta Vertebrata 20: 35–48.

Acevedo, P. et al. 2005. Environmental constraints in the colonization sequence of roe deer (*Capreolus capreolus* Linnaeus, 1758) across the Iberian Mountains, Spain. – J. Biogeogr. 32: 1671–1680.

Acevedo, P. et al. 2007. Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. – Epidemiol. Infection 135: 519–527.

Acevedo, P. et al. 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. – J. Zool. 276: 37–47.

Acevedo, P. et al. 2011. Evaluación del estado de la población de cabra montés de los Montes de Toledo: relaciones con el ciervo. – Pirineos 166: 29–49.

Arnold, G. W. and Dudzinski, M. L. 1967. Comparison of faecal nitrogen regressions and in vitro estimates of diet digestibility for estimating consumption of herbage by grazing animals. – J. Agric. Sci. 68: 213–219.

Barrio, I. C. et al. 2012. Can cover crops reduce rabbit-induced damages in vineyards in southern Spain? – Wildlife Biol. 18: 88–96.

Barrios-Garcia, M. N. and Ballari, S. A. 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. – Biol. Invas. 14: 2283–2300.

Bosch, J. et al. 2012. Distribution, abundance and density of the wild boar on the Iberian Peninsula, based on the CORINE program and hunting statistics. – Folia Zool. 61: 138–151.

Briedermann, L. 2009. Schwarzwild (new edition updated by Stöcker, B). – Franckh-Kosmos. Verlags-GmbH and Co. KG, Stuttgart.

Buckland, S. T. et al. 2004. Introduction to distance sampling: estimating abundance of biological population. – Oxford Univ. Press.

Bueno, C. G. et al. 2010. Does wild boar rooting affect livestock grazing areas in alpine grasslands? – Eur. J. Wildlife Res. 56: 765–770.

Bueno, C. G. et al. 2011. Effects of large wild boar disturbances on alpine soil seed banks. – Basic Appl. Ecol. 12: 125–133.

Bugalho, M. N. and Milne, J. A. 2003. The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint? – For. Ecol. Manage. 181: 23–29.

Bugalho, M. N. et al. 2011. Establishing grazing and grazing-excluded patches increases plant and invertebrate diversity in a Mediterranean oak woodland. – For. Ecol. Manage. 261: 2133–2139.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. – Springer.

Cabezas-Díaz, S. et al. 2011. The presence of a "competitor pit effect" compromises wild rabbit (*Oryctolagus cuniculus*) conservation. – Anim. Biol. 61: 319–334.

Calvete, C. et al. 2006. Habitat factors related to wild rabbit population trends after the initial impact of rabbit haemorrhagic disease. – Wildlife Res. 33: 467–474.

Caughley, G. and Grigg, G. C. 1981. Surveys of the distribution and density of kangaroos in the pastoral zone of South Australia, and their bearing on the feasibility of aerial survey in large and remote areas. – Austral. Wildlife Res. 8: 1–11.

Côté, S. D. et al. 2004. Ecological impacts of deer overabundance. – Annu. Rev. Ecol. Evol. Syst. 35: 113–147.

Cuevas, M. F. et al. 2010. Food habits and impact of rooting behaviour of the invasive wild boar, *Sus scrofa*, in a protected area of the Monte Desert, Argentina. – J. Arid Environ. 74: 1582–1585.

Delibes-Mateos, M. et al. 2008a. Key role of European rabbits in the conservation of the western Mediterranean Basin Hotspot. – Conserv. Biol. 22: 1106–1117.

Delibes-Mateos, M. et al. 2008b. Rabbit populations and game management: the situation after 15 years of rabbit haemorrhagic disease in central–southern Spain. – Biodivers. Conserv. 17: 559–574.

Delibes-Mateos, M. et al. 2009a. Long-term changes in game species over a long period of transformation in the Iberian Mediterranean landscape. – Environ. Manage. 43: 1256–1268.

Delibes-Mateos, M. et al. 2009b. Rabbit (*Oryctolagus cuniculus*) abundance and protected areas in central–southern Spain: why they do not match? – Eur. J. Wildlife Res. 55: 65–69.

Fernández-Alés, R. et al. 1992. Recent changes in landscape structure and function in a Mediterranean region of SW of Spain (1950–1984). – Landscape Ecol. 7: 3–18.

Ferreira, C. and Alves, P. C. 2009. Influence of habitat management on the abundance and diet of wild rabbit (*Oryctolagus cuniculus algirus*) populations in Mediterranean ecosystems. – Eur. J. Wildlife Res. 55: 487–496.

Focardi, S. et al. 2000. Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. – J. Zool. 250: 329–334.

Gil-Sánchez, J. M. et al. 2011. Habitat assessment to select areas for reintroduction of the endangered Iberian lynx. – Wildlife Biol. Practice 7: 1–19.

Guerrero-Casado, J. et al. 2013. Restocking a keystone species in a biodiversity hotspot: recovering the European rabbit on a landscape scale. – J. Nat. Conserv. 21: 444–448.

Hamel, S. et al. 2009. Spring normalized difference vegetation index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. – J. Appl. Ecol. 46: 582–589.

Häsler, H. and Senn, J. 2012. Ungulate browsing on silver fir: the role of occasions, food shortage, and diet preferences. – Wildlife Biol. 18: 67–74.

Junta de Andalucía 2007. Mapa de Usos y Coberturas Vegetales del Suelo de Andalucía, Escala 1: 25 000.

Lazo, A. et al. 1992. Evaluation of hare abundance allowed by their use of attraction points. – Z. Säugetierkunde 57: 373–379.

Leslie, D. M. and Starkey, E. E. 1987. Fecal indexes to dietary quality – a reply. – J. Wildlife Manage. 51: 321–325.

Lozano, J. et al. 2007. Increase of large game species in Mediterranean areas: is the European wildcat (*Felis silvestris*) facing a new threat? – Biol. Conserv. 138: 321–329.

Macci, C. et al. 2012. Effects of wild boar (*Sus scrofa*) grazing on soil properties in Mediterranean environment. – Catena 98: 79–86.

Mohr, D. et al. 2005. Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. – Soil Biol. Biochem. 37: 693–700.

Putman, R. et al. 2011. Identifying threshold densities for wild deer in the UK above which negative impacts may occur. – Mamm. Rev. 41: 175–196.

Ritchie, M. E. et al. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. – Ecology 79: 165–177.

San Miguel, A. et al. 1996. Ordenación del monte mediterráneo para la caza mayor. – Ecosistemas 16: 7–13.

Simonne, A. H. et al. 1997. Could the dumas method replace the Kjeldahl digestion for nitrogen and crude protein determinations in foods? – J. Sci. Food Agric. 73: 39–45.

Sirami, C. et al. 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the northwestern Mediterranean. – Biol. Conserv. 141: 450–459.

Villafuerte, R. et al. 1995. Incidence of viral haemorrhagic disease in wild rabbit populations in Spain. – Mammalia 59: 651–659.

Villafuerte, R. et al. 1997. Influence of food abundance and quality on rabbit fluctuations: conservation and management implications in Doñana National Park (SW Spain). – Rev. d'Écol. Terre Vie 52: 345–356.

Viñuela J. et al. 1994. Nesting dispersion of a black kite population in relation to location of rabbit warrens. – Can. J. Zool. 72: 1680–1683.

Virgós, E. and Travaini, A. 2005. Relationships between small-game hunting and carnivore diversity in central Spain. – Biodivers. Conserv. 14: 3475–3486.

Virgós, E. et al. 2003. Factors shaping European rabbit abundance in continuous and fragmented populations of central Spain. – Acta Theriol. 48: 113–122.

Virgós, E. et al. 2007. Is the wild rabbit (*Oryctolagus cuniculus*) a threatened species in Spain? Sociological constraints in the conservation of species. – Biodivers. Conserv. 16: 3489–3504.

Ward, D. 2005. Reversing rabbit decline: one of the biggest challenges for nature conservation in Spain and Portugal. Technical report. – World Conservation Union, Gland, Switzerland.

Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.