Factors Affecting Red-Legged Partridge Alectoris rufa Abundance on Big-Game Hunting Estates: Implications for Management and Conservation

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FACTORES QUE AFECTAN A LA ABUNDANCIA DE LA PERDIZ ROJA *ALECTORIS RUFA* EN COTOS DE CAZA MAYOR: IMPLICACIONES PARA LA GESTIÓN Y CONSERVACIÓN

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Summary.—The red-legged partridge *Alectoris rufa* is not only the most important bird game species but also an important prey species for many predators in Iberia. However, its populations have significantly declined in recent decades, principally as the result of agricultural intensification on arable land. Its abundance has also undergone a significant decline in forested areas over the last few decades, where wild ungulate management and abundance have increased. In this scenario, we aimed to test the factors that affect red-legged partridge abundance in relation to high wild ungulate (wild boar and red deer) abundance in south-central Spain. The factors included as predictors were carnivore, wild boar and red deer abundances, vegetation features, nest predation rate and invertebrate availability. Red deer abundance showed a negative relationship with partridge abundance in spring (non-significant negative trends were also evident for carnivore and wild boar), whereas variables related to food availability (grass biomass, Hemipteran abundance and total invertebrate mass) had a positive effect in the same season. Moreover, deer and carnivore abundances and spring nest predation rate were negatively associated with partridge abundance in autumn. Plant biomass and Hemipteran abundance were negatively correlated with wild boar abundance, whereas maximum pasture height was negatively related to red deer and wild boar abundance. Overall, our results show that high ungulate densities may

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negatively affect partridge abundance, which may be mediated by (i) a reduction in food availability (invertebrate and herbaceous plant biomass) and (ii) nest predation by wild boar. This research has shown that current intensive big-game hunting management schemes in south-central Spain are often incompatible with red-legged partridge conservation, and that these effects should be taken into account when defining big-game management and conservation policies.

Key words: *Alectoris rufa*, food availability, game management, interspecific competition, invertebrates, red deer, wild boar.

RESUMEN.—La perdiz roja *Alectoris rufa* no solo es el ave de caza más importante, sino que también es una importante presa para muchos depredadores en Iberia. Sin embargo, sus poblaciones han disminuido significativamente en las últimas décadas, principalmente como resultado de la intensificación de la agricultura en zonas agrícolas. Sus abundancias también han sufrido un descenso significativo en zonas forestales durante los últimos decenios donde la gestión de ungulados silvestres y sus abundancias se han incrementado. En este escenario, nuestro objetivo ha sido evaluar los factores que afectan a la abundancia de perdiz roja en un contexto de alta abundancia de ungulados silvestres (jabalí y ciervo) en el centro-sur de España. Los factores incluidos como predictores fueron la abundancia de carnívoros, jabalí y ciervo, las características de la vegetación, la proporción de nidos depredados y la disponibilidad de invertebrados. La abundancia de ciervo mostró una relación negativa con la abundancia de perdiz en primavera (también se evidenciaron tendencias negativas no significativas para carnívoros y jabalí), mientras que las variables relativas a la disponibilidad de alimento (biomasa herbácea, abundancia de hemípteros y el peso total de los invertebrados) tuvieron un efecto positivo en la misma estación. Por otra parte, en otoño, la abundancia de ciervos y carnívoros, y la tasa de depredación de nidos en primavera se asociaron negativamente con la abundancia de perdiz. La biomasa de herbáceas y la abundancia de hemípteros se correlacionaron negativamente con la abundancia de jabalíes, mientras que la altura máxima del pasto estuvo negativamente asociada con la abundancia de ciervo y jabalí. En general, nuestros resultados muestran que las altas densidades de ungulados podrían afectar negativamente a la abundancia de perdiz mediado por (i) una reducción en la disponibilidad de alimento (invertebrados y biomasa de herbáceas) y (ii) la depredación de nidos por el jabalí. Esta investigación ha puesto de manifiesto que los actuales sistemas intensivos de gestión de la caza mayor en el centro-sur de España no son compatibles con la conservación de la perdiz roja, y que por lo tanto, estos efectos deben ser considerados a la hora de definir las políticas para la gestión de la caza mayor y la conservación.

Palabras clave: *Alectoris rufa,* ciervo, competencia interespecífica, disponiblidad de alimento, gestión cinegética, invertebrados, jabalí, perdiz roja.

INTRODUCTION

The abundance and range of wild ungulates have increased throughout Europe and North America over the last century (Clutton-Brock and Albon, 1992; Côté *et al*., 2004; Gordon *et al*., 2004). This expansion has been facilitated by several factors, including the regulation of exploitation and the control of poaching (Gortázar *et al*., 2000), the abandoning of agricultural land in mountain and forest areas (Acevedo *et al*., 2006; Vargas *et al*., 2007), and the establishment of protected and conservation areas (Côté *et al*., 2004). However, the key factor is considered to have been anthropogenic expansion, which has primarily been carried out for hunting purposes (Gortázar *et al*., 2000; Acevedo and Cassinello, 2009).

In the Iberian Peninsula, and particularly in central and southern areas, there are high densities of red deer *Cervus elaphus his-*

panicus and wild boar *Sus scrofa* on many hunting estates. Indeed, in areas with intensive game management aimed to boost big-game species, red deer can reach densities of over 50 individuals/km² (Vicente *et al.*, 2007; Acevedo *et al.*, 2008), and wild boar densities can even attain 90 individuals/km² (Acevedo *et al.*, 2007; Bosch *et al.*, 2012). However, despite the large increase in the densities of wild boar and deer, little is known about the ecological impacts of the over-abundance of these species on Mediterranean ecosystems (but see Carpio *et al.* [2014a; 2014b; 2014c] for its impacts on other species; Gortázar *et al.* [2006] for disease-related constraints; Perea *et al.* [2014] for impacts on vegetation).

One species that could be sensitive to the abundance of wild ungulates is the red legged-partridge *Alectoris rufa*, which has high socio-economic and ecological value as a game species and through its role as important prey for several species of predators in Iberia (Calderón, 1983). Despite the importance of the red-legged partridge in Spain and Portugal, its natural populations are estimated to have undergone a significant decline of over 50% between 1973-2002 (Blanco-Aguiar, 2007). Furthermore, recent results of the SACRE programme (SEO/BirdLife, 2014) show that the red-legged partridge is one of the ten species that have declined most severely in recent years (the abundance was 33% lower in 2013 with respect to that in 1998). However, despite the negative population trend, the red-legged partridge is currently listed as "least concern" worldwide (BirdLife International, 2012, www.iucnredlist.org).

According to several studies, the most harmful factor for partridge distribution is habitat change resulting from agricultural intensification (Vargas *et al.*, 2006; Blanco-Aguiar *et al.*, 2007), which has had direct effects, such as the deterioration of suitable nesting sites (Newton *et al.*, 2004), a reduc-tion in food availability, an increase of pre-dation risk owing to habitat simplification (Benton *et al.*, 2003) and exposure to toxic biocides, for example through ingestion of dressed seeds (Mineau and Palmer, 2013; López-Antia *et al.*, 2015). In addition, other factors such as overhunting and releases of farmed partridges have also been identified as harmful to wild partridges (Caro *et al.*, 2014).

The factors affecting partridge populations in forest and mountain areas have received less attention than those acting in lowland and agricultural areas. In woodland and forest ecosystems from southern Spain (often de-voted to big-game), one of the main factors that explains the decrease in partridge popu-lations is the impoverishment of habitat quality as a consequence of land-use changes (Delibes-Mateos *et al.*, 2012). Such changes include increases in large patches of dense homogeneous scrublands, pine reforesta-tion characterised by a high tree density that prevents the growth of scrubland and pas-tureland, and the spread of oak-savannas ("dehesas") that offer scarce scrub cover (refuge) as a consequence of intensive grazing pressure (Fernández-Alés *et al.*, 1992). This has led to a loss of habitat heterogeneity, thus making many woodland and mountain areas unsuitable as partridge habitat (see Lucio, 1991).

Nonetheless, in these areas, one factor that may also affect partridge populations could be the high densities of wild ungulates: resulting in food competition, trampling or changes in habitat structure, and nest pre-dation by wild boars (Carpio *et al.*, 2014a). High densities of wild ungulates are known to affect the growth, reproduction and survival of plants, since they consume their stems, flowers, leaves and fruits, thus favouring species that are less frequently consumed (Côté *et al.*, 2004; Mohr *et al.*, 2005; Aceve-do *et al.*, 2008; Putman *et al.*, 2011; Cuevas *et al.*, 2012; Perea *et al.*, 2014). Plant species, moreover, closely determine the insects and

other invertebrates that are present and that are critical for partridge nestlings during their first weeks after hatching (Holland *et al.*, 2006). Therefore, an intense disturbance in plant communities as a result of high ungulate densities may reduce their diversity and the species richness that is available for partridges (Stein *et al.*, 2010). We consequently hypothesise that high abundances of wild ungulates could reduce partridge abundances as a consequence of a decrease in food availability (plants and insects), and nest predation by wild boar. To assess this, the factors that affect red-legged partridge abundance in relation to high wild ungulate (wild boar and red deer) abundances were tested on big-game estates in south-central Spain.

MATERIAL AND METHODS

Study area

Data were collected on nine different hunting estates in southern Spain (fig. 1), averaging 2,470 hectares in extent (range 1,480-3,600 ha; table 1). The dominant vegetation includes tree species such as holm oak *Quercus ilex* and cork oak *Quercus suber*, together with pine plantations (*Pinus pinea* and *Pinus pinaster*) and scrubland dominated by species of *Cistus*, *Erica*, *Pistacia*, *Phyllirea* and *Rosmarinus* with scattered pastures. The study sites are mainly devoted to recreational hunting of wild boar and red deer. The red-legged partridge is not hunted in the study area and no management measures, such as releases or habitat improvement, are applied to enhance their populations.

Estimating ungulate and carnivore abundances

Deer population size was estimated at the hunting estate level, each estate being con-

sidered as a discrete management unit. Two spotlight counting events (two replicates on consecutive days) between September and October 2011 were used to estimate the deer population size on each estate. Transects (mean length = 20.3 km ± 2.34 S.E.) were driven at 10-15 km/h along dirt tracks covering the whole estate but excluding those tracks close to the estate boundary. The distance from the observer to the deer or to the centre of a deer group was measured with a Leica LRF 1200 Scan telemeter (Solms, Germany) (range 15-1100 m; precision ±1 m/±0.1%), and compass bearings were taken to determine the angle between these and the transect line. Deer population densities (indi-
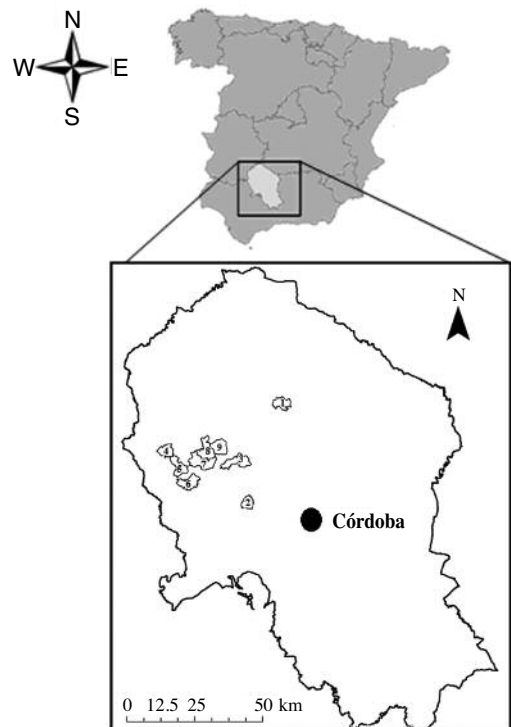

FIG. 1.—Map of Córdoba Province showing the location of the sampling sites.
[Mapa de la provincia de Córdoba mostrando la localización de los puntos de muestreo].

viduals per hectare) were estimated using Distance 5.0 software (Buckland *et al.*, 2004). 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 was based on Akaike's Information Criterion (AIC).

TABLE 1

Description of the nine study areas. Red deer density (red deer/ha), wild boar abundance (FBII: frequency based indirect index), carnivore abundance (KAI: droppings/km), carnivore abundance (Spotlight: carnivores/km), spring and autumn partridge abundance (KAI: partridges/km), surface area (ha), scrubland, woodland and pasture (% of total surface area) and transect length for red deer census (Total km: census 1 + census 2).
[Descripción de las nueve áreas de estudio. Densidad de ciervos (ciervos/ha), abundancia de jabalí (FBII: índice de frecuencia), abundancia de carnívoros (IKA: excrementos/km), abundancia de perdiz en primavera y otoño (IKA: perdices/km), área (ha), matorral, arbolado y pastizal (% con respecto a la superficie total) y longitud de los transectos para los censos de ciervo (kilómetros totales: censo 1 + censo 2).]

Estate code	Red deer density (ind/ha)	Wild boar abundance (FBII)	Carnivore abundance (KAI)	Carnivore abundance (Spotlight)	Spring partridges abundance (KAI)	Autumn partridges abundance (KAI)
1	0.25	0.15	3	0.1	0.63	1.02
2	0.4	0.25	2.7	0.07	0.45	0.6
3	0.26	0.04	12.6	0.24	0.42	0.43
4	0.29	0.34	0.6	0.02	0.35	0.66
5	0.37	0.38	1.86	0.19	0.29	0.75
6	0.32	0.17	0.4	0.16	0.26	0.47
7	0.53	0.41	0.74	0.02	0.14	0
8	0.68	0.47	5.9	0.16	0.11	0.3
9	0.41	0.08	13.2	0.16	0.44	0.44

Estate code	Surface (ha)	% Shrubland	% Woodland	% Pasture	Total Transect length for red deer census (km).
1	2200	32	6	63.7	40
2	1590	30.7	23	40	42.2
3	3600	28.5	15.8	70	41.2
4	1480	14.7	24.5	59.8	37.2
5	2540	32.6	12	58.6	42
6	2747	31.1	16	51.2	37
7	3343	31.2	37.5	39	41.2
8	3308	40	26	47.2	36
9	1860	26.2	27.5	75.7	30.5

Wild boar abundance was estimated following the methodology employed by Acevedo *et al*. (2007) based on dung frequency along a walked transect. According to this method, two 4-km transects per estate, located at least two kilometres apart, were performed in September and October 2011. Each transect comprised 40 segments 100 m in length and 1 m wide, divided into ten sectors of 10 m in length. Sign frequency was defined as the average number of 10 m sectors containing dung per 100-m transect (Carpio *et al*., 2014a), and a mean value of wild boar abundance was calculated per estate using the following formula:

$$\text{FBII} = \frac{1}{n} \sum_{i=1}^{n} S_i$$

where S_i is the number of sign-positive sectors and n the total number of sampled sectors.

The number of carnivore scats per km in these transects was also recorded (similarly to Carpio *et al*., 2014a). Carnivore abundances were additionally estimated through the use of spotlight counts during July and August 2011 in order to obtain a kilometric abundance index (KAI). Two 20-km routes (two replicates on consecutive days) were spotlighted per estate, and any carnivores observed were noted. Those detected were the red fox *Vulpes vulpes*, stone marten *Martes foina* and common genet *Genetta genetta*.

Estimating red-legged partridge abundance

Red-legged partridge abundance was estimated during two seasons in 2011 (April and October), coinciding with the population minimum just before breeding and the population peak following juvenile recruitment respectively (Borralho *et al*., 1996; Gortázar *et al*., 2002). The transects on each estate, whose average length was 20.6 km ± 3.5 (± S.E.), were measured by driving at a speed of 10-15 km/h, and two replicates of each transect per estate and season were carried out, at no more than 3-day intervals. The transects were conducted by two people (one driver and one observer) during the first three hours after sunrise and in good weather conditions (Gortázar *et al*., 2002), and they covered optimal habitats for partridges (oak savannahs, pastures and sparse scrublands), avoiding dense pine forest and dense scrubland patches, in which detectability/visibility is poor. Simple counts were made and a kilometric abundance index (KAI) was calculated for each estate by dividing the number of observations by the total length of the transect (the low number of observations preventing using "Distance software" to estimate partridge densities).

Invertebrate sampling

Since invertebrates are important food resources for partridge chicks, two invertebrate surveys were conducted at random points 50-100 m from transects for estimating partridge abundance. The first took place in the last two weeks of March 2012 while the second was carried out in late April 2012. Five sampling points were established on each of the nine estates and two pitfall traps were placed at each one (90 pitfalls in total). The pitfall traps were buried at ground level and consisted of plastic receptacles with a capacity of 0.75 litres and an opening diameter of 12 cm (Paschetta *et al*., 2013). They were half-filled with a solution of salts (to preserve the specimens caught) and soap (to break the water surface tension). The trapped invertebrates were collected 14 days after the traps had been set (Allombert *et al*., 2005) and were preserved in 100 ml plastic containers with 70% alcohol. The inverte-

brates were subsequently identified to order level under a stereomicroscope, this degree of identification having figured in earlier studies of partridge diet (Holland *et al*., 2006). The diversity and structure of invertebrates larger than 0.02 mm (mesofauna and macrofauna) were studied and any microfauna (< 0.02 mm) were excluded. The invertebrate dry mass and taxon richness were calculated for each sampling point. In order to obtain the dry mass, pitfall trap contents were dehydrated in an oven at 80ºC for 24 hours before weighing on a precision scale (0.001 g). All index values were calculated from the average of the two pitfall traps in each pair of sampling periods. In addition, for each sampling point, the number of invertebrates belonging to the following groups was determined: a) Hemiptera (including Homoptera and Heteroptera), b) Coleoptera (both larvae and adults), c) Hymenoptera, d) Diptera, e) Collembola and f) class Arachnida (which includes subclass Acari, and the orders Scorpionida, Pseudoscorpionida, Opilionida, Solifugae and Araneae). These groups are considered to be the most important in the partridge diet (Holland *et al*., 2006).

Vegetation structure and plant sampling

Ten circular walking transects were conducted on each estate during May 2011 around the insect sampling points, using a 50 m cord to measure the distance. Shrub and pasture cover, along with maximum grass height, were measured on these transects, since these indexes have been considered as indirect measures of pasture availability for different herbivore species (Affleck *et al*., 2005). Finally, all individuals of the plant families identified as the most important in the partridge diet (Fabaceae, Poaceae and Asteraceae, according to Holland *et al*., 2006)

within the transect were noted and the percentage cover of each family was calculated.

In addition, plant biomass (g) was assessed from cuttings in an area of 25 cm² of herbaceous vegetation randomly selected around every transect. The vegetation sampled was dried to constant mass in a drying oven with hot air circulation at 60°C and weighed using an electric balance (precision: 0.01 g).

Nest predation

The nest predation rate by wild boar was obtained using data recorded by Carpio *et al*. (2014a) on the same hunting estates in 2012, using only nests located in areas accessible to wild boars (N = 45), i.e. five artificial nests per estate. In this experiment, nests were formed using four natural red-legged partridge eggs supplied by a game farm and two plaster eggs (N = 270). Egg predators were identified from tooth marks on the plaster eggs and by automatic cameras placed at 14 nests. All nests were checked for predation after 23 days and to discover the percentage of eggs depredated by different predators (for more details see Carpio *et al*., 2014a).

Statistical analysis

The variables red deer density, vegetation height, Collembola and Coleoptera, were log-transformed to fit the parameters of normality in accordance with the Kolmogorov-Smirnov test. A Principal Component Analysis was performed for carnivore abundance, which brought together the two carnivore abundance estimates (scats/km and KAI) into a single factor that explained 90.3% of the variance. The absence of spatial autocorrelation was checked by calculating the Moran's indices of each variable. The Partial Least Squares Regression (PLSR) technique

was used to construct two initial general models and four specific models (see below). PLSR is a useful regression calibration technique when the number of predictor variables is similar to or higher than the number of observations, and/or the predictors are highly correlated (Carrascal *et al*., 2009). This modelling procedure was based on a linear transformation of the original descriptors into a small number of orthogonal factors (latent variables), and an attempt was made to maximise the covariance between the descriptors and the dependent variable. In the general models, the dependent variables were partridge abundances in spring and autumn respectively, and the independent variables were: red deer, wild boar and carnivore abundances; plant biomass, maximum pasture height, rate of nest predation, percentage cover of shrub and pasture land, invertebrate species richness and biomass, frequency of the most important invertebrate groups (Collembola, Coleoptera, Diptera, Hemiptera, Hymenoptera and Arachnida), and finally, percentage cover of the plant families that are most important to partridges (Fabaceae, Asteraceae and Poaceae). Final models were constructed using only the variables with the highest standardised regression coefficient obtained in the full models, which allowed the optimal of the regression coefficient (Q^2) to be obtained, and both models were validated by following the full cross-validation technique.

In addition, four specific PLSRs were performed using as response variables those previously indentify as important predictors in the partridge abundance models (PLSR general models) that could be affected by high ungulate density (Hemiptera, invertebrate mass, vegetal biomass and maximum height of grass). In these specific models, red deer and wild boar abundances together with habitat related variables were included as independent ones. Statistical analyses were performed using Unscrambler 9.7 software.

RESULTS

Red deer density ranged from 25 to 67 individuals per km² (mean 39 ± 0.14 S.E.), and the abundance index for wild boar ranged from 0.04 to 0.47 (mean 0.26 ± 0.15 S.E.). The kilometric abundance index (KAI) for partridge ranged from 0.11 to 0.64 individuals/km (mean 0.34 ± 0.15 S.E.) in spring and from 0 to 1.02 (mean 0.51 ± 0.27 S.E.) in autumn. 65% of the eggs were predated, and only 20% of nests were not totally or partially predated. The wild boar was the main predator and consumed 45.8% of predated eggs (for more details on predation rates see Carpio *et al*., 2014a). With regard to invertebrate sampling, 2,580 animals were identified, 2,047 of which were of the most important taxa in the partridge diet (fig. 2).

The general PLSR analysis for spring abundance resulted in a significant model (with two principal components) that explained 59% ($R^2X = 0.59$) of the variance from the independent variables ($R^2X_{PC1} = 0.45$ & $R^2X_{PC2} = 0.14$) and 83% ($R^2Y = 0.83$) of the
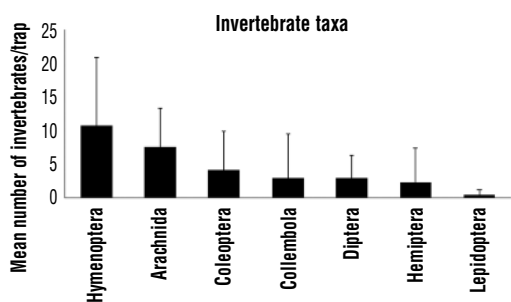

FIG. 2.—Mean number of individuals (±S.E.) per pitfall trap belonging to the most important invertebrate taxa in the partridge diet, according to Holland *et al*. (2006).
[Número medio de individuos (±S.E.) por trampa de caída pertenecientes a los taxones de invertebrados más importantes en la dieta de la perdiz según Holland et al. *(2006)].*

variance of the dependent variable ($R^2Y_{PC1} = 0.71$ & $R^2Y_{PC2} = 0.12$). The PLS autumn abundance analysis resulted in another significant model (with only one principal component) that explained 37% ($R^2X = 0.37$) of the variance from the independent variables and 60% ($R^2Y = 0.60$) of the variance in the dependent variable. Table 2 shows the regression coefficients of the variables retained in the final models, which summarise the effect of each parameter on partridge abundance in the spring and autumn models. In the spring model, three parameters had a significant effect on partridge abundance:

TABLE 2

Regression coefficients of the variables retained in the final PLSR general models. *p < 0.05.
*[Coeficientes de regresión de las variables importantes en los modelos PLSR generales. *p < 0,05].*

Spring model
$R^2X = 0.59$ $R^2Y = 0.83$ $Q^2 = 0.73$

Variable	Coefficients
Deer Density	–0.44*
Carnivores Abundance	–0.233
Wild boar density	–0.223
Maximum height	0.188
Hemiptera	0.192*
Invertebrates mass	0.196*
Vegetal Biomass	0.211*

Autumn Model
$R^2X = 0.37$ $R^2Y = 0.60$ $Q^2 = 0.55$

Variable	Coefficients
Deer Density	–0.505*
Carnivores Abundance	–0.436*
% Non depredated eggs	0.308*

red deer abundance had a negative effect, whereas Hemiptera, invertebrate mass and vegetal biomass had a positive correlation. In the autumn model, deer density and carnivore abundance had a negative effect on partridge abundance, and only the percentage of unpredated eggs had a positive effect.

Finally, the specific PLSR models (table 3), using as response variables those which affect red-legged partridge abundance (Hemiptera, vegetal biomass, invertebrate mass and maximum grass height), showed that the wild boar abundance index was negatively correlated with Hemiptera, vegetal biomass and grass height, whereas red deer abundance was only negatively correlated with grass height. The PLSR model using the invertebrate mass as a response variable was not significant (*$R^2X = 0.5$; $R^2Y = 0.11$; $Q^2 = –0.041$*), and therefore those results are not given.

DISCUSSION

This study has shown that red legged partridge abundance on big-game hunting estates in Southern Spain is (i) negatively associated with high red deer abundance, (ii) positively associated with variables indicative of higher food availability, some of which were affected by both wild boar and red deer, and (iii) negatively affected by nest predation. This highlights the fact that big and small game species are currently spatially segregated in southern Spain (Vargas *et al*., 2007; Delibes-Mateos *et al*., 2009), probably not only as a consequence of land-use changes and big game management leading to high abundances, but also through direct and indirect effects of wild ungulates on small game species. Therefore, the high population densities that ungulates reach in some woodland areas could be considered as an additional threat to partridge populations. Among other aspects, Caughley, 1981

TABLE 3

Regression coefficients of the important variables retained in the PLSR specific models. *p < 0.05.
*[Coeficientes de regresión de las variables importantes en los modelos PLSR específicos *p < 0,05].*

Hemiptera (PLSR 1)	
$R^2X = 0.58$ $R^2Y = 0.26$ $Q^2 = 0.21$	Coefficients
Wild boar abundance	–0.14*
Vegetal Biomass	0.13*
Fabaceae	0.14*
Maximum height of grass	0.09
Vegetal Biomass (PLSR 2)	
$R^2X = 0.65$ $R^2Y = 0.29$ $Q^2 = 0.26$	Coefficients
Wild boar abundance	–0.24*
Fabaceae	0.17
Maximum height of grass	0.13
Red deer	–0.11
Maximum height of grass (PLSR 3)	
$R^2X = 0.65$ $R^2Y = 0.29$ $Q^2 = 0.26$	Coefficients
Wild boar abundance	–0.23*
Red deer abundance	–0.22*
Fabaceae	0.24*
% of pasture land	0.26*

(reviewed by Côté *et al*., 2004 in the case of red deer) proposed that animals are over-abundant when they cause ecosystem dysfunction, including a loss of biodiversity. In the light of this consideration, our results suggest that the current ungulate densities attained on many hunting estates can be considered as cases of overabundance, since they can reduce the abundance of other species as a consequence of a reduction in food resources (invertebrate and vegetation) and an increase in nest predation rates (by wild boars), particularly in the case of ground-nesting birds (Barrios-García and Ballari, 2012). What is more, this reduction in numbers of partridges and other birds may result in additional trophic cascade effects, thus affecting the prey resources of endangered predators (Lozano *et al*., 2007).

Our results further show that partridge abundance was negatively correlated with red deer density in both seasons (fig. 3). These negative relationships could result from a decrease in food availability as a consequence of overgrazing and trampling in areas of high red deer densities. In fact, our

results show that partridge abundance was positively related with vegetal biomass, which is a good estimator of pasture availability (Lazo *et al*., 1991). Although the maximum grass height did not show a significant effect, it was included in the best model showing a negative association with partridge abundance in spring, being in turn negatively affected by red deer density. Grass shortening may not only affect partridges as a result of food reduction but may also indirectly affect their vulnerability to predation (Hudson and Rands, 1988), since partridges (and their nests) are much more vulnerable in low herbaceous cover (Lucio, 1991).

Although wild boar abundance was not significantly correlated with partridge abundance, our results indicate that they may affect partridges by direct predation of nests (Carpio *et al*., 2014a), by a negative impact on invertebrates (Carpio *et al*., 2014c), and by reducing grass biomass and height. In the present study, wild boar abundance was negatively correlated with Hemiptera frequency (table 2), which showed a significant positive relationship with partridge abundance in spring, suggesting that wild boar overabundance could also decrease the availability of

insects for partridges. Moreover, this negative effect on invertebrates could affect chick development, since invertebrates are the main protein source for young chicks and protein intake is essential for proper growth and the development of thermoregulatory mechanisms (Liukkonen-Anttila *et al*., 2002; Southwood and Cross, 2002). Wild boar abundance was also negatively correlated with grass biomass and height, which were previously identified as important predictors of red-legged partridge abundance in spring. This highlights the strong impact that boar rooting behaviour can have on grassland communities (Bueno *et al*., 2010).

Our results also show that partridge abundance in autumn was also negatively affected by egg predation in spring, wild boar being the main nest predators in the study area (Carpio *et al*., 2014a). This negative association in autumn suggests that juvenile recruitment and population growth (which takes place from late spring to autumn) may be strongly affected by nest predation, and the role of the wild boar as a nest predator can therefore be considered as an important harmful factor on hunting estates with high densities of this ungulate. Boar feeding behaviour may not only affect red-legged partridge populations but also those of other ground-dwelling birds (Barrios-García and Ballari, 2012). Indeed, Selva *et al*. (2014) have similarly recently shown that the proportion of depredated nests was higher in areas adjacent to ungulate feeding sites than at control sites, suggesting that game management should always consider potential indirect effects and the complex interactions that occur at ecosystem level.

Finally, it is also noteworthy that partridge abundance was negatively correlated with carnivore abundance in autumn. However, considering only this negative relationship may not be sufficient for understanding the possible effects of predation on partridges, and it is necessary to test the dietary and
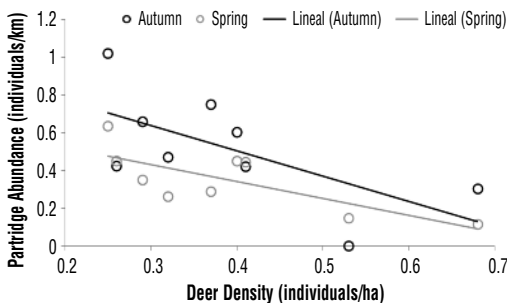

FIG. 3.—Red-legged partridge abundance in spring (grey) and autumn (dark) as a function of red deer density.

[Abundancia de perdiz roja en primavera (gris) y otoño (negro) en función de la densidad de ciervo].

numerical responses of the carnivores to red-legged partridge abundance in order to elucidate predator-partridge relationships (Fernández de Simón, 2013).

Although this was a short study at a limited number of sites we consider that our results may be extrapolated to other hunting estates characterised by high densities of wild ungulates. The relationships between partridge abundance, food availability indicators and ungulate densities shown here may similarly be extrapolated to other areas of Spain in which there is an increase in the abundance of wild ungulates but it is necessary to confirm plausible effects of wild ungulates on partridges and other birds over a wider range of habitats and locations. This matter may be of major conservation concern in woodland areas in Southern Spain, in which several endangered predators persist and rabbits and red-legged partridges remain at low densities (Delibes-Mateos *et al.*, 2009; Guerrero-Casado *et al.*, 2013). In conclusion, this paper further shows that current big-game hunting management schemes in South Central Spain are often incompatible with the conservation of the main bird game species. The effects shown must therefore be considered as signs of ungulate overabundance and should be taken into account when deciding the most appropriate big-game management and conservation policies. Wild ungulate density should be therefore managed in order to make big-game hunting compatible with partridge conservation, although more studies are needed to determine the threshold value of ungulate abundance. An additional management option to promote partridge populations in areas of south-central Spain that are devoted to big game could be the establishment of ungulate exclusion areas, since nest predation rates are lower in the absence of wild boar (Carpio *et al.*, 2014a); and pasture cover and height as well as invertebrate richness is higher within ungulate exclusion fences (Carpio *et al.*, 2014c).

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