Bird Conservation International (2015) 25:166–181. © BirdLife International, 2014
doi:10.1017/S0959270914000197

Effects of hunting management on Mediterranean farmland birds

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Summary

Hunting and its associated management have significant costs and benefits for biodiversity conservation, which makes this socio-economic activity highly controversial at both international and regional levels. We investigated relationships between management for small game species (mainly Red-legged Partridges *Alectoris rufa* and rabbits *Oryctolagus cuniculus*) and both abundance and richness of farmland and scrubland songbirds, raptors and ground-nesting birds, and on the abundance of three species of conservation concern (Little Bustard *Tetrax tetrax*, Eurasian Thick-knee *Burhinus oedicnemus* and Montagu's Harrier *Circus pygargus*) in southern Portugal farmland. We compared 12 game estates and 12 matching areas with similar sizes and land uses but no game management. Richness and abundance were estimated from fixed point counts, and were related to game regime (managed or unmanaged), habitat characteristics and census period. Our results showed that game management was associated, albeit weakly, with higher abundance of raptors and ground-nesting birds, but no relationship (either positive or negative) was found for other guilds and species. Habitat was generally the most important factor explaining bird species richness and abundance. Our results suggest possibilities for promoting management systems that could maximize both hunting sustainability and conservation value of managed areas, particularly when management helps to improve or maintain beneficial habitats or practices for farmland birds.

Introduction

The increasing pressure from human activities implies that current rates of biodiversity loss are unparalleled in historical times (Mace *et al.* 2005). There is a widespread agreement among a variety of stakeholders that halting biodiversity loss will only be possible through the implementation of land-use strategies that integrate the needs of both human activities and biodiversity conservation (Woodroffe *et al.* 2005). Hunting is one of those activities that interact with biodiversity, and all over the world it is undertaken by millions of people over large areas across a broad range of ecosystems (Mustin *et al.* 2011).

A number of studies have exemplified negative impacts of hunting on biodiversity through overexploitation (Halliday 1980, Keane *et al.* 2005), and disturbance of wildlife (Evans and Day 2002, Casas *et al.* 2009). Also, undesirable effects of some game management practices on both game and non-game species have been documented; e.g. the release of farm-reared animals for shooting may compromise the genetic integrity of some game species (Blanco-Aguiar *et al.* 2008, Chazara *et al.* 2010), and predator control carried out by hunters may threaten some predators of conservation concern (Whitfield *et al.* 2003). In contrast, other studies have pointed out that hunting may contribute to biodiversity conservation, highlighting the potential for hunters to be active collaborators with conservation organizations (Paulson 2012). For example, game management may contribute to safeguard valuable habitats for biodiversity on private land

(Oldfield *et al.* 2003), and may also benefit other non-target species through the provision of food or the removal of generalist predators (Stoate and Szczur 2001, Beja *et al.* 2009). Overall, the relationships between hunting and biodiversity are still a matter of controversy among researchers, conservationists and the general public, at both international and regional levels (Mustin *et al.* 2011).

Most studies addressing the effects of hunting on biodiversity have been carried out in northern Europe, whereas species and populations from more diverse southern European ecosystems have received less attention (but see Suárez *et al.* 1993, Stoate *et al.* 2000, Beja *et al.* 2009). There is thus a need to examine the interactions between hunting and biodiversity in a wider range of ecological circumstances and geographic regions, thereby helping to develop generalisations that may be useful in setting guidelines for enhancing the conservation value of game management, while decreasing some of its negative impacts. The Iberian Peninsula is a region where examining these issues is particularly relevant, both because of its importance from the conservation standpoint (Myers *et al.* 2000), and also because hunting there is a significant and widespread socio-economic activity (Martínez *et al.* 2002).

In principle, the potential impact of hunting on biodiversity will depend not only on the occurrence of the activity as such, but also on the management applied, including the regulation of animals hunted (i.e. whether extraction is adjusted in relation to abundance), and the management tools applied with the objective of improving populations of game. In fact, game management to boost game populations is becoming progressively more intensive in the Iberian Peninsula, which may have negative consequences for biodiversity (Virgós and Travaini 2005, Villanúa *et al.* 2008, Macaulay *et al.* 2013). For example, the decline of the Red-legged Partridge *Alectoris rufa* and the European rabbit *Oryctolagus cuniculus*, mainly as a consequence of changes in agricultural practices, overhunting or epidemic diseases (Villafuerte *et al.* 1995, Blanco-Aguiar *et al.* 2004), has led to increases in potential detrimental practices, such as the large scale release of farm-reared animals (Blanco-Aguiar *et al.* 2008), and the implementation of intensive predator control campaigns (Villafuerte *et al.* 1998). In contrast, some studies suggested that actions aimed at benefitting small-game species in Iberian contexts may also have positive consequences on other species sharing the same habitats, such as predator control benefitting ground-nesting passerines (Suárez *et al.* 1993) or the provision of water points benefitting some farmland bird species (Gaudioso Lacasa *et al.* 2010). Additionally, in this region, income from hunting can provide an economic incentive to maintain areas of relatively undisturbed wildlife habitat, including high conservation value 'montados' and 'dehesas' (areas of sparse oak *Quercus* spp. woodland which may be cultivated or grazed underneath; see Díaz *et al.* 2009, Macaulay *et al.* 2013). Overall, we can presume that hunting may have conservation value if it improves populations of game and other wild species (especially species of conservation concern) or, at least, if it is not harmful to species of conservation concern and contributes to maintain the viability of high-value land-use systems.

Within this context, the aim of this study was to investigate the effects of game management on non-game species in the Iberian Peninsula. The study focused on farmland bird assemblages, because small game hunting mainly occurs on farmland, and farmland birds have suffered major population declines at the European level in recent decades, mainly due to agricultural intensification (Donald *et al.* 2001, BirdLife International 2004). Specifically, the study was based on a treatment-control natural experiment, comparing areas with and without management for small game species in southern Portugal, and analysing the relative effects of game management and habitat conditions on: (i) species richness and abundance of species grouped according to ecological characteristics; and (ii) abundance of individual species of conservation concern. Results were then used to discuss the conservation implications of game management in Mediterranean farmland.

Methods

Study area

The study was conducted in the region of Alentejo, southern Portugal (Figure 1). Climate is Mediterranean, with hot summers, fairly cold winters and > 75% of annual rainfall (500–700 mm)

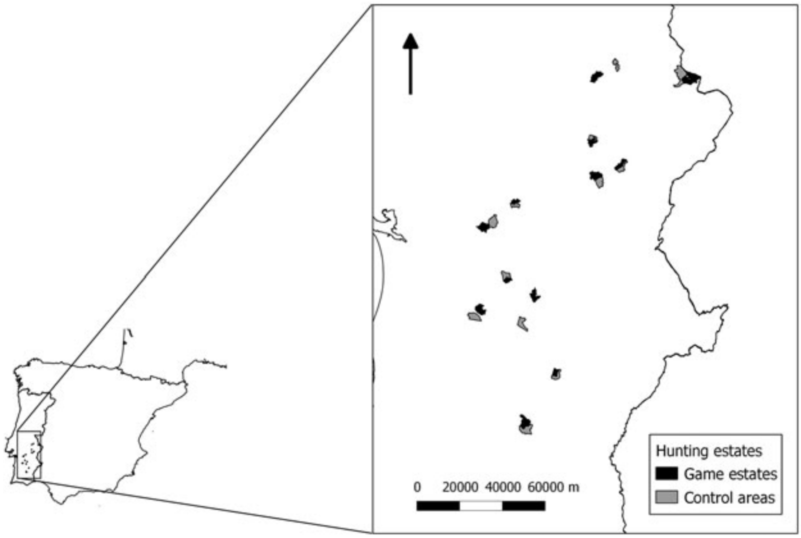

Figure 1. Location of the study area in southern Portugal.

concentrated in October–March. The landscape is dominated by savanna-like woodlands ('montados') of cork oak *Quercus suber* or holm oak *Q. ilex*, with understorey frequently grazed by cattle, sheep and pigs. Other important land uses include annual crops (mostly winter cereals, e.g. barley *Hordeum vulgare*, wheat *Triticum* spp.) and permanent crops (e.g. olive groves *Olea europaea*, vineyards *Vitis vinifera*), as well as pine *Pinus* spp. and eucalyptus *Eucalyptus* spp. plantations. There are marked trends for agricultural intensification in the most productive areas, as well as scrub encroachment and afforestation in marginal agricultural lands (Pinto-Correia and Mascarenhas 1999, Van Doorn and Bakker 2007).

Hunting is important in Alentejo, involving both residents and a large number of hunters from urban centres throughout the country. In recent years, the economic importance of hunting has increased along with modifications in hunting regulations and the decline of traditional rural economies (Van Doorn and Bakker 2007). Hunting regimes changed from open hunting in the mid-1970s, in which there was neither game management nor restrictions of access to hunting areas, to the present situation of primarily private hunting estates, with large areas managed by hunter associations or landowners (Coelho 2011).

Sampling design

The study was akin to a treatment-control natural experiment, involving comparisons between 12 estates managed to promote game species (private hunting regime, hereafter 'Game estates'), and 12 matching control areas, open to hunters but with no game management (open hunting regime, hereafter 'Control areas') (Figure 1). Hunting estates were randomly selected from a database of all hunting estates in Alentejo, and Game estates and Control areas were required to be as similar as possible, both in terms of size, habitat and land use (see Beja *et al.* 2009 for details). All Game estates and Control areas selected were required to have more than three years of continuous similar conditions in terms of game management.

Mean surface area and standard deviation of the 24 areas was 12 ± 6 km^2 (range 5.5–25.7). Management practices were assessed from enquiries to landowners and game managers, but they could not be quantified in detail for each study area because in most cases the information provided was incomplete. However, enquiries revealed that all game estates provisioned water and grain

https://doi.org/10.1017/S0959270914000197 Published online by Cambridge University Press

(watering and feeding sites), 91.7% admitted carrying out predator control (the single exception did not provide information), at least 41.7% cultivated game crops to provide cover and food for game species, and at least 91.7% released small game, mainly Red-legged Partridge (eight estates) and European rabbit (five estates). More details can be found in Beja *et al.* (2009). Species legally controlled were red foxes *Vulpes vulpes*, Egyptian mongooses *Herpestes ichneumon*, feral cats *Felis catus*, dogs *Canis familiaris*, Carrion Crows *Corvus corone*, Eurasian Jays *Garrulus glandarius* and Common Magpies *Pica pica*. The illegal culling of protected carnivores and birds of prey occurred to an unknown extent (Beja *et al.* 2009).

Avian surveys

Field surveys were carried out in 2000 and 2001. Thirty point counts were randomly selected in each of the 24 study sites. Point selection was restricted to land uses covering more than 5% of the total area. To minimise the probability of overlapping counts, a minimum distance of 700 m between successively census points was used. Each set of thirty points consisted of three different sub-sets of points, each one visited in one of the three sampling periods during the breeding season: early season (late March to mid-May), mid-season (late April to early June) and late season (mid-June to mid-July). On average, each subset consisted of 10 points, but there was some variation among areas (SD ± 2.7) due to logistic constraints. In each sampling period, surveyed points were widely scattered along tracks distributed throughout the whole of the estate. This sampling protocol aimed to obtain a more realistic census of the breeding community, given the large temporal variation in breeding phenology and activity among bird species in southern Portugal, including sedentary and migratory species (both pre- and trans-Saharan migrants). A total of 91.1% of point counts were conducted by a single experienced observer (LG), and the remaining by an equally experienced observer (LR). We identified all individuals and flocks seen or heard, during 15 minutes in each sampling point. Bird censuses were made during the first three hours after dawn and the last three hours before dusk, corresponding to the period of highest bird activity. Each Game estate and its corresponding Control area were always sampled by the same observer, on consecutive days, at around the same time.

Bird guilds

Bird species were clustered in four ecological groups (guilds; see Verner 1984): farmland songbirds, scrubland songbirds, raptors, and medium-sized ground-nesting birds, mainly steppe-birds (a list of all species can be found in Table S1 in the online Supplementary Materials). The focus on songbirds (i.e. all Passeriformes except the family Corvidae) is justified, because this heterogeneous group of species (Tellería *et al.* 1999) is a widely used indicator of both habitat and wildlife conservation value (Stoate and Szczur 2001, Litteral and Wu 2012, Morales *et al.* 2012). Farmland songbirds were considered because previous studies have shown that they may be favoured by cultivation of game crops and by seeds provided in feeding stations for game (Mustin *et al.* 2011), as well as by reduced predation pressure due to predator control (Yanes and Suárez 1996), and so they could be expected to react positively to game management. Scrubland songbirds were considered because they might also be favoured by reduced predation pressure, though they are unlikely to be affected by the provisioning of seeds and game crops. We excluded Spotless Starling *Sturnus unicolor* from analyses, as the much higher abundance of Spotless Starling in Control areas (1,860 contacts) than in Game estates (870 contacts) was likely to be unrelated to game management, probably resulting to a large extent from more unoccupied rural constructions in non-managed areas (LG and LR pers. obs.), which may enhance breeding sites for the species (Tellería *et al.* 1999).

The guild of raptors included diurnal birds of prey and owls feeding at least occasionally on small game species (rabbits or partridges). This guild was considered because it includes species of conservation concern, which may either benefit from management due to an increase of small prey abundance (Delibes-Mateos *et al.* 2007), or be negatively affected if illegal control is directed against predators seen as competitors by hunters (Beja *et al.* 2009).

The ground-nesting guild included medium-sized bird species and one wader (Pratincole *Glareola pratincola*), which frequently uses farmland areas. We excluded ground-nesting songbirds and raptor species to avoid representation of species in more than one guild. Additionally, we excluded game species as the Red-legged Partridge, the Common Quail *Coturnix coturnix* and wildfowl, as these may be affected by shooting pressure, rather than by game management. This guild was considered because it included species of conservation concern, which might be affected by management carried out to increase suitable habitats for breeding and feeding of game birds, as well as by predator control reducing the naturally high predation pressure on ground nests (Yanes and Suárez 1996, Beja *et al.* 2014).

Finally, we were also specifically interested in evaluating the impact of hunting on individual species of conservation concern in Portugal (Cabral *et al.* 2008). Among those, we focused our analyses on the species most frequently recorded in our study areas (> 70 observations), including Little Bustard *Tetrax tetrax*, Eurasian Thick-knee *Burhinus oedicnemus* and Montagu's Harrier *Circus pygargus*.

Explanatory variables

We were interested in evaluating the effect of small game management on richness and abundance of bird guilds (thus testing for differences between Control areas and Game estates) after controlling for habitat variables. The habitat composition of each Game estate and Control area was characterised in terms of six dominant land cover categories (Table 1). At each sampling point, the proportion of each land cover category was visually estimated within a 200 m radius centred on the observer, immediately after the bird count. An overall estimate for each estate was then obtained by averaging the estimates from the 30 points sampled within the estate. Habitats were considered at the level of the entire estate rather than at the scale of each individual point, because we were interested on the overall landscape composition resulting from the joint effects of farmland and game management practices.

Table 1. Variables measured in the 24 areas and used in the Principal Component Analysis and modelling procedure.

Variable	Description
Census period	Categorical variable with three different levels: early season (late March to mid-May), mid-season (late April to early June) and late season (mid-June to mid-July)
Habitat	
Open farmland	Percentage cover of arable land (pastures, cereal fields, fallows and/or ploughed fields)
Permanent crops	Percentage cover of olive groves, vineyards and fruit orchards
'Montados'	Percentage cover of open woodlands dominated by *Quercus ilex* and/or *Q. suber* with pastures, arable crops, or shrubs in the understorey
Mediterranean scrubland	Percentage cover of medium-height Mediterranean shrubs, dominated by species of *Cistus*, *Genista*, and *Ulex* among many others, with a strong component of *Q. ilex* and/or *Q. suber*, the latter sometimes achieving full tree height
Streams, reservoirs and riparian vegetation	Percentage cover of streams, riparian vegetation, farm ponds, and small reservoirs
Forest stands	Percentage cover of pine *Pinus* spp. or eucalyptus *Eucalyptus* spp. plantations
Game category	
Game management	Categorical variable with two different levels: Game estates and Control areas

Additionally, as raptors that feed on small game species (rabbits and partridges) may respond positively to small game abundance (Delibes-Mateos *et al.* 2007), we also considered abundance of both small game species as further explanatory variables for this guild. Partridge abundance was estimated in the surveys described above, and it is presented as total partridges observed in each sampling period in each surveyed area. Rabbits were surveyed once in each area (May–June) from diurnal transects walked along dirt tracks, and observations of individual animals and signs of their presence (faeces) were counted (Beja *et al.* 2009). Latrines defined as discrete clusters of 20 or more droppings in a 10 cm radius were used as counting units instead of individual pellets (Calvete *et al.* 2006).

Statistical analyses

We modelled richness and abundance of each guild considered, and abundance of individual species of conservation concern. Richness was expressed as the total number of different species observed in each surveyed area and abundance was measured as the total number of individuals observed in each sampling period within each surveyed area (see above). For richness of each bird guild, we used only one value per surveyed area (maximum number of species observed in 30 points), as species richness observed in each estate only reached asymptotic values after c.19–22 points (results not shown here). Prior to this analysis, we $\log_{10}(x+1)$ transformed variables with skewed distributions in order to approach normality and reduce the influence of a few large values (Zar 1999). We initially used the paired t-test to identify differences in abundance and species richness between Game estates and Control areas.

We reduced the six habitat categories into two orthogonal factors using a Principal Component Analysis (PCA; e.g. Atauri and Lucio 2001). Subsequently, we modelled the richness of each guild using Generalised Linear Mixed Models (GLMMs), fitting response variables to a Poisson distribution and using a log link function, and included 'grouping area' (i.e. encompassing each pair of matching Game estate and Control area) as a random effect. As explanatory variables, we used the type of estate (managed or not managed), the two PCA habitat axes, and small game abundance in the case of raptors. We also used GLMMs to model the abundance of each guild and the abundance of the three species of conservation concern, fitting response variables to a Poisson distribution with log link. Response variables were number of individuals observed, and we used as an offset the $\log_{10}$ number of points surveyed. We used as a random term 'surveyed area' (i.e. each Game estate or Control area) nested within 'grouping area', thereby accounting for the repeated observations in each monitored area, and for the lack of independence between each pair of areas due to spatial proximity (see above). Explanatory variables were as above and additionally we included census period as a fixed categorical variable. Models were calculated with the function *glmmADMB* (Fournier *et al.* 2012), implemented using R statistical software, Version 2.15.1 (R Development Core Team 2011).

We used a model-averaging, information-theoretic approach to assess the magnitude and direction of the effects of predictor variables (Burnham and Anderson 2002). We performed all possible combinations of the independent variables with the R-function *dredge* (library *MuMIn*; Bartoń 2012). Models were ranked according to Akaike's Information Criterion (AIC_c for small sample sizes). Akaike weights were also obtained for each model using the R-package *AICcmodavg* (Mazerolle 2012). Then we calculated an averaged model with all the models that presented a difference of $AIC_c < 2$. Akaike weights indicate the probability that the model is the best among the set of plausible candidate models (Burnham and Anderson 2002), so we calculated the importance of each variable in the averaged model by summing the Akaike weights over all models in which the variable was present (Naidoo *et al.* 2011). We only interpreted the effects of variables for which the standard errors were smaller than the average coefficient, because otherwise estimates were considered too imprecise.

Results

Overall, we observed 22,188 individual birds from 127 species during the censuses. About half of the individuals (48.6%) were recorded in Game estates and another 51.4% in Control areas. In terms of guild membership, 13.4% of the species were classified as farmland songbirds, 25.2% were scrubland songbirds, 9.4% were raptors, and 3.9% were ground-nesting birds. Species that did not belong to any of these groups (48.1%) were not considered further. Preliminary analyses based on paired t-tests showed no differences in richness and abundance between Game estates and Control areas (paired t-tests, $P > 0.05$ in all cases, Table 2).

The PCA with habitat variables produced two orthogonal axes which together accounted for more than 95% of the variance (Table 3). The first axis can be interpreted as a gradient from sites dominated by open arable land to those including oak woodlands (whether closed or open). The second axis reflects a gradient of land abandonment, contrasting the 'montados' (open and managed oak woodland) *versus* encroached Mediterranean scrubland.

Model selection revealed a single candidate model for farmland songbird abundance, ground-nesting bird richness and Montagu's Harrier abundance, while there were a rather large number of plausible models for the other guilds and species (Table S2). The model-averaged approach supported the effect of explanatory variables on bird species richness and abundance (Table 4), which we describe subsequently for each guild considered.

Farmland and scrubland songbirds

Habitat was the most influential variable explaining richness and abundance of both guilds. Species richness and abundance of farmland songbirds increased with rising proportion of open habitat, while richness and abundance of scrubland songbirds declined over the same gradient (Table 4). Census period also affected abundance of farmland songbirds, which was highest in late season and game management was not related to the richness and abundance of both guilds (Table 4).

Table 2. Mean and standard error of richness (total different species observed in each estate) and abundance (number of individuals observed per point) of species guilds in Game estates and Control areas of southern Portugal. Results of paired *t*-tests between groups are also presented. Although most tests were performed on long-transformed data, summary statistics are presented in the original scale.

	Control areas Mean ± SD	Game estates Mean ± SD	t_{11}	*P*
Guild species richness				
Farmland songbirds	10.583±2.503	11.667±1.874	-2.169	0.053
Scrubland songbirds	12.667±3.312	13.500±4.661	-0.882	0.396
Raptors	3.500±0.904	4.000±1.348	-1.483	0.166
Ground-nesting birds	1.417±1.164	1.333±1.155	0.432	0.674
Bird abundance				
Farmland songbirds	9.423±9.726	8.401±4.014	-0.087	0.931
Scrubland songbirds	8.859±4.770	9.202±4.538	-0.771	0.446
Raptors	0.441±0.514	0.478±0.428	-1.202	0.238
Ground-nesting birds	0.416±0.837	0.388±0.693	0.091	0.928
Bird species abundance				
Eurasian Thick-knee	0.105±0.191	0.110±0.197	-0.068	0.946
Little Bustard	0.230±0.573	0.237±0.522	-0.058	0.954
Montagu's Harrier	0.156±0.325	0.123±0.260	1.015	0.317
Game species abundance				
Red-legged Partridge	0.155±0.196	0.468±0.633	-3.276	0.002
Rabbit	0.458±1.079	5.942±8.836	-2.677	0.021

Table 3. Summary results of the Principal Component Analysis of habitat variables.

Habitat variable	PC1	PC2
Open farmland	-0.830	0.225
Permanent crops	0.037	-0.093
'Montados'	0.510	0.673
Mediterranean scrubland	0.213	-0.692
Streams, reservoirs and riparian vegetation	0.007	-0.022
Forest stands	0.061	-0.089
Eigenvalue	958.1	534.1
Explained variance (%)	60.7	95.6

Raptors

Habitat was also the most influential variable explaining richness and abundance of raptors. Game management was also included in the best AIC_c models for raptor abundance (Table S2), which was highest in Game estates (Table 4). The strongest habitat effects were found for PC1, suggesting that both species richness and abundance of raptors were increased with the amount of open land. Finally, abundance was highest earlier in the season (Table 4).

Ground-nesting birds

Game management was included in the set of best AIC_c models for ground-nesting bird abundance (for richness, the standard error was higher than the average coefficient), with a tendency for higher abundance in Game estates (Table 4 and Table S2). Again, habitat variables were the most important in explaining ground-nesting bird abundance and richness, which declined with a decrease of open arable land and with an increase in encroachment through land abandonment (Table 4). Abundance was highest earlier in the season (Table 4).

Species of conservation concern

Game management did not have a significant effect on the abundance of any of the species of conservation concern considered, after taking into account habitat and census period (Table 4 and Table S2). Even if it appeared in the set of best models for the Little Bustard, the standard deviation was higher than the parameter estimate (Table 4). Open land was positively related to the abundance of all three species, and there was a strong effect of census period on Little Bustard and Montagu's Harrier, with the highest counts recorded earlier in the season.

Discussion

Hunting is a traditional activity that may be compatible with the conservation of biodiversity, but that may also threaten biodiversity if sustainable practices are not established (Leopold 1986). We argue that hunting would be detrimental to conservation if it leads to decreases of populations of wild species of conservation concern. Alternatively, it would be beneficial to conservation if it either improves populations of species of conservation concern, or if it is not harmful to those species and contributes to maintain high-value land-use systems. Studies in northern Europe and North America have found either positive or negative effects of hunting or hunting management practices on conservation (Thiollay 2005, Valkama *et al.* 2005, Mustin *et al.* 2011).

Until now, there was little information on the effects of hunting and its associated management on non-game birds in Mediterranean ecosystems (Díaz *et al.* 2009), where farming is still relatively non-intensive and where biodiversity is high (Pain and Pienkowski 1997, Sokos *et al.* 2013). Broadly, our study did not find any evidence that in game estates there is lower richness or abundance

Table 4. Model-averaged coefficients of Poisson GLMM relating the richness and abundance of three bird guilds, and the abundance of species of conservation concern, to land cover types (PC_1 and PC_2, see text for details) and game management in Alentejo (southern Portugal). RVI= Relative variable importance.

		Variable name														
		Intercept	Game management (Game estate)		Census period (early season)		Census period (late season)		PC1		PC2		Rabbits		Partridges	
		Parameter (S.E.)	Parameter (S.E.)	RVI	Parameter (S.E.)	RVI	Parameter (S.E.)	RVI	Parameter (S.E.)	RVI	Parameter (S.E.)	RVI	Parameter (S.E.)	RVI	Parameter (S.E.)	RVI
Farmland songbirds	Richness	2.401 (0.062)							-0.004 (0.002)	0.74	0.003 (0.003)	0.20				
	Abundance	3.455 (0.065)			-0.189 (0.033)	1	0.097 (0.030)	1	-0.007 (0.002)	1	0.014 (0.003)	1				
Scrubland songbirds	Richness	2.549 (0.060)							0.006 (0.002)	1	-0.005 (0.002)	0.68				
	Abundance	3.362 (0.085)							0.020 (0.002)	1	-0.007 (0.003)	0.64				
Raptors	Richness	1.296 (0.116)							-0.005 (0.003)	0.34					0.174 (0.207)	0.18
	Abundance	0.382 (0.155)	0.209 (0.200)	0.27	0.151 (0.134)	1	-0.281 (0.144)	1	-0.014 (0.003)	1	0.014 (0.005)	1			0.145 (0.193)	0.20
Ground-nesting birds	Richness	0.037 (0.290)	0.044 (0.350)	1					-0.017 (0.005)	1	0.024 (0.012)	1				
	Abundance	-1.285 (0.386)	0.578 (0.502)	0.35	0.702 (0.148)	1	-0.320 (0.172)	1	-0.040 (0.008)	1	0.050 (0.015)	1				
Eurasian Thick-knee		-1.524 (0.241)							-0.027 (0.005)	1	0.017 (0.010)	0.62				
Little Bustard		-3.522 (0.931)	0.678 (0.779)	0.30	1.251 (0.207)	1	-1.050 (0.288)	1	-0.057 (0.016)	1	0.131 (0.048)	1				
Montagu's Harrier		-2.078 (0.380)			0.393 (0.240)	1	-0.568 (0.288)	1	-0.045 (0.007)	1	0.055 (0.019)					

of bird guilds, or reduced abundance of species of conservation concern. In contrast, we found some positive associations, albeit relatively weak, between management for small game and the abundance of some guilds that comprise several species of conservation concern. Results thus suggest that some of the management activities carried out within game estates may be beneficial at least for some species, although the magnitude of the effects was small.

We found a positive effect of game management for ground-nesting bird abundance (Table 4) and these could be related to predator control. Predation is an important cause of nest failure and chick survival for Red-legged Partridges, as well as for many other ground-nesting birds (Casas and Viñuela 2010, Magaña *et al.* 2010 and references therein, Mateo-Moriones *et al.* 2012). For this reason, on most game estates (including our study area, Methods and Beja *et al.* 2009) mammalian predator control is a common management practice to reduce predation pressure on game species. Although predator control is aimed at reducing predation on game species, it may also benefit other species, including ground-nesting birds, as controlled carnivore species frequently prey on nest and chicks of these avian species (Fletcher *et al.* 2010, Magaña *et al.* 2010, Hartway and Mills 2012). In this sense, a recent study suggested that Egyptian mongooses may be one of the main predators of ground nests in Mediterranean farmland (Beja *et al.* 2014), and this is one of the species most strictly controlled in game estates of southern Portugal (Beja *et al.* 2009). In contrast to the predation hypothesis, however, our results did not show a significant relationship between game management and abundance of either Eurasian Thick-knee, Little Bustard or Montagu's Harrier (all ground-nesting species). This may be because our sampling protocol was not accurate enough to detect differences for individual species, as differences between managed and unmanaged areas were overall small. Alternatively, this may suggest that the relationship between game management and abundance of the guild ground-nesting bird species is not related to predator control. This could indicate that game management is largely ineffective in reducing predator populations. For instance, there may have been movements of predators between managed and unmanaged areas (Towerton *et al.* 2011), and predator control may be compensated by the attraction of predators from neighbouring areas due to an increase in prey availability (Delibes-Mateos *et al.* 2007, Beja *et al.* 2009). Indeed, in our study, paired Game estates and Control areas (where predator control did not occur) were close (Figure 1), which may have resulted in a lack of marked differences in predator abundance paired managed and unmanaged areas.

As an alternative to the predation hypothesis, it is possible that positive effects on ground-nesting species were due to factors such as habitat management. For instance, the cultivation of game crops to provide cover and food for game birds (Reino *et al.* 2000) may be beneficial for a range of farmland species (Martínez 1994, Stoate *et al.* 2003, Sage *et al.* 2005, Moreira *et al.* 2012), such as the steppe-birds included in our ground-nesting guild. Moreover, management of game crops may include delaying crop harvesting to protect nests from destruction of partridges (Casas and Vinũela 2010), which would also favour other ground-nesting species (Morgado and Moreira 2000). Additionally, provision of food and water for small game may have benefitted these species (Gaudioso Lacasa *et al.* 2010, Estrada *et al.* 2012). In any case, these trends were only apparent when taking into account habitat differences, and the overall magnitude of the effect was small (Table 4). In summary, although we provide evidences of some benefits of game management for some farmland birds (ground-nesting steppe-birds), suggesting a potential positive effect of food provision or cultivation of game crops, further studies are required to confirm this finding.

Raptor abundance was also higher in areas managed for Game estates than in Control areas. This may be related to the higher availability in managed areas of small game species such as partridges and rabbits (Beja *et al.* 2009, Table 2), which are potential prey for the species considered in our guild (Valkama *et al.* 2005). However, and contrary to our expectation, we did not find an important positive effect of partridge or rabbit abundance on both richness and abundance of raptors in the best AIC_c models (Table 4). This suggests that other management tools, such as cultivation of game crops, could also favour higher abundance of raptors in Game estates, if there are better foraging grounds than other land uses, due to higher prey abundance or detectability (Janes 1985, Ferrer and Harte 1997, Ontiveros *et al.* 2005).

Although the observed higher abundance of raptors in game estates suggests that hunting management may benefit this guild, it should also be noted that it would be necessary to evaluate whether source-sink dynamics are occurring, and whether higher observed richness and abundance are not also hiding a higher mortality. In this sense, Beja *et al.* (2009) found in the same study area that the abundance of certain raptor species was less than that expected from habitat or prey availability in areas with higher density of gamekeepers, suggesting potential persecution of raptors. Something similar has been also observed in other studies conducted in northern Europe (Anderson *et al.* 2009). Therefore, more studies should be carried out to completely understand the global effect of game management on raptor species.

Finally, our results showed that habitat was the most important variable for explaining variation in richness and abundance of guilds and species. Vegetation structural heterogeneity is quite often related to abundance or richness of songbirds (Mönkkönen 1994, Reino *et al.* 2009, Castro *et al.* 2010, Concepción and Díaz 2011, Pickett and Siriwardena 2011). In this sense, we found a positive relationship between habitat structural simplicity (large treeless areas, having only herbaceous or dwarf shrub cover) and farmland songbirds, but negative with scrubland songbirds. Also, abundance and richness of other guilds, and abundance of the three species of conservation concern, were explained by habitat, and were higher where habitat structural simplicity was more widespread. This is not surprising since many of the species observed during the surveys mainly occupy large areas of treeless and extensive cereal cultivation known as 'cereal pseudosteppes' (Suárez *et al.* 1997, Traba *et al.* 2007). In addition, these species generally avoid nesting in, or close to, tall or thick vegetation, which may favour higher abundances of generalist predators (Reino *et al.* 2009, 2010a,b, Červinka *et al.* 2011).

Conclusions

Broadly, our results suggest that low-intensity management actions directed at small game in the Iberian Peninsula do not seem to detrimentally affect any of the species or guilds studied, while it may have positive effects (albeit weak) on other species. Our findings are in agreement with those shown in earlier studies in Portugal (Borralho *et al.* 1998, Stoate *et al.* 2000) and elsewhere in Europe (Stoate and Szczur 2001, Mustin *et al.* 2011). This indicates that there is a potential for shared benefits and common objectives among hunters and those generally interested in wildlife conservation (Knezevic 2009), and that there are possibilities for developing management systems that specifically maximise both hunting sustainability and conservation value of managed areas.

With our data it was not possible to differentiate which management activities had higher (positive) impact on non-game species, and so there is a need to further investigate the consequences of specific game management on biodiversity, at both the local and landscape scales. However, the fact that our results showed that habitat variables were more important than game management for all guilds suggests that habitat improvement and maintenance of sustainable game populations is possibly the basis for the most long-term and large-scale benefits of hunting on bird conservation. Game management has resulted at times in improvements of habitat quality that have benefited directly (through increasing productivity or breeding success) and indirectly (improving or increasing their foraging and nesting habitats) other bird species (Chiverton and Sotherton 1991, Tharme *et al.* 2001, Sage *et al.* 2005). Additionally, the more common explanation for declines in many farmland bird populations, including game ones like the Red-legged Partridge, is habitat change, in the form of degradation, fragmentation or destruction (Donald *et al.* 2006, Reino *et al.* 2009). Therefore, management for game that leads to better habitat quality, associated with sustainable harvest strategies, could result in areas that have large conservation value (e.g. Robertson *et al.* 2001). In these cases, the maintenance of hunting would provide great opportunities to maintain the viability of these high-quality habitats, thus contributing to the conservation of farmland bird species.

Supplementary Material

The supplementary materials referred to in this article can be found at journals.cambridge.org/bci

Acknowledgements

This study was funded by the Portuguese Foundation for Science and Technology (FCT) (PRAXIS/C/AGR/11062/1998) and by the European Commission under the 7th Framework Programme for Research and Technological Development through the project HUNT (212160, FP7-ENV-2007-1), and contributes to the project CGL2009-13029 from the Spanish Ministry of Science. J.C. had postdoctoral contract jointly financed by the ESF and by the Junta de Comunidades de Castilla-La Mancha (JCCM, Spain), in the framework of the Operational Programme FSE 20072013; AE has a postdoctoral contract funded by the project BIODIVERSA/0003/2011; LR and LG were funded by FCT through grants SFRH/BPD/62865/2009 and SFRH/BD/64645/2009, respectively; and MDM was supported by a JAE-doc contract (Programa Junta Para la Ampliación de Estudios), funded by CSIC and the European Social Fund. We thank the staff of ERENA, SA the Centre for Applied Ecology 'Baeta Neves' (Instituto Superior de Agronomia) and the Centre for Environmental Biology (Lisbon Faculty of Science) for collaboration in the development of the Project. We thank landowners and game managers who allowed access to their property and their willingness to provide information on their game management practices. Finally we thank Mario Díaz, José Tella, Phil Atkinson and an anonymous referee for constructive comments on the manuscript.

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Received 28 May 2013; revision accepted 15 January 2014;
Published online 8 October 2014