Grazing improves habitat suitability for many ground foraging birds in Mediterranean wooded grasslands

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Abstract

Wooded grasslands, usually grazed, cover vast areas in Southern Europe and Northern Africa. They host rich resident bird communities and, in winter, receive large numbers of migrants from Central and Northern European woodlands. Many species are partly or entirely dependent on ground foraging, and since in winter food is often the most limiting factor for birds, maintaining suitable ground habitat is crucial.

To study how grazing influences suitability of winter ground habitat for birds, we carried out an experiment in a wooded grassland in Southern Iberia, whereby grazing was controlled in 12 purposely fenced two-hectare plots (4 x 15 sheep/ha, 4 x 3 sheep/ha and 4 x no grazing). We quantified ground habitat features, food abundance and intensity of use by ground-foraging birds in each of these 12 plots. In addition, we made focal observations of birds feeding on the ground and compared the habitat of $1m^2$ foraging patches with those of nearby control patches.

We found that virtually all birds prefer to forage in patches with short ground vegetation and high food abundance. Measurements of these parameters in the experimental plots showed that while grazing shortens vegetation it decreases food availability, and thus has opposing effects on important determinants of habitat suitability. Nevertheless, the numbers of birds foraging in the plots indicate that, overall, grazing benefits the assemblage of ground-feeding birds, presumably because for most species the advantages of foraging in less cluttered habitats more than compensate the lower abundance of prey. However, arboreal bird species that make short foraging forays to the ground had lower numbers in grazed plots.

Most bird species that forage on the ground benefited from grazing, and although they can forage under a broad range of grazing levels, some showed clear preferences along the gradient of grazing intensity. Such preferences should be taken into consideration by managers. In general, grazing

should be maintained at a level sufficient to open up ground vegetation, increasing the area occupied by patches of short vegetation, in which almost all bird species prefer to forage. At moderate levels, grazing is thus a valuable management tool to promote winter bird habitat quality in Mediterranean wooded grasslands, while increasing the economic value of these threatened landscapes.

Highlights

- Birds select to feed in ground patches with short vegetation and abundant prey
- Grazing improved foraging habitat, but decreased prey abundance
- Most species benefited from grazing, but a few were negatively affected by heavy grazing
- Grazing should be kept at levels sufficient to shorten and open up ground vegetation
- Moderate grazing results in best overall habitat for wintering ground-foraging birds

Keywords

Wooded pastures; Grazing impact; Ground-foraging birds; Landscape management; Conservation; Agroecosystems

1. Introduction

Wooded grasslands, characterized by a usually well-developed herb layer associated with tree cover of variable composition and density, cover vast areas in the Western Palearctic and often host a rich biodiversity (Plieninger *et al.*, 2015; Centeri *et al.*, 2016). Grazing may have been of great importance shaping Palearctic ecosystems (e.g. Bradshaw *et al.*, 2003; Dengler *et al.*, 2014), which were once populated by a rich fauna of wild large herbivores, such as bison, aurochs, wild horses, mammoths and rhinoceros (Blondel *et al.*, 2010). Humans drove most of them to extinction and vegetation structure is now greatly driven by human activities (Barnosky *et al.*, 2004; Blondel *et al.*, 2010). In these new anthropogenic ecosystems, domestic grazers play some of the roles of the original herbivores (Vera, 2000), particularly at the level of the ground vegetation. Wooded grasslands often host rich bird assemblages that include many ground-foraging species. Such species that once relied on wild herbivores to maintain areas with ground cover suitable for foraging may now be mostly dependent on grazing by domestic ungulates, however, the impacts of this activity on birds and other wildlife are highly variable and still poorly understood (Schieltz and Rubenstein, 2016).

From Iberia to the Balkans, Southern Europe hosts important areas of different types of wooded grasslands (Plieninger *et al.*, 2015; Centeri *et al.*, 2016), some of which are also present in the North African Maghreb. They all harbor rich resident bird assemblages (e.g. Hartel *et al.*, 2014; Correia *et al.*, 2015; Catarino *et al.*, 2016) and, during the winter, receive a large proportion of the populations of migratory bird species nesting in central and northern Europe (e.g. Díaz *et al.*, 1997; Tellería, 2001; Leal *et al.*, 2011; Arizaga *et al.*, 2012). Food availability tends to be particularly low during winter, when food acquisition is often the most important constraint for birds (Hutto, 1985). Since many species wintering in the grazed wooded grasslands of southern Europe are partially dependent on food collected on the ground (e.g. Cramp and Perrins, 2006), it is critical to manage grazing pressure to maintain suitable ground foraging habitats. In the absence of grazing or artificial maintenance, their usually well-developed herb layer can be progressively replaced by scrub vegetation. In the western Mediterranean, both in Europe and Northern Africa, the most extensive of these wooded grasslands have a tree cover dominated by cork and holm oaks. In Portugal and Spain, these wooded grasslands, which are often also used for low-intensity agriculture, are considered as an agro-silvo-pastoral system known as *Montado* or *Dehesa*, respectively, and are recognized by their high economic value and rich biodiversity (e.g. Pinto-

Correia *et al.*, 2011; Leal *et al.*, 2016; Moreno *et al.*, 2016). This resulted in their classification as High Nature Value Farmlands (HNVF) (Hoogeveen *et al.*, 2004) and inclusion in the Annex I of the European Union (EU) Habitats Directive (92/43/CEE). Traditionally, these wooded grasslands have been mainly grazed by sheep (Moreno and Pulido, 2009; López-Sánchez *et al.*, 2016), but management practices are changing rapidly in response to ecological and economic pressures. For example, EU policies of financial incentives have led to an increase in stocking rates and a progressive replacement of sheep by cattle (Moreno and Pulido, 2009; Bugalho *et al.*, 2011).

Not only does grazing decrease vegetation height (Vickery *et al.*, 2001), but it can also influence spatial heterogeneity and plant species composition (Putman *et al.*, 1991; Adler *et al.*, 2001; Bugalho *et al.*, 2011). These can, in turn, influence nutrient distribution (Haynes and Williams, 1993; Dahlgren *et al.*, 1997; Peco *et al.*, 2017) and invertebrate abundance (e.g. Gibson *et al.*, 1992; Vickery *et al.*, 2001; Batáry *et al.*, 2007; Dennis *et al.*, 2008). However, access to prey can be just as important for birds as prey abundance (Buckingham and Peach, 2005), and grazing may also influence this parameter through its effect on vegetation height and density (Fuller and Gough, 1999). This is very important for ground-foraging birds because they may struggle to find and capture food in dense ground cover or even avoid it altogether to minimize predation risk (Buckingham and Peach, 2005).

Since many of the birds wintering in Southern European wooded grasslands feed on the ground, and ground cover depends on grazing, it is important to evaluate how grazing should be managed to maintain adequate foraging conditions for birds. However, information to guide management is very scarce and is mostly based on studies done in temperate grasslands of central and northern Europe (e.g. Buckingham and Peach, 2005; Buckingham *et al.*, 2006; Evans *et al.*, 2006; Hartel *et al.*, 2014) where conditions are potentially very different from those prevailing in their southern wooded counterparts. Moreover, even in those better studied regions virtually all existing information has been obtained during the nesting season and there is little information for the winter (e.g. Perkins *et al.*, 2000; Moreira *et al.*, 2005).

Birds choose feeding sites at different spatial scales. First at the landscape level, which results in the choice of a particular foraging habitat and then at the microhabitat level, selecting the exact location of feeding patches (Hutto, 1985). For ground-foraging birds in grasslands, the availability of high-quality ground feeding patches is critical. The overall objective of this study was to investigate how grazing affects wintering bird species feeding on the ground in Mediterranean wooded grasslands, thus contributing to the knowledge required for a science-based management of these valuable ecosystems. We predicted that (i) feeding patch preferences would vary among bird species, (ii) grazing would affect ground-level habitat structure and prey availability, (iii) and that, as a consequence, grazing would influence the abundance of birds feeding on the ground. We discuss the implications of our findings for the management of Mediterranean wooded grasslands.

2. Methods

2.1 Study area and experimental design

This study was carried out in Portugal, in "*Herdade do Freixo do Meio*" (38º 42´12''N, -8º 19´29'' W). This is a large organic farm that covers 650 ha and is dominated by cork and holm oak (*Quercus suber* and *Q. rotundifolia*) woodlands and small olive groves. The ground cover is mostly composed of grasses and forbs, and grazed by cattle, sheep, goats and pigs. We collected data on bird use and habitat variables at two scales: a plot-scale involving measurements in large (2 ha) experimental plots, and a patch-scale based on measurements made in 1m^2 patches and nearby controls, within the same experimental plots.

We manipulated grazing intensity in 12 experimental plots separated by electric fences, in a mixed cork and holm oak woodland. The plots were roughly homogeneous in terms of soil type and ground cover and avoided the proximity of water courses; tree density varied somewhat across the study area, but we made an effort to balance the representation of the different tree densities in the three grazing levels (Figure 1). In this system, a grazing pressure of three sheep per hectare is generally considered sustainable (Olea and San Miguel-Ayanz, 2006). Therefore, four plots were continuously grazed by six sheep (Light Grazing), four plots were grazed by 30 sheep (Heavy Grazing) and four plots were left without sheep (Not Grazed). According to local farmers these density treatments are representative of sheep densities in the study region. The sheep were placed in the plots in December 2010 and remained there until data collection was completed at the end of February 2012, except around the shearing period. Water was made available in all plots throughout the study. During the peak of the long and dry summer bales of straw were provided. Prior to the establishment of the experimental plots the entire study area was used for sheep grazing.

2.2. Choice of ground foraging sites at the patch-scale

To locate foraging patches, the area within each experimental plot was scanned for birds on the ground during January and February 2012. We did this by walking during the morning along a zig-zag route within each plot, avoiding its edges. Search effort was equal across the three treatment levels, and proximity between plots guaranteed that they were equally available to all birds in the study area. When a bird was detected foraging, we characterized the patch by measuring several habitat variables, as described in Table 1, within a 1m^2 quadrat centered on the location of the bird. The abundance of invertebrates in these foraging patches was estimated using quadrat counts (Samways *et al.*, 2010). A square frame delimiting an area of 0.5 m^2 was placed on the ground minimizing disturbance and trampling by the observer. We then searched the quadrat for surface or sward active invertebrates during a standardized period of one minute. Invertebrates were identified to order level. All these variables were also quantified within two 1m^2 control patches, located 5 m to the north and south of each foraging patch. In the case of flocks, the first bird observed was chosen for the characterization of foraging patches. Invertebrate abundance was not used to model chaffinch (*Fringilla coelebs*) habitat selection, because in the winter it mainly eats seeds (Cramp and Perrins, 2006).

To determine the set of microhabitat variables that influenced the choice of ground foraging patch by each bird species within its activity area, we used conditional paired logistic regression (Clogit model). We paired each foraging patch with the two corresponding controls. This paired technique is suitable to model choices that individual birds are making at the microhabitat scale (Compton *et al.*, 2002). Variables with Spearman correlation values > 0.7 were excluded from the modelling procedure, retaining the variable with potentially greater biological relevance (Tabachnick and Fidell, 1996; Hosmer and Lemeshow, 2000). Further preliminary reduction of predictor variables was performed with univariate modelling, eliminating those variables with $p > 0.25$. Finally, a model was constructed for each species using a backward stepwise method, retaining the models with the lowest AIC (*Akaike Information Criterion*). Model fit was evaluated using the area under the ROC curves (AUC, *Area under the Receiver Operating Characteristics curve*) (Pearce and Ferrier, 2000).

Table 1. Variables and methods used for the characterization of bird foraging patches and experimental plots.

Variable	Methodology	Range	Patch/Plot
Distance to tree	Distance of center of patch to the nearest tree (m)	0 - 17	Patch
Dung	Count of the number of dung pellets within a $1m^2$ quadrat	0 - 109	Patch/Plot
Leaf litter	Point interception method using a meter long 11-pin frame placed along the two diagonals of each quadrat (Bråthen and Hagberg, 2004) (%)	0 - 100	Patch/Plot
Bare ground	Point interception method using a meter long 11-pin frame placed along the two diagonals of each quadrat (Bråthen and Hagberg, 2004) (%)	0 - 100	Patch/Plot
Overturned soil	Visual estimation of the percentage of soil that was disturbed by wild boars or domestic pigs when searching for food in a $1m^2$ quadrat	0 - 100	Patch/Plot
Ground vegetation	Median herb layer height (cm) measured with a vertical ruler within a $1m^2$ quadrat, excluding emergent swards	0 - 24	Patch/Plot

2.3 Effect of grazing on the structure of ground habitat and prey availability

To characterize the influence of grazing on the structure of ground habitat, we used 30 $1m^2$ quadrats, placed five meters apart along a diagonal of each of the 12 plots. In each quadrat, we measured several habitat variables as described in Table 1.

To evaluate the effects of grazing on prey availability, we sampled epigeal invertebrates using pitfall traps (Ø 9.5 cm, filled with water, biodegradable detergent and salt) (Topping and Sunderland, 1992; Samways *et al.*, 2010). Each plot was sampled at three sites with five traps each. Traps were set forming a one square meter quadrat with one trap at the center, and placed in flat terrain, avoiding tree canopies. Traps were left open for two weeks, and the arthropods collected were preserved in 70º alcohol with glycerin. Specimens with a body length greater than 2 mm were identified to order level.

We only included in the analyses taxa known to be regularly consumed by farmland birds across Europe (Cramp and Perrins, 2006; Holland *et al.*, 2006). All data on habitat structure and prey availability were collected during January and February 2012, 13 to 14 months after the sheep were placed in the experimental plots.

The effect of grazing on habitat variables and prey availability was tested with generalized linear models (GLM). Each of the three grazing levels was represented in this test by four replicates (plots). Variables expressed as percentages were logit transformed prior to analysis to approximate normality. We assumed a Poisson error structure for the variables expressed as counts and a Gaussian error structure for all the remaining variables.

2.4 Association between grazing and number of birds foraging on the ground at the plot-scale

We estimated the use of each experimental plot by counting birds foraging on the ground along a series of parallel line transects, separated by 25 m and avoiding the edge of the plot. The length and number of individual parallel transects in each plot varied because of constraints imposed by the different shapes of plots, but they always totaled 600 m. These counts were repeated 16 times in each plot, between sunrise and 11:00, alternating sampling times across plots to minimize potential biases due to time-of-day (Palmeirim and Rabaça, 1994). The transect was only 2x25m wide because birds foraging on the ground can be difficult to spot in dense ground cover unless they flee from the observer (Buckingham *et al.*, 2006). However, all birds detected within the transect were registered independently of their distance to the observer. The objective of this sampling strategy was to obtain indexes of relative abundance, rather than estimates of density. The association between grazing intensity and the use by the most common ground-foraging bird species was assessed with GLMs, using four replicated plots for each of the three grazing levels. We also used GLMs to test if the numbers of birds were influenced by the average ground vegetation height and invertebrate abundance in the sampled plots. Since the three tit species present in the study area have similar environmental and feeding needs (Cramp 1998), for this analysis, we pooled their data to increase sample size.

Clogit modelling was carried out using package Survival (Therneau and Lumley, 2017), and the remaining statistical computations in Deducer (Fellows, 2012) in the R environment (R Development Core Team, 2015).

3 Results

3.1 Determinants of choice of ground foraging sites at the patch-scale

We obtained data on the structure of ground habitat and prey abundance from 270 foraging patches of 17 bird species and 540 control patches. However, for this analysis, we only considered species for which we had data from a minimum of 20 foraging patches: meadow pipit, robin, chaffinch, white wagtail and chiffchaff (Table 2).

Results of the final Clogit models, assessing the importance of habitat variables and prey availability on the choice of foraging habitat at the patch-scale, are shown in Table 2. Height of the vegetation was the only factor that was present in virtually all final species' models, in all cases with a negative coefficient. Number of invertebrates had a positive influence on all insectivorous species. Distance to trees had a positive effect for the white wagtail, but a negative one for the chiffchaff.

Table 2. Final Clogit models for bird species at the foraging patch-scale, including the Area Under the ROC curve (AUC), the coefficients of variables in the models and corresponding standard errors (SE) (*p < 0.05, **p < 0.01, ***p < 0.001).

	AUC	Coefficient	SE (Coef)	Z value	p-value	
Chaffinch *Fringilla coelebs*						
Vegetation	0.67	-0.37	0.14	-2.72	0.00	**
Chiffchaff *Phylloscopus collybita*						
Distance to tree	0.85	-0.55	0.19	-2.87	0.00	**
Invertebrates		0.65	0.36	1.79	0.07	.
Vegetation		-0.22	0.12	-1.86	0.03	*
Meadow pipit *Anthus pratensis*						
Invertebrates	0.66	1.08	0.43	2.54	0.01	*
Robin *Erithacus rubecula*						
Invertebrates		1.07	0.46	2.33	0.02	*
Vegetation	0.85	-0.65	0.16	-4.01	0.00	***
Overturned soil		0.06	0.04	1.75	0.08	.
White-wagtail *Motacilla alba*						
Distance to tree		0.43	0.15	2.79	0.01	**
Invertebrates		1.02	0.46	2.21	0.03	*
Vegetation	0.87	-0.73	0.32	-2.27	0.02	*
Dung pellets		0.02	0.02	1.29	0.20	

3.2 Effect of grazing on the structure of ground habitat and prey availability

GLMs revealed a significant influence of grazing on all measured ground habitat variables ($p < 0.05$). Grazing increased the abundance of dung pellets, the proportion of bare ground and of ground mostly covered by leaf litter. However, it greatly decreased vegetation height (mean ground vegetation height in ungrazed plots was 8.4 cm and in the heavily grazed plots just 1.5 cm). Percentage of soil overturned by wild boars and domestic pigs was lower in grazed areas, presumably because the vegetation in ungrazed areas provided better cover for these animals (Figure 2). We captured 1371 invertebrates >2mm, of which 479 belonged to taxa known to be consumed by birds in European farmland. Ungrazed control plots had more captures of invertebrates than grazed areas (Figure 2).

Since the Clogit models showed that ground vegetation height is the single most import factor determining choice of feeding patches by birds (Table 2), we compared the vegetation heights in those patches used by each species with the heights available in the three studied levels of grazing (Figure 3). It is evident that, overall, grazing increases the availability of the vegetation height class most often used by the focal species (from 1 to 4 cm, the 25 and 75 % quartiles of the use by all species, Figure 3). In the ungrazed plots, 75 % of the vegetation is taller than that preferred by any of the species when foraging on the ground. Under light grazing, this value is reduced to 53 % and is virtually 0 % in heavily grazed areas.

3.3 Association between grazing and number of birds foraging on the ground at the plot-scale

A total of 1 113 birds of 21 species were observed in the control and treatment plots (335 individuals of 15 species in ungrazed plots, 382 individuals of 17 species in lightly grazed and 396 individuals of 18 species in heavily grazed plots (Appendix 1)). Only the eight species with more than 30 observations were used in analyses (Figure 4). For five of these species there was a statistically significant association between grazing and the numbers of individuals feeding on the ground. White wagtail, robin and chaffinch were more abundant in grazed plots, whereas blue tit and great tit were more abundant in ungrazed areas. Goldfinch, chiffchaff and meadow pipit did not show a clear response to grazing intensity.

Vegetation height and invertebrate abundance were particularly important predictors of habitat selection by birds at the patch-scale, therefore we also evaluated the importance of these variables at the plot-scale. Plots with low average vegetation height tended to be more used by chaffinch ($p=0.03$), white wagtail (p=0.004) and robin (nearly significant, p=0.07), but less used by tits (p=0.002). Chaffinch and robin used more frequently plots with low average invertebrate abundance (p=0.03 and p=0.04, respectively).

4 Discussion

4.1 At the patch-scale choice of foraging sites is mostly determined by vegetation height and arthropod abundance

The analysis of foraging-patch selection showed that, when foraging on the ground, all studied bird species select areas with specific characteristics. These characteristics varied from species to species but two were important for most of them: invertebrate abundance and vegetation height. Patches with greater invertebrate abundance than controls were selected by all insectivorous species. This is to be expected because food acquisition is a major constraint for wintering birds (Hutto, 1985). Vegetation height is also of general importance and, with the exception of the Meadow pipit, all species foraged in patches where the vegetation was shorter than the local average. This preference for patches with short ground vegetation may be explained by an easier access to prey and reduced predation risk. In fact, it has been shown that in patches with short vegetation both granivorous and insectivorous birds locate food items more efficiently (Butler and Gillings, 2004) and the detection of approaching predators tends to be easier (Devereux *et al.*, 2004; Whittingham and Evans, 2004). Moreover, if the perceived predation risk is lower, birds can spend less time in surveillance and thus increase their intake rates (e.g. Whittingham *et al.*, 2004; Whittingham and Evans, 2004). It has been experimentally demonstrated for ground foraging birds that taller vegetation decreases patch profitability (Powolny *et al.*, 2015).

4.2 Grazing influences the structure of ground habitat and prey availability

Our analysis shows that the selection of ground foraging sites by birds in Mediterranean wooded grasslands is greatly influenced by the characteristics of ground habitat. The comparison of ground habitat structure across the three treatments shows that grazing has a major impact on some of those characteristics, such as vegetation height and invertebrate abundance.

Our pitfall capture data show a significant, but relatively small, decrease of invertebrate abundance with grazing. Other studies have reported declines of invertebrates with grazing (e.g. East and Pottinger, 1983; Morris, 2000; van Klink *et al.*, 2015). However, it is important to note that the decrease that we report is probably substantially underestimated because of known biases of pitfall trapping (Greenslade, 1964). In fact, captures depend not only on the abundance of invertebrates, but also on trappability (Melbourne, 1999) which is known to be greater in the shorter and sparser vegetation of more intensely grazed areas (Greenslade, 1964; Melbourne, 1999). This bias may thus inflate the apparent abundance of invertebrates in grazed areas. In contrast with the negative impact on most invertebrates, grazing can facilitate the occurrence of coprophagous insects (Vickery *et al.*, 2001; Jay-Robert *et al.*, 2008).

Finally, it is important to note that, although in general the impact of grazing on vegetation features increased progressively along the three grazing intensities, the differences between ungrazed and lightly grazed areas tended to be less accentuated than those between lightly grazed and heavily grazed regimes. This suggests that the impact of light grazing on habitat is comparatively less pronounced.

4.3 Grazing is associated with the numbers of birds feeding on the ground

The studied grasslands are typical of managed Mediterranean oak landscapes and have a fairly high density of trees. Therefore, the majority of birds observed feeding on the ground are woodland species, such as robin, chaffinch, chiffchaff and tits, which tend to spend much of their time on trees (Ceia and Ramos, 2014; Pereira *et al.*, 2014). Nevertheless, at least during winter, many species obtain much of their food on the ground (Cramp and Perrins, 2006), and we found that grazing was associated with the number of birds feeding in this stratum. However, the strength and direction of this association differed between species.

Three species showed a statistically significant positive association with grazing: chaffinch, robin and white wagtail. These birds search for food (seeds or invertebrates) on the ground surface or swards while walking or hopping on the ground. They may thus benefit from the opening up of the ground layer by grazers that facilitates the mobility of birds and increases prey and seed visibility. Moreover, sparser vegetation allows greater visibility for birds while on the ground, and thus decreases their investment in vigilance against predators (e.g. Whittingham *et al.*, 2004). For this group of species, such advantages more than compensate the lower abundance of food caused by grazing. Grazing may reduce not only the abundance of invertebrates but also of seeds (Bertiller, 1996; Sternberg *et al.*, 2003), and this should be relevant for the chaffinch and other seedeaters. However, we did not sample seed availability because granivorous species were a small proportion of the birds feeding on the ground in the wooded grasslands that we studied. The most extreme example in this group is the white wagtail, a ground bird that searches for prey while walking and running (Cramp and Perrins, 2006), and thus benefits greatly from the reduction of obstacles resulting from grazing. Studies conducted in other habitats have also reported a positive influence of grazing on various ground-foraging birds, both through the shortening of ground vegetation and the creation of areas of bare ground (e.g. Atkinson *et al.*, 2004; Buckingham *et al.*, 2006; Schaub *et al.*, 2010).

Only two species were negatively associated with grazing, blue tit and great tit. They are both predominantly arboreal gleaners that make forays to feed on the herb layer or soil (Cramp and Perrins, 2006). They made little use of heavily grazed areas, where prey tend to be scarcer. Finally, there are also species that seem to be unaffected by grazing, such as goldfinch chiffchaff and meadow pipit. However, this lack of a significant effect may also be due to the relatively small number of plot-scale replicates; more replicates would presumably result in significant effects for a greater number of species.

The greater usage of plots with short average vegetation by most birds is in line with the observed preference for foraging in patches with short vegetation. However, the results of the two scales did not match in the case of invertebrate abundance, as some species were more abundant in plots with fewer invertebrates. We suggest that this is explained by a dominant role of vegetation height in the selection of foraging habitat; the higher number of birds in plots with low invertebrate abundance is due to a preference to forage in plots with low average vegetation height, which tend to have fewer invertebrates. However, it is worth noting that, within those plots, they chose patches with more invertebrates.

Our results suggest that, during winter, Mediterranean wooded grasslands are important for both resident and migratory bird species that forage on surface or sward-dwelling invertebrates, and that they tend to benefit from grazing because it decreases ground clutter. The generalized use of these grasslands by such species in winter contrasts with the situation in grasslands further north, mostly used in this season by birds that feed on soil-dwelling invertebrates (Perkins *et al.*, 2000; Buckingham *et al.*, 2006).

4.4 Conclusions and management implications

In the studied Mediterranean wooded grasslands grazing has opposing impacts on two very important determinants of the suitability for most birds foraging on the ground: it decreases vegetation height and density, which is beneficial, but reduces the abundance of food. Differences in the way species respond to this trade-off are likely to explain variations in the impact of grazing on birds. In line with this hypothesis, our patch and plot level analyses indicate that, overall, grazing benefits the assemblage of birds that feed on the ground, presumably because for most species the advantages of foraging in less cluttered habitats more than compensate the lower abundance of prey. However, arboreal bird species that make short foraging forays to the ground have lower numbers in grazed plots. The response of birds to grazing is not homogeneous and is influenced by the foraging strategy of each species.

Our results indicate that it is not possible to identify a single level of grazing that benefits all bird species. However, we can suggest a number of management options that, with the necessary adjustments to the specific area and type of livestock, may be useful for decision makers involved in management.

(1) Most birds are flexible and able to forage in all levels of grazing, even though some have clear preferences along the gradient of grazing intensity. However, there were comparatively few birds foraging in ungrazed areas, and none of the species had a clear preference for them. Therefore, keeping Mediterranean wooded grasslands ungrazed results in a loss of economic value of these ecosystems without any significant conservation benefit, at least for birds that forage on the ground. In the long term, eliminating grazing results in scrub encroachment which changes bird assemblages substantially, as shown in previous studies (Rabaça, 1990; Nikolov *et al.*, 2011; Santana *et al.*, 2012; Listopad *et al.*, 2018).

(2) Moderate grazing by sheep and presumably other domestic ungulates, at a level considered sustainable in the studied system (Olea and San Miguel-Ayanz, 2006), does not have negative impacts on any of the focal species, and results in the best overall habitat for the assemblage of birds that forage on the ground. Grazing should be maintained at a level sufficient to open up ground vegetation, increasing the area occupied by patches of short vegetation, in which almost all bird species prefer to forage. This is important during the winter, but it is likely to be even more important in the early spring, when higher temperatures result in fast growth of the herb layer (Buckingham and Peach, 2005).

(3) Heavy grazing (15 sheep per ha) greatly increases the availability of vegetation heights preferred by most birds, but it is probably only better than light grazing for insectivorous specialist ground foragers, or for species that feed on coprophagous invertebrates. Moreover, grazing with a very high impact on ground vegetation makes it unsuitable for foraging by some bird species, and is likely to affect other components of the ecosystem, such as tree recruitment (Carmona *et al.*, 2013; López-Sánchez *et al.*, 2016), so it should only be prescribed for specific situations.

In Mediterranean wooded grasslands most ground foraging birds benefit from grazing by domestic ungulates, which partly replace the ecological functions once fulfilled by wild ungulates, many of which are now extinct. It is thus evident that well-managed grazing is a potentially important tool to maintain the high biodiversity value of these grasslands. For birds that forage on the ground in winter, and considering that the preferences of species vary, our results support fostering mosaics of variable grazing intensity. The optimal representation of grazing intensities in such mosaics depends on conservation priorities, but when the target of conservation is the overall species assemblage then a gradient of different levels of moderate grazing should be maintained. Birds are just one of the many values to consider in the definition of grazing strategies, particularly in ecologically rich systems, such as Mediterranean wooded grasslands. More research is needed to better understand the effects of grazing at different times of the year and on other taxa (Schieltz and Rubenstein, 2016). Nevertheless, our results are reassuring evidence that, at moderate levels, this economically important activity is compatible with the preservation of bird biodiversity in wooded grasslands.

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6. References

Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128, 465-479.
Arizaga, J., Diez, E., Aranguren, I., Asenjo, I., Cuadrado, J.F., Elosegi, Z., Goikoetxea, J., Herrero, A., Jauregi, J.I., Mendiburu, A., Sanchez, J.M., 2012. Wintering survival of insect-eating passerines in southern Europe. Bird Study 59, 37-42.
Atkinson, P.W., Buckingham, D., Morris, A.J., 2004. What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? Ibis 146, 99-107.
Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. Science 306, 70-75.
Batáry, P., Orci, K.M., Báldi, A., Kleijn, D., Kisbenedek, T., Erdős, S., 2007. Effects of local and landscape scale and cattle grazing intensity on Orthoptera assemblages of the Hungarian Great Plain. Basic Appl. Ecol. 8, 280-290.
Bertiller, M.B., 1996. Grazing effects on sustainable semiarid rangelands in Patagonia: The state and dynamics of the soil seed bank. Environ. Manag. 20, 123-132.
Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G., 2010. The Mediterranean region: Biological diversity in space and time. Oxford University Press, Oxford.
Bradshaw, R.H., Hannon, G.E., Lister, A.M., 2003. A long-term perspective on ungulate–vegetation interactions. For. Ecol. Manag. 181, 267-280.
Bråthen, K.A., Hagberg, O., 2004. More efficient estimation of plant biomass. J. Veg. Sci. 15, 653-660.
Buckingham, D., Peach, W., 2005. The influence of livestock management on habitat quality for farmland birds. Anim. Sci. 81, 199-203.
Buckingham, D.L., Peach, W.J., Fox, D.S., 2006. Effects of agricultural management on the use of lowland grassland by foraging birds. Agric. Ecosyst. Environ. 112, 21-40.

Bugalho, M.N., Lecomte, X., Gonçalves, M., Caldeira, M.C., Branco, M., 2011. Establishing grazing and grazing-excluded patches increases plant and invertebrate diversity in a Mediterranean oak woodland. For. Ecol. Manag. 261, 2133-2139.

Butler, S.J., Gillings, S., 2004. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. Ibis 146, 123-130.

Carmona, C.P., Azcárate, F.M., Oteros-Rozas, E., González, J.A., Peco, B., 2013. Assessing the effects of seasonal grazing on holm oak regeneration: Implications for the conservation of Mediterranean dehesas. Biol. Conserv. 159, 240-247.

Catarino, L., Godinho, C., Pereira, P., Luís, A., Rabaça, J.E., 2016. Can birds play a role as High Nature Value indicators of montado system? Agrofor. Syst. 90, 45-56.

Ceia, R., Ramos, J., 2014. Birds as predators of cork and holm oak pests. Agrofor. Syst., 1-18.

Centeri, C., Renes, H., Roth, M., Kruse, A., Eiter, S., Kapfer, J., Santoro, A., Agnoletti, M., Emanueli, F., Sigura, M., 2016. Wooded grasslands as part of the European agricultural heritage. Biocultural Diversity in Europe. Springer, pp. 75-103.

Compton, B.W., Rhymer, J.M., McCollough, M., 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83, 833-843.

Correia, R.A., Franco, A.M.A., Palmeirim, J.M., 2015. Role of the Mediterranean Sea in differentiating European and North African woodland bird assemblages. Community Ecol. 16, 106-114.

Cramp, S., Perrins, C.M., 2006. Birds of the Western Palearctic interactive. BirdGuides, UK., Oxford.

Dahlgren, R.A., Singer, M.J., Huang, X., 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. Biogeochemistry 39, 45-64.

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment 182, 1-14.

Dennis, P., Skartveit, J., McCracken, D.I., Pakeman, R.J., Beaton, K., Kunaver, A., Evans, D.M., 2008. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. J. Appl. Ecol. 45, 279-287.

Devereux, C.L., Mckeever, C.U., Benton, T.G., Whittingham, M.J., 2004. The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. Ibis 146, 115-122.

Díaz, M., Campos, P., Pulido, F.J., 1997. The Spanish dehesas: a diversity in land-use and wildlife. In: Pain, D.J., Pienkowski, M.W. (Eds.), Farming and birds in Europe. The Common Agricultural Policy and its implications for bird conservation. Academic Press, London, pp. 178-209.

Evans, D.M., Redpath, S.M., Evans, S.A., Elston, D.A., Gardner, C.J., Dennis, P., Pakeman, R.J., 2006. Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. Biology Letters 2, 636-638.

Fellows, I., 2012. Deducer: a data analysis GUI for R. Journal of statistical Software 49, 1-15.

Fuller, R.J., Gough, S.J., 1999. Changes in sheep numbers in Britain: implications for bird populations. Biol. Conserv. 91, 73-89.

Gibson, C., Hambler, C., Brown, V., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. J. Appl. Ecol., 132-142.

Greenslade, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol. 33, 301-310.

Hartel, T., Hanspach, J., Abson, D.J., Máthé, O., Moga, C.I., Fischer, J., 2014. Bird communities in traditional wood-pastures with changing management in Eastern Europe. Basic Appl. Ecol. 15, 385-395.

Haynes, R.J., Williams, P.H., 1993. Nutrient cycling and soil fertility in the grazed pasture ecosystem. In: Sparks, D.L. (Ed.), Adv. Agron. Academic Press, pp. 119-199.

Holland, J., Hutchison, M., Smith, B., Aebischer, N., 2006. A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. Ann. Appl. Biol. 148, 49-71.

Hoogeveen, Y., Petersen, J.-E., Balazs, K., Higuero, I., 2004. High Nature Value Farmland - Characteristics, trends and policy challenges, in EEA report. No 1/2004. In: European Environment Agency (Ed.).

Hosmer, D.W., Lemeshow, S., 2000. Applied logistic regression. Wiley, New York.

Hutto, R.L., 1985. Habitat selection by nonbreeding, migratory land birds. In: Cody, M.L. (Ed.), Habitat selection in birds. Academic Press, Inc., pp. 455-476.

Jay-Robert, P., Niogret, J., Errouissi, F., Labarussias, M., Paoletti, É., Luis, M.V., Lumaret, J.-P., 2008. Relative efficiency of extensive grazing vs. wild ungulates management for dung beetle conservation in a heterogeneous landscape from Southern Europe (Scarabaeinae, Aphodiinae, Geotrupinae). Biol. Conserv. 141, 2879-2887.

Leal, A.I., Martins, R.C., Palmeirim, J.M., Granadeiro, J.P., 2011. Influence of habitat fragments on bird assemblages in cork oak woodlands. Bird Study 58, 309-320.

Leal, A.I., Rainho, A., Martins, R.C., Granadeiro, J.P., Palmeirim, J.M., 2016. Modelling future scenarios to improve woodland landscapes for birds in the Mediterranean. Journal for Nature Conservation 30, 103-112.

Listopad, C.M.C.S., Köbel, M., Príncipe, A., Gonçalves, P., Branquinho, C., 2018. The effect of grazing exclusion over time on structure, biodiversity, and regeneration of high nature value farmland ecosystems in Europe. Sci. Total Environ. 610–611, 926-936.

López-Sánchez, A., Perea, R., Dirzo, R., Roig, S., 2016. Livestock vs. wild ungulate management in the conservation of Mediterranean dehesas: Implications for oak regeneration. For. Ecol. Manag. 362, 99-106.

Melbourne, B.A., 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. Aust. J. Ecol. 24, 228-239.

Moreira, F., Beja, P., Morgado, R., Reino, L., Gordinho, L., Delgado, A., Borralho, R., 2005. Effects of field management and landscape context on grassland wintering birds in Southern Portugal. Agric. Ecosyst. Environ. 109, 59-74.

Moreno, G., Gonzalez-Bornay, G., Pulido, F., Lopez-Diaz, M., Bertomeu, M., Juárez, E., Diaz, M., 2016. Exploring the causes of high biodiversity of Iberian dehesas: the importance of wood pastures and marginal habitats. Agrofor. Syst. 90, 87-105.

Moreno, G., Pulido, F.J., 2009. The functioning, management and persistence of dehesas. In: Rigueiro-Rodríguez, A., McAdam, J., Mosquera-Losada, M.R. (Eds.), Agroforestry in Europe. Current Status and Future Prospects. Springer, Dordrecht, Netherlands, pp. 127-160.

Nikolov, S.C., Demerdzhiev, D.A., Popgeorgiev, G.S., Plachiyski, D.G., 2011. Bird community patterns in sub-Mediterranean pastures: the effects of shrub cover and grazing intensity. Anim. Biodivers. Conserv. 34, 11-21.

Olea, L., San Miguel-Ayanz, A., 2006. The Spanish dehesa. A traditional Mediterranean silvopastoral system linking production and nature conservation. 21st General Meeting of the European Grassland Federation, Badajoz, pp. 1-15.

Palmeirim, J.M., Rabaça, J.E., 1994. A method to analyze and compensate for time-of-day effects on bird counts. J. Field Ornithol. 65, 17-26.

Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133, 225-245.

Peco, B., Navarro, E., Carmona, C.P., Medina, N.G., Marques, M.J., 2017. Effects of grazing abandonment on soil multifunctionality: The role of plant functional traits. Agriculture, Ecosystems & Environment 249, 215-225.

Pereira, P., Godinho, C., Roque, I., Marques, A., Branco, M., Rabaça, J.E., 2014. Time to rethink the management intensity in a Mediterranean oak woodland: the response of insectivorous birds and leaf-chewing defoliators as key groups in the forest ecosystem. Ann. For. Sci. 71, 25-32.

Perkins, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Barnett, P.R., 2000. Habitat characteristics affecting use of lowland agricultural grassland by birds in winter. Biol. Conserv. 95, 279-294.

Pinto-Correia, T., Ribeiro, N., Sá-Sousa, P., 2011. Introducing the *montado*, the cork and holm oak agroforestry system of Southern Portugal. Agrofor. Syst. 82, 99-104.

Plieninger, T., Hartel, T., Martín-López, B., Beaufoy, G., Bergmeier, E., Kirby, K., Montero, M.J., Moreno, G., Oteros-Rozas, E., Van Uytvanck, J., 2015. Wood-pastures of Europe: geographic coverage, social–ecological values, conservation management, and policy implications. Biol. Conserv. 190, 70-79.

Powolny, T., Eraud, C., Masson, J.-D., Bretagnolle, V., 2015. Vegetation structure and inter-individual distance affect intake rate and foraging efficiency in a granivorous forager, the Eurasian Skylark Alauda arvensis. Journal of ornithology 156, 569-578.

Putman, R., Fowler, A., Tout, S., 1991. Patterns of use of ancient grassland by cattle and horses and effects on vegetational composition and structure. Biol. Conserv. 56, 329-347.

R Development Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Viena, Austria. http://www.R-project-org

Rabaça, J.E., 1990. The influence of shrubby understory in breeding bird communities of cork oak (*Quercus suber*) woodlands in Portugal. Portugaliae Zoologica 1, 1-6.

Samways, M.J., McGeoch, M.A., New, T.R., 2010. Insect conservation: a handbook of approaches and methods. Oxford University Press, Oxford.

Santana, J., Porto, M., Gordinho, L., Reino, L., Beja, P., 2012. Long-term responses of Mediterranean birds to forest fuel management. J. Appl. Ecol. 49, 632-643.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. PLoS One 5, 5.

Schieltz, J.M., Rubenstein, D.I., 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? Environ. Res. Lett. 11, 18.

Sternberg, M., Gutman, M., Perevolotsky, A., Kigel, J., Lepš, J., 2003. Effects of grazing on soil seed bank dynamics: An approach with functional groups. J. Veg. Sci. 14, 375-386.

Tabachnick, B., Fidell, L., 1996. Using Multivariate Statistics. HarperCollins Publishers Inc., New York.

Tellería, J.L., 2001. Passerine bird communities of Iberian dehesas: A review. Anim. Biodivers. Conserv. 24, 67-78.

Therneau, T.M., Lumley, T., 2017. Package 'survival'. R package version, 2.41-43.

Topping, C., Sunderland, K., 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. J. Appl. Ecol., 485-491.

Vera, F.W.M., 2000. Grazing ecology and forest history. CABI publishing.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647-664.

Whittingham, M.J., Butler, S.J., Quinn, J.L., Cresswell, W., 2004. The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. Oikos 106, 377-385.

Whittingham, M.J., Evans, K.L., 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis 146, 210-220.

Figure Captions

Figure 1. Study area in "Herdade do Freixo do Meio" (38º 42´12''N, -8º 19´29'' W), Alentejo, Portugal. Experimental plots with different grazing pressures are identified as Not grazed – NotG, Light grazing – LightG, and Heavy grazing – HeavyG.

Figure 2. Characterization of the ground habitat and prey abundance. Bars are averages of the four replicates of each grazing level; lines represent one SE. Significance level are indicated with . p<0.1, *p < 0.05, ***p<0.001.

Figure 3. Boxplots showing vegetation height (cm) in the foraging patches for species with more than 20 focal observations (white), for all the species combined (black), and experimental plots with different grazing pressure (grey tones). A few outliers are not visible because they exceed the upper limit of the scale. The height of vegetation preferred by all the studied species is very scarce in the ungrazed experimental plots.

Figure 4. Number of birds per transect (± SE) in plots with different grazing pressure (Not grazed, Light grazing and Heavy grazing). Significant results are marked with *p < 0.05, **p < 0.01.