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Effects of wilderness grazing on ground-breeding birds in Pannonian grasslands

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Abstract: The acceleration of grassland loss on the global scale has been reported in many studies, which is often attributed to the combination of land use change and increased variability of climatic processes. Extensive steppe national parks serve as an ideal study site for grassland conservation, especially wilderness areas where the natural effects of grazing on wildlife can still be tracked. In our study we aim to investigate the effects of habitat structure, grazing type and intensity as well as climatic variables on species abundance, species richness and abundance of functional groups of ground-breeding bird species in the largest compact alkali grassland area of central Europe. We applied the information theoretic approach estimating the importance of ecological predictors according models of substantial support. The main result of our study shows that ground-breeding bird communities in steppe areas exhibit highly species-specific responses to the species of grazers, grazing intensity, habitat composition and climatic predictors. Across the most supported models, species-specific habitat composition values were the most supported predictors. Our findings show that although the response of ground-breeding birds to vegetation, grazing and climatic predictors is highly species-specific, consistent patterns of responsiveness to grazing and climatic patterns emerge, which calls for long-term studies on the combined effects of climatic variability and management of grazing systems.

Nomenclature: Hadarics (2008).

Abbreviations: GLMM – General Linear Mixed Models; HNP – Hortobágy National Park, UD – Utilization Distribution

Introduction

Recently, a number of studies reported on the accelerated disappearance of native grasslands at global scale, often attributed to increasing human activities (Ceballos et al. 2010, Turner and Dakota 2013). Additionally, land use change seriously affects the underlying ecological processes maintaining grassland biodiversity (Garnier et al. 2007). For example, traditional grazing systems have collapsed in many parts of Europe leading to adverse structural changes in grassland ecosystems (Pykälä 2000, Fuhlendorf et al. 2006). Consequently, a number of ground-breeding birds show declining trends in native grasslands (Batáry et al. 2007, Fisher and Davis 2010).

These processes have urged conservationists to try to maintain or re-establish traditional grazing systems, using locally adapted breeds of large ungulates and sheep (Pykälä 2000), resulting in a number of successful grassland management projects. Traditional cattle and sheep breeds are usually less efficient milk-, meat- and wool-producers but require less human intervention, which allows more natural grazing processes. Further, they are adapted to local circumstances and able to utilise low quality food (Metera et al. 2010), thus controlling alien shrubs (Fernández-Lugo et al. 2011). The effects of large herbivores, such as horse, cattle, sheep, goat, have been investigated by a number of previous studies which reported that moderate grazing can help preserving biodiversity of open landscapes, especially on wetlands with fast vegetation growth (Loucougaray et al. 2003, Metera et al. 2010).

Another approach of managing grassland communities is the establishment of wilderness areas using wild herbivores or descendants of those that lived here in prehistoric times (e.g., deer and Przewalski's horses) as well as traditional species and Heck cattle. The latter breed originates from an attempt to "breed back" domestic cattle to their ancestral form, the extinct aurochs (Vuure 2005). Such areas in Europe include Oostvaardersplassen in the Netherlands, Camargue in France and Pentezug in Hortobágy National Park, Hungary. While Oostvaardersplassen is a 5600 ha area grazed by Polish ponies (also known as Konik), Heck cattle and red deer (Vera 2009, Sutherland 2002), Camargue hosts three traditional cattle breeds of Camargue horses (Menard et al. 2002). In contrast, the eastern part of the Eurasian steppe zone is still largely managed by traditional grazing systems, especially in Mongolia and Kazakhstan with a tendency towards intensification and land use change (Robinson et al. 2003, Jiang et al. 2006).

In Hortobágy National Park (HNP) in East-Hungary, both the maintenance of traditional grazing systems and a re-establishment of wilderness-like grassland area occur. The traditional Hungarian breeds, such as Hungarian Grey Cattle, Racka Sheep, as well as Water Buffalo and domestic horses have been grazing for centuries in this area. In contrast, the re-establishment of wilderness areas in Hortobágy has started only recently. "Pentezug Project" was initiated by the Cologne Zoo and the Hortobágy National Park Directorate in 1997. The strictly protected Pentezug area is located 10 kilometers away from public roads and is bordered by electric fence, allowing no public access. The project has two main aims: (1) to maintain a grassland area using large ungulates for grazing, and (2) to breed, protect and study behaviour and habitat selection of Przewalski's horses (Zimmermann 2005). Nowadays, more than 280 horses and 300 cattle roam on the 2500 ha area. A growing body of evidence suggests that ancient aurochs and wild horses coexisted in grasslands (Menard et al. 2002), suggesting that several aspects of prehistoric conditions are re-established in Pentezug.

Current analyses predict accelerated climatic variability in the Eurasian steppe zone which might lead to the collapse of grassland-wetland complexes (McCarthy 2001). Indeed, a decline of wetlands in the western part of the Eurasian steppe zone have been reported, which forecasts population decreases in a number of grassland birds, already disappearing from Western Europe (Batáry et al. 2007). In our study we aim to investigate the effects of vegetation structure, grazing type and intensity as well as climatic variables on: (i) the number of territorial males; (ii) species richness; (iii) abundance of functional groups of ground-breeding birds, classified as bird species the nests of which are built directly on the ground or in low vegetation affected by grazing pressure, in the largest compact alkali grassland area of Central Europe. We hypothesize that both species richness and abundance of functional groups are governed by grazing pressure and climatic conditions (Pykälä 2000, Pearce-Higgins and Green 2014)

Materials and methods

Study area

Our study sites were located in the central and eastern part of Hortobágy National Park (HNP) in Eastern Hungary (N 47° 30', E 21°10'). The national park covers 80,200 hectares and is considered the most extensive continuous alkaline grassland in Central Europe, consisting of dry alkali grassland areas interspersed with alkali marshes, which would be a semi-open landscape without grazing. Out of this area, 27 000 hectares are designated as Ramsar site, being a stopover site of key importance for migratory and breeding waterbirds inside the country and in Central Europe as well (Ecsedi 2004). For our study two sample areas were selected which contain similar habitat composition values (Mann-Whitney U-test, $p < 0.002$ for all habitat types, classified reedbeds, alkali marshes, wet meadows, grasslands, barren alkali patches, weedy areas, roads, loess vegetation and woodlands). Both areas were 2 km × 2 km in size, each divided into N=100 contiguous 4.0 ha squares. The eastern area is characterized by traditional sheep grazing, while the other area is located within the Pentezug wilderness area.

Bird data

Records of breeding birds were collected between 2001-2010 twice a year, between 20 April – 10 May and between 15 May – 10 June in the two 400 hectares large areas. Observations were carried out in the centroid of the 4.0 hectares large squares as point counts on fixed survey transects in both areas (Angyalháza and Pentezug) where we followed randomized directions to avoid possible biases caused by the effect of the time of the day.

During each survey, territorial males were counted for five minutes in each count point (N=200 count points in total; map of Appendix 1). To obtain the best estimate of the number of territorial males in each observation square, we always used the larger of the values recorded in the two surveys (Voříšek 2008, Schmeller et al. 2012).

We classified bird species based on their diet types following the recommendations of Santana et al. (2012), as species feeding predominantly on insects (insectivorous), invertebrates in general, seeds (graminivorous), plants (herbivorous) or on vertebrates (bird of prey). In our study area the ground-breeding bird communities are primarily characterised by waders feeding on invertebrates, insectivorous *Locustella* and *Acrocephalus* warblers as well as ducks, harriers, members of the *Gruiformes*, larks, pipits, wagtails and buntings.

Bird populations

During our ten years of study, we detected territorial behaviour in 40 species within the study sites, eight species of which had less than seven years of observation and were excluded from further analyses (Table 1). Therefore we found that populations of all common bird species are stable thus no control for population changes is necessary when analyzing the effects of environmental variables on the number of territorial males.

Grazing data

Grazing data were collected all year round between 2000-2007, approximately on 200 days in total from the two study areas. Observations were carried out between sunrise and sunset on foot or on vehicle, recording the animals' locations on a map of Pentezug using WGS84 GPS coordinates. After data collection, habitat types were associated with each observation point using the landuse maps provided by the HNP Directorate which include polygon shapes of reedbeds, alkali marshes, wet meadows, grasslands, barren alkali patches, weedy areas, roads, loess vegetation and woodlands. The proportion of habitat types was calculated for each square of the study area.

After compiling the dataset of grazing wild horses and cattle, we calculated 50% and 95% home ranges of large ungulates by calculating Utilization Distribution (UD), as suggested by Worton (1995). UD is the bivariate function providing the probability density that an animal is found at a point

Table 1. Bird species with territorial males observed in the study area at least in seven years, indicating the functional group as well as mean and standard deviation of the total number of territorial males calculated across the study years.

Common name	Scientific name	Functional group (diet)	Number of years	Mean	SD
great bittern	*Botaurus stellaris*	invertebrates	9	2.40	21.8348
mallard	*Anas platyrhynchos*	herbivorous	9	0.80	12.6744
garganey	*Anas querquedula*	herbivorous	7	0.54	10.3695
marsh harrier	*Circus aeruginosus*	bird of prey	10	3.48	26.171
Montagu's harrier	*Circus pygargus*	bird of prey	7	0.54	10.3695
quail	*Coturnix coturnix*	graminivorous	7	5.92	33.9244
water rail	*Rallus aquaticus*	invertebrates	7	0.26	7.3373
coot	*Fulica atra*	herbivorous	8	1.08	14.6351
stone curlew	*Burhinus oedicnemus*	invertebrates	9	1.88	21.9019
lapwing	*Vanellus vanellus*	invertebrates	9	4.28	28.9747
common snipe	*Gallinago gallinago*	invertebrates	7	2.42	21.8929
redshank	*Tringa totanus*	invertebrates	8	0.80	12.6829
skylark	*Alauda arvensis*	graminivorous	10	279.84	178.5758
tawny pipit	*Anthus campestris*	insectivorous	7	0.26	7.3373
yellow wagtail	*Motacilla flava*	insectivorous	10	90.72	122.2696
winchat	*Saxicola rubetra*	insectivorous	7	0.26	7.3373
stonechat	*Saxicola torquata*	insectivorous	7	1.62	25.3828
wheatear	*Oenanthe oenanthe*	insectivorous	7	1.08	14.6449
grasshopper warbler	*Locustella naevia*	insectivorous	9	4.02	28.0923
Savi's warbler	*Locustella luscinioides*	insectivorous	10	6.66	35.9251
sedge warbler	*Acrocephalus schoenobaenus*	insectivorous	10	78.12	173.4666
reed warbler	*Acrocephalus scirpaceus*	insectivorous	7	0.54	10.3695
great reed warbler	*Acrocephalus arundinaceus*	insectivorous	8	2.68	23.0308
reed bunting	*Emberiza schoeniclus*	graminivorous	10	43.86	104.0749
corn bunting	*Miliaria calandra*	graminivorous	7	4.30	29.051

according to its geographical coordinates. Using this model, home range is defined as the minimum area in which animals are attributed some specified probability of being located. Accordingly, we generated shape files defining 50 and 95% probability of occurrence for the data of horses and cattle separately, as the ecological effects of these large ungulates are differential for ground-breeding birds (Ryder 1980, Reino et al. 2010). In the following step we calculated new variables, which indicated if a particular survey plot was included or not in the 50 and 95% home ranges for both large ungulates in each year.

Habitat predictors

Habitat composition values of each survey plot were recorded in every year and were classified as woodland, loess vegetation, dry alkali grassland, wet alkali grassland, alkali marsh, barren alkali soil, weedy vegetation and road (Török et al. 2011).

Climate data

To control for wetland conditions, we used winter and spring precipitation totals, summed for December to February and March to May, respectively. As spring temperature predicts habitat conditions for breeding birds primarily by modifying vegetation phenology, we calculated spring temperature averaging monthly mean values of March, April and May (Pearce-Higgins and Green 2014). All climatic variables were measured at the nearest weather station in Hortobágy, Eastern Hungary (N 47°20', E 21°24').

Statistical analyses

The records of the final database included the following information: species name, functional group classified by diet types, survey plot ID, year, annual maximum of territorial males, proportion of each habitat type, included or not in 95 and 50% home ranges of horses, cattle, and sheep as well as climatic variables. As the 95 and 50% home ranges for each grazing animal significantly correlated ($p < 0.0001$ for all cases), we used 50% home range values for further analyses. In the following step we calculated temporal trends in bird population sizes by species calculated as the slope of linear regression fitted on the annual sum of territorial males as a function of years, using the pooled data of both areas. In the next step, for all species we developed general linear mixed models (GLMM) fitted on the number of territorial males as a function of habitat types, climatic parameters and grazing pressure, where none of the variables were transformed due to the original data recording procedures which provided the same scaling for the same type of data. Additionally, year was added as fixed factor and area as random factor assuming Poisson error distribution. Data of the two areas were pooled after providing an area identity record to each observation; to control for possible spatial autocorrelation, area identity was treated as a random factor during all analyses. Next, we

Table 2. Model-averaged parameter values of predictors across best supported models (Δ > 2.0) for species richness. Predictors with significant z-values are indicated in bold.

Predictor	θ	SEu	z-value	p-value
Intercept	4.8193	3.1749	1.5171	0.1293
Grassland	-0.5654	0.1901	2.9696	**0.0030**
Marsh	6.2374	1.3829	4.5031	**< 0.0001**
Reedbed	1.8006	0.3748	4.7958	**< 0.0001**
Spring temp.	-0.4428	0.2236	1.9771	0.0593
Barren areas	-0.0711	0.6041	0.1176	0.8577
Cattle 95%	0.2527	0.1371	1.8455	0.0613
Horse 95%	**-0.2635**	**0.1306**	**1.9887**	**0.0401**

Table 3. Model-averaged parameter values of predictors across best supported models (Δ > 2.0) for insectivorous birds. Predictors with significant z-values are indicated in bold.

Predictor	θ	SEu	z-value	p-value
(Intercept)	**4.8221**	**2.1359**	**2.2536**	**0.0242**
Horse 95%	-0.1703	0.1209	1.405	0.16
Grassland	**-0.7078**	**0.1751**	**4.0276**	**< 0.0001**
Marsh	**2.8728**	**0.6712**	**4.2667**	**< 0.0001**
Spring temp.	**-0.3295**	**0.1329**	**2.4719**	**0.0134**
Winter prec.	**-0.0061**	**0.0026**	**2.3331**	**0.0196**
Cattle 95%	0.166	0.1304	1.269	0.2044
Reedbed	0.3698	0.3031	1.2161	0.2239
Barren area	0.2489	0.5288	0.4691	0.639

Table 4. Model-averaged parameter values of predictors across best supported models (Δ > 2.0) for graminivorous birds. Predictors with significant z-values are indicated in bold.

Predictor	θ	SEu	z-value	p-value
Intercept	**4.0963**	**0.6664**	**6.1373**	**< 0.0001**
Sheep 95%	-0.1057	0.0756	1.3954	0.1629
Spring prec.	-0.0007	0.0005	1.5656	0.1174
Spring temp.	**-0.2293**	**0.0493**	**4.6457**	**< 0.0001**
Winter prec.	**-0.0048**	**0.001**	**4.6527**	**< 0.0001**
Reedbed	0.285	0.2071	1.3739	0.1695
Cattle 95%	0.0484	0.0634	0.7623	0.4459
Horse 95%	0.0384	0.0569	0.6737	0.5005
Barren area%	0.246	0.3296	0.7451	0.4562
marsh	-0.5999	0.9027	0.6635	0.507
grassland	0.0689	0.1085	0.6341	0.526

developed GLMM on species richness as well as abundance of functional groups applying the same model structure as outlined above, where the number of records to assess the importance of environmental predictors on the abundance of functional groups were sufficient only for insectivorous and graminivorous birds.

After model fitting, the relative importance of ecological predictors was calculated using model-comparison techniques (Anderson and Burnham 2002) applied in information-theoretic framework. In the first step we obtained the values of Akaike's information criterion corrected for small sample size (AICc) which expresses the trade-off between the goodness of fit of the model and its complexity, thus functioning as a measure of information entropy. As a result, we calculated partial model-averaged parameter estimates (θ) and unconditional standard errors (SEu; Anderson and Burnham 2002) of each variable by the sums of their Akaike weights across all models with substantial support containing the given predictor.

For all analyses we used the R statistical computing environment (R Development Core Team 2013, version 3.2.5). Spatial statistics were calculated using the "maptools" (Lewin-Koh et al. 2011) and "spatstat" packages (Baddeley and Turner 2005). Model fitting and consequent model selection was performed applying "lme4" (Bates et al. 2014) and "MuMIn" (Barton 2011) packages.

Results

Model selection

Considering the predictors using the confidence intervals (excluding zero inflated intervals) between the supported models (dAICc < 2) for all species, we found that the number of the territorial males as the best proxy for population size were

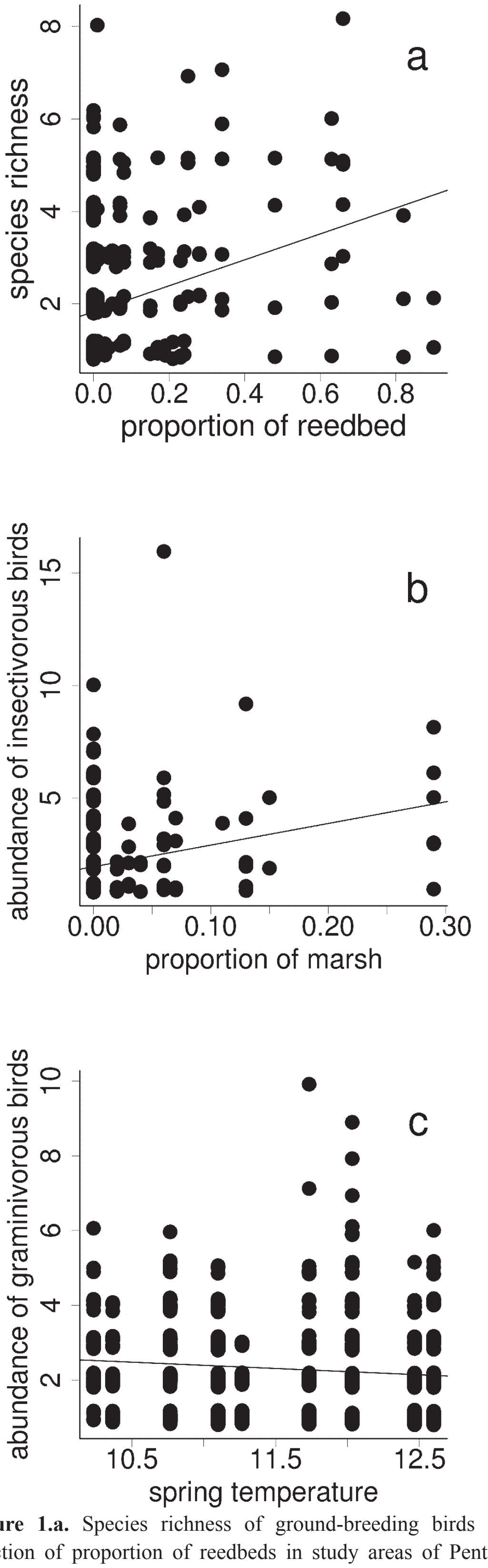

Figure 1.a. Species richness of ground-breeding birds as a function of proportion of reedbeds in study areas of Pentezug and Angyalháza areas between 2001-2010 **b.** Abundance of ground-breeding insectivorous birds as a function of proportion of marshes. **c.** Abundance of ground-breeding graminivorous birds as a function of mean spring temperature in study areas of Pentezug and Angyalháza areas between 2001-2010.

affected by the size (proportion?) of the marshes, followed by reedbed and grasslands and the spring temperatures (Table 2, Fig 1a) Horse grazing were also affected the species richness of all birds observed (Appendix 2)

For insectivorous birds, we revealed that their abundance was most influenced by the are of marshes and then the grassland, however the spring temperatures and the winter precipitation was also an influential predictors (Table 3, Fig 1b).

For graminivorous birds only the environmental condition such as spring temperatures and the winter precipitation affected their abundance (Table 4, Fig 1c.)

Discussion

The main result of our study shows that ground-breeding bird communities in steppe areas exhibit highly guild-specific responses to the species of grazers, grazing intensity, habitat composition and climatic predictors. Across the most supported models, species-specific habitat composition provided the strongest effects as shown by significant z-values. Interestingly, significant relationships between the number of territorial males and grazing proxies indicate that while grazing of large ungulates showed no relationship with male numbers, sheep grazing was influential for several bird species, including wetland taxa. However, the inclusion of large ungulate grazing among supported models implies that traditional grazing support ground-breeding bird communities. This pattern may be related to that large herbivore mammals graze differently, primarily due to anatomical and behavioural characteristics. In our case, the effects of horse grazing was not among supported predictors. To understand the lack of this effect, we propose the following hypotheses. First, considering grazing physiology, daily intake of horses is higher than in cattle, and cattle consume more broadleaved plants and dicotyledons (Menard et al. 2002), which is predicted to result in different invertebrate fauna affecting habitat choice of breeding birds. Second, temporal dynamics of movements of groups of cattle and horses substantially differ, which is expected to result in different spatial heterogeneity of habitats which influences the spatial distribution of territories of ground-breeding birds (Ryder 1980). Additionally, sheep are more likely to graze vegetative parts of plants, while cattle prefer reproductive parts (Metera et al. 2010); these differences result in small-scale heterogeneity (Fuhlendorf and Engle 2001). Therefore, moderate grazing with various species seems to increase biodiversity of the flora compared to grazing with one species (Loucougaray et al. 2004, Evans et al. 2006). Remarkably, both over- and undergrazing may exert negative effects on biodiversity, which is rather habitat-specific, however (Metera et al. 2010, Hadjigeorgiou et al. 2005).

Our findings are in line with a number of studies reporting that as wetlands seem to be highly important for maintaining bird communities in steppe areas, the grazing of large ungulates can play a vital role in managing wet habitats, increasing the biodiversity of wetlands in general and supporting bird communities (Báldi et al. 2013). Importantly, our study area is considered a wilderness area where the movements of grazers are only limited by the electric fence surrounding it. As a result, these animals roam freely between water surfaces, food patches or shelters. This results in heterogeneity of spatial patterns in habitat use (for example vegetation close to water surfaces is heavily grazed in summer). Due to the temporal and spatial grazing patterns of herbivores, vegetation shows large-scale spatial heterogeneity, both in our study sites and in a number of European wilderness areas (Fuhlendorf and Engle 2001). This variance in plants affects the habitat quality or feeding conditions of a broad range of taxa. Grazing by wild animals requires no intensive human intervention, resulting in decreased levels of human disturbance.

We found that a few ground-breeding species were sensitive to spring temperature with lower levels of abundance of both insectivorous and graminivorous birds in warmer springs, such as for example *Coturnix coturnix, Alauda arvensis, Motacilla flava, Acrocephalus specie*s, *Locustella luscinioides* and *Miliaria calandra*. This finding is in line with several recent studies demonstrating that bird population decline as a result of temporal mismatch between spring migration phenology and the timing of prey emergence peaks (Pearce-Higgins and Green 2014). Although we were not able to measure the temporal dynamics of a broad spectrum of invertebrates serving as potential food resource for ground-breeding birds, increasing spring mean temperatures and the increasing frequency of heat extremities during the breeding season support this pattern (Bartholy et al. 2007). Similarly, increasing spring temperatures predicted declining species richness, with no significant z-statistics, however.

Spring precipitation showed significant effects for several bird species and was included among the best supported models for 10 out of 32 taxa with positive parameter estimates in majority of the cases. This implies that wet springs might induce population increase in the main food items of birds with no preference for wetlands. Indeed, a number of animal species preferring dry steppe habitats have been shown to exploit wetlands during reproduction. For example, *Otis tarda* prefers habitats classified as wetlands during displaying, breeding or moulting, as these spots provide food and shelter during droughts (Végvári et al. 2016). Further, bird numbers were smaller in warmer springs which suggests that the interaction of spring temperature and precipitation might be important in driving the number of established territories possibly through food availability (Møller et al. 2006). Although the interaction term did not emerge as a supported predictor calculated using monthly values, the combined effects of temperature and precipitation on finer temporal scales might be a relevant factor for ground-breeding birds when selecting territories (Møller et al. 2006). Thus, the importance of wetlands in territory selection of ground-breeding birds in steppe habitats further supports the evidence of current climatic models that consistently predict a decline of wetlands in the western part of the Eurasian steppe zone, forecasting population decreases in a number grassland birds, already disappearing from Western Europe (Barbet-Massin et al. 2012).

In summary, our results show that although the response of ground-breeding birds to vegetation, grazing and climatic predictors are species-specific, consistent patterns emerge in the effects of grazing and climatic predictors which call for long-term studies on the combined effects of climatic variability and management of grazing systems (Lal et al. 2011, Ryals et al. 2014).

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Appendices

Appendix 1. Map of the study area indicating survey plots, major wetlands and spatial distribution of various grazing types.

Appendix 2. Model-averaged parameter values of predictors with standard errors, z-values and related p-values, across best supported models ($\Delta > 2.0$) for all species. Predictors with significant z-values are indicated in bold.

Appendix 3. Mean values and standard deviations of habitat proportions of both study areas.

Appendix 4. Full model selection table of GLMM-s fitted for all species.

The file may be downloaded from www.akademiai.com.