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RESEARCH ARTICLE

Associations of grassland birds with vegetation structure in the Northern Campos of Uruguay

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Submitted March 20, 2015; Accepted August 24, 2015; Published November 4, 2015

ABSTRACT

Grassland birds are declining as a consequence of habitat modification, and these declines have generated efforts to determine how birds cope with changes in habitat features, especially in agricultural landscapes. The objective of our study was to examine the relationship between grassland birds and vegetation structure in the Northern Campos of Uruguay. Vegetation variables were sampled on 4 sites that differed in agricultural management: (1) “Crop” site, a combination of annual crops and seeded pastures; (2) “Pasture” site, seeded pastures only; (3) “Native 1” site, natural grasslands under sheep and cattle grazing; and (4) “Native 2” site, natural grasslands grazed by native Pampas deer (*Ozotoceros bezoarticus*) and cattle. We used multivariate analyses to examine the relationship between bird abundance and vegetation variables. Vegetation structure varied among sites, and most of these differences can be linked to specific management activities typical of each site. Mean vegetation height was greater (and more variable) in cultivated grasslands (Crop and Pasture sites), whereas mean percentage grass contacts (grass cover) was greater in natural grasslands (Native 1 and 2 sites). Vegetation variables accounted for a significant amount of variation in bird distribution and abundance (14.8%). Grassland birds were associated most strongly with vegetation height, grass cover, and vegetation patchiness. Some of the species associated with the highest values for these environmental gradients were Dark-throated Seedeater (*Sporophila ruficollis*), with vegetation height; Pampas Meadowlark (*Sturnella defilippii*), with grass cover; and Burrowing Owl (*Athene cunicularia*), with vegetation patchiness. Unlike facultative species, many grassland-specialist birds were associated with characteristic features (i.e. high grass cover) of natural grasslands used by livestock. Others, however, were associated with typical features (i.e. taller vegetation) of cultivated grasslands. Thus, Pampas grassland bird populations would benefit not only from native-grassland preservation efforts, but also from management guidelines for agriculture-dominated lands.

Keywords: agricultural gradient, bird–vegetation associations, Pampas grasslands

Asociaciones de Aves de Pastizal a variables de estructura de vegetación en los Campos del Norte de Uruguay

RESUMEN

Las aves de pastizal están declinando como consecuencia de la modificación de hábitat y es importante entender como las aves enfrentan cambios en las características del hábitat, especialmente en agroecosistemas. Examinamos la relación entre aves de pastizal y estructura de la vegetación en los Campos del Norte de Uruguay. Se muestrearon variables de vegetación en cuatro sitios con diferentes manejos agropecuarios: (1) “Cultivo”, cultivos anuales y pasturas exóticas; (2) “Pastura”, pasturas exóticas exclusivamente; (3) “Nativo 1”, pastizales nativos pastoreados por ovinos y vacunos, y (4) “Nativo 2”, pastizales nativos pastoreados por *Ozotoceros bezoarticus* (herbívoro nativo) y vacunos. Utilizamos análisis multivariados para examinar la relación entre la abundancia de las aves y la vegetación. La estructura de la vegetación varió entre sitios y la mayoría de las diferencias pueden ser relacionadas con las actividades de manejo características de cada lugar. La altura de vegetación fue mayor en los pastizales cultivados (“Cultivo” y “Pastura”) mientras que la cobertura de pasto fue mayor en los pastizales naturales (Nativo 1 y 2). Las variables de vegetación explicaron una parte significativa de la variación en la distribución y abundancia de aves (14.8%). Las aves mostraron una asociación más fuerte a la altura de la vegetación, la cobertura de pastos y el parcheado. Algunas de las especies que mostraron las asociaciones más fuertes fueron *Sporophila ruficollis* con la altura de vegetación, *Sturnella defilippii* con la cobertura de pastos y *Athene cunicularia* con el parcheado. Muchos especialistas de pastizal estuvieron asociados con características típicas (i.e. alta cobertura de pastos) de los pastizales naturales. Otros, sin embargo, estuvieron asociados con características típicas (i.e. vegetación alta) de pastizales cultivados. Las aves pampeanas no

sólo se beneficiarían con la preservación de pastizales nativos sino también con la implementación de lineamientos de manejo en áreas dominadas por la agricultura.

Palabras clave: asociaciones aves-vegetación, gradiente agropecuario, pastizales pampeanos

INTRODUCTION

Vegetation composition and structure can directly affect bird survival and reproduction, and thus they are considered important influences on avian assemblages and bird–habitat relationships (Rotenberry 1985, Skowno and Bond 2003, Suárez et al. 2003, Whittingham et al. 2006). For grassland birds in particular, empirical evidence indicates that species may show strong associations with vegetation structure (Cody 1985, Patterson and Best 1996). This factor is thought to influence bird distributions and numbers because it affects food and nesting resources and provides protection from the elements and from predators (e.g., Rotenberry and Wiens 1980, Grzybowski 1983, Cody 1985, Fisher and Davis 2010). During foraging, vegetation structure can influence both prey availability and detectability. In regard to nesting resources, it can provide spatial clues that help birds relocate their nests, it can influence nest microclimate, it can provide thermoregulatory advantages to incubating individuals, and—probably most important for grassland birds—it can reduce nest predation risks by increasing nest concealment (Walsberg 1985, Hoekman et al. 2002, Davis 2005). Finally, vegetation structure influences predation risk not only for nests, but also for individuals themselves (Grzybowski 1983, Lima 1993, Whittingham et al. 2006).

The Pampas biome of southeast South America is dominated by grassland ecosystems that extend from southern Brazil into Uruguay and central-eastern Argentina. The region's extraordinarily favorable conditions for agriculture have resulted in a drastic modification of its native vegetation since European settlement (Vervoort 1967, León et al. 1984, Di Giacomo and Krapovickas 2005). Most of the Pampas have now been converted to either rangelands or croplands. High conversion rates have continued in recent times. In the Northern Campos, for example, the area occupied by native grasslands was reduced by ~9% between 1990 and 2000 in Uruguay and by 15.6% between 1976 and 2002 in Rio Grande do Sul, Brazil (Martino and Methol 2008, Cordeiro and Hasenack 2009). Not surprisingly, habitat modification has been identified as the most likely factor behind declines of populations of Pampas grassland birds (Collar et al. 1992, Stotz et al. 1996, Vickery et al. 1999, Azpiroz et al. 2012). Even though detailed information from this region is limited, there is evidence that many species have suffered substantial population reductions, coupled with significant range contractions (Fraga et al. 1998, Tubaro and Gabelli 1999, Gabelli et al. 2004). Despite the need for relevant

ecological data, the region has received little research attention, especially compared with other grassland biomes and agricultural landscapes in the Northern Hemisphere.

Identification of habitat attributes that influence bird numbers can guide the design of sound management strategies (Davis et al. 1999, Rotenberry and Knick 1999, Fisher and Davis 2010). We have only limited data on the vegetation structure of fields under alternative management practices in the Pampas, and the habitat requirements of many Pampas grassland birds remain largely unknown. The available information suggests contrasting responses of bird species to agriculture-related activities: Some species are associated with ungrazed or lightly grazed natural grasslands, but others are more abundant in areas where suitable habitat is maintained by intensive livestock grazing (Lanctot et al. 2002, Fernández et al. 2003, Isacch and Cardoni 2011, Dias et al. 2014).

In a previous study, we characterized bird assemblages found on 4 sites that differed in land use (crops, pastures, and 2 native grassland settings), representing a gradient from highly modified to nearly natural grasslands in the Northern Campos of Uruguay. We found that (1) bird communities in the 4 grassland types were distinct; (2) obligate grassland birds tended to use natural grasslands, whereas facultative grassland species were typical of cultivated grasslands (croplands and planted pastures); and (3) threatened species attained relatively high densities only in natural grasslands (Azpiroz and Blake 2009). Variability in vegetation structure among sites might be one important factor driving differences among these bird populations. Here, to address this possibility in the framework of our earlier findings, we examine the role of vegetation structure as a possible driver of differences in the composition of grassland-bird assemblages. Grassland birds (*sensu* Vickery et al. 1999) include obligate species (i.e. grassland specialists) that are “exclusively adapted to and entirely dependent on grassland habitats and make little or no use of other habitat types,” as well as facultative species (i.e. grassland generalists) that “use grasslands as part of a wider array of habitats...[and thus] are not entirely dependent on grasslands but use them commonly and regularly.” We sampled vegetation and combined it with the bird-abundance dataset we had used previously (Azpiroz and Blake 2009). Our objectives were to determine differences in vegetation structure among the 4 sites under different management schemes that are characteristic of the Northern Campos of Uruguay and to identify the most important vegetation variables with

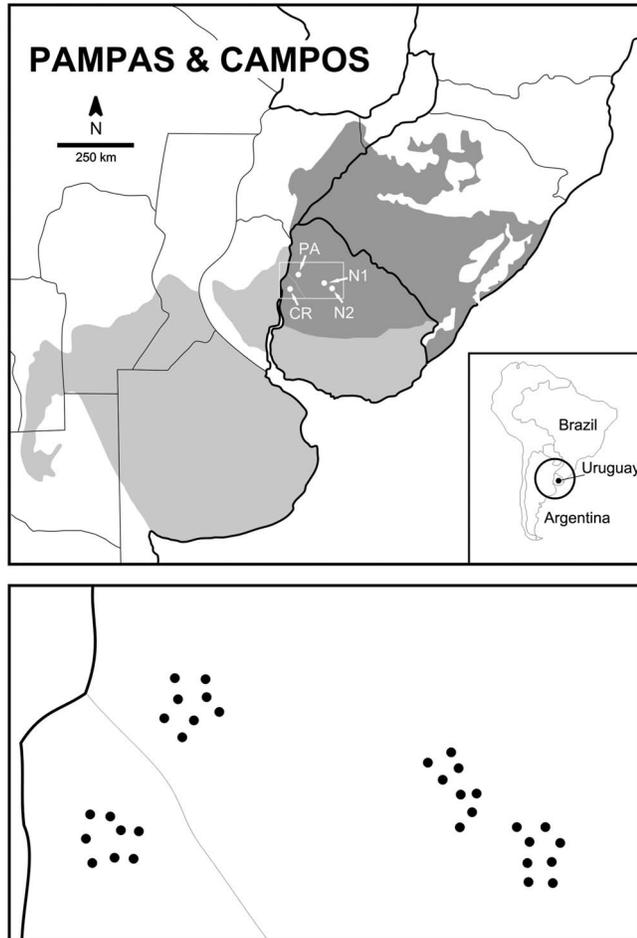


FIGURE 1. Location of Pampas and Campos grasslands in southeastern South America. Within the Northern Campos (dark gray) of Uruguay, 4 sites were sampled: “Crop” (CR), “Pasture” (PA), “Native 1” (N1), and “Native 2” (N2). The diagonal line inside the white square approximately separates agricultural dominated areas (to the left) and livestock grazing areas to the right (adapted from Martino and Methol 2008). Lower panel shows the approximate location of transects within each of the 4 sites.

which obligate and facultative grassland birds are associated. On the basis of findings from other grassland studies, we expected vegetation height, vegetation density, and litter depth to vary among sites and to be the main features with which grassland-bird abundance would be correlated (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Patterson and Best 1996, Delisle and Savidge 1997, Davis 2004, Dias et al. 2014).

METHODS

Study Area and Grassland Sites

The study was conducted in northwest Paysandú department and southern Salto department, northwest Uruguay ($31^{\circ}19'–31^{\circ}44'S$ and $56^{\circ}42'–57^{\circ}56'W$). This area is located

in the Northern Campos of Uruguay within the southeastern South American grasslands (Azpiroz et al. 2012) and the Pampas biome (Stotz et al. 1996). The study was conducted on several ranches and farms near Chapicuy in Paysandú department and near San Antonio and Cerros de Vera in Salto department (Figure 1). Within this general area, we selected 4 large patches (500–1,200 ha) of grasslands under different land uses (for more details of the study area and sites, see Azpiroz and Blake 2009). Two sites (“Crop” and “Pasture”) were located within a matrix of croplands and planted pastures. By contrast, the other 2 sites (“Native 1” and “Native 2”) were in a matrix dominated by extensive cattle ranching (Figure 2). The Crop site included cultivated land that was plowed and seeded to annual crops (i.e. barley and sunflower), which grew during spring and summer in the first half of the sampling period. Barley was planted in austral winter 2004 and harvested in late October 2004, and a residual crop of sunflower was grown on these fields from December 2004 to March 2005. Throughout the second half of the sampling period, the fields included a phase of planted pastures after crops were harvested. The Pasture site included lands that were plowed and seeded with nonnative species and used as cattle pastures. The other 2 sites were characterized by native grasslands that had never been plowed and that were grazed by free-ranging livestock, native herbivores, or both. Grasslands on the Native 1 site were used for cattle and sheep grazing, resulting in lower vegetation diversity than on Native 2 (Sturm 2001). Grasslands in the Native 2 site were grazed by cattle and free-ranging Pampas deer (*Ozotoceros bezoarticus*). Because there was little grazing by sheep (only about 20–30 sheep were maintained on these fields), this site supported a more complex and taller vegetation structure than Native 1 (Sturm 2001).

Typical grass (G) and forb (F) species in planted pastures were *Festuca arundinacea* (G), *Bromus catharticus* (G), *Lolium multiflorum* (G), and *Trifolium repens* (F). Common taxa in natural grasslands within the study area included *Stipa* spp. (G), *Paspalum* spp. (G), *Aristida* spp. (G), *Danthonia montevidensis* (G), *Bothriochloa laguroides* (G), *Baccharis coridifolia* (F), *Wahlenbergia linarioides* (F), *Richardia humistrata* (F), *Rhynchosia senna* (F), *Chevreulia sarmentosa* (F), *Oxypetalum microphyllum* (F), and *Eryngium echinatum* (F).

The spatial distribution of study sites (Figure 1) was constrained by the distribution of these different land uses. Croplands, for example, are primarily restricted to the western part of the study region, whereas native grasslands are found in the eastern part. Grasslands grazed by Pampas deer are particularly limited in distribution and further constrained the selection of study sites. The Crop and Pasture sites were the closest available to Native 2 grasslands. Despite the spatial nonindependence of these



FIGURE 2. Images of the 4 sites within the Northern Campos of Uruguay where birds and vegetation were sampled: “Crop” (upper left); “Pasture” (upper right); “Native 1” (lower left, with cattle and sheep); and “Native 2” (lower right, with Pampas deer).

land-use types, there were no similar constraints in relation to the distribution patterns of birds. That is, all species found during the study had distributions that extended beyond the limits of our area of study (for additional details, see Azpiroz and Blake 2009:29). When reporting some of our findings, we distinguish between “cultivated” (Crop and Pasture sites) and “natural” grasslands (Native 1 and Native 2 sites).

Bird Dataset

We used the same bird dataset as Azpiroz and Blake (2009), which was obtained from September 2004 to November 2005. Birds were sampled every 2 mo in eight 500-m-long variable-width transects on each of 4 sites (>95% of birds were recorded within 0–150 m from the transect center line; Figure 1). Transects were placed in plots with homogeneous vegetation; they were ≥ 400 m apart and avoided the intersection of fencerows and other nongrassland habitats (i.e. gallery forest). We selected transects randomly after considering these constraints. Within each site, an area of ~ 120 ha was sampled. Analyses had a total sample size of 256 (8 periods \times 4 sites \times 8 transects on each site). This dataset contained a total of 4,968 individuals of 50 grassland-bird species observed on all transects combined during the whole sampling period (Azpiroz and Blake 2009); 36 species were recorded on ≥ 5 occasions. In our previous study, we reported density estimates at the site level for the 15 most abundant species (Azpiroz and Blake 2009). Here, we used relative

abundance data (number of individuals per transect) because we wanted to assess comparable information for whole bird assemblages recorded in the study area and were also interested in bird patterns at a finer scale (transect level). Although this approach does not account for differences in detectability, we consider our results informative despite this limitation because data were obtained in habitats with similar structural characteristics (i.e. grassland and grassland-like habitats). In fact, among the 15 species for which both relative abundance and density estimates were available, these 2 sets of measures were largely congruent: Higher numbers of a given bird in 1 of the 4 sites were indicative of greater density in that particular site (see Azpiroz and Blake 2009: table 4 and appendix 1). In this context, we feel confident that our relative-abundance data are useful for comparative inference. Scientific and English names follow Remsen et al. (2015).

Sampling of Vegetation Structure

On the same bird transects and during the same periods, five 100-m vegetation transects were placed at 100-m intervals; the first vegetation transect crossed the bird transect perpendicularly at 50 m from its starting point, and the last one at 450 m from its starting point. In this way, half of each vegetation transect lay to the right of the bird transect, and the other half to the left (Figure 3). Each vegetation transect was divided into ten 10-m sections; within each section, a sampling point was randomly

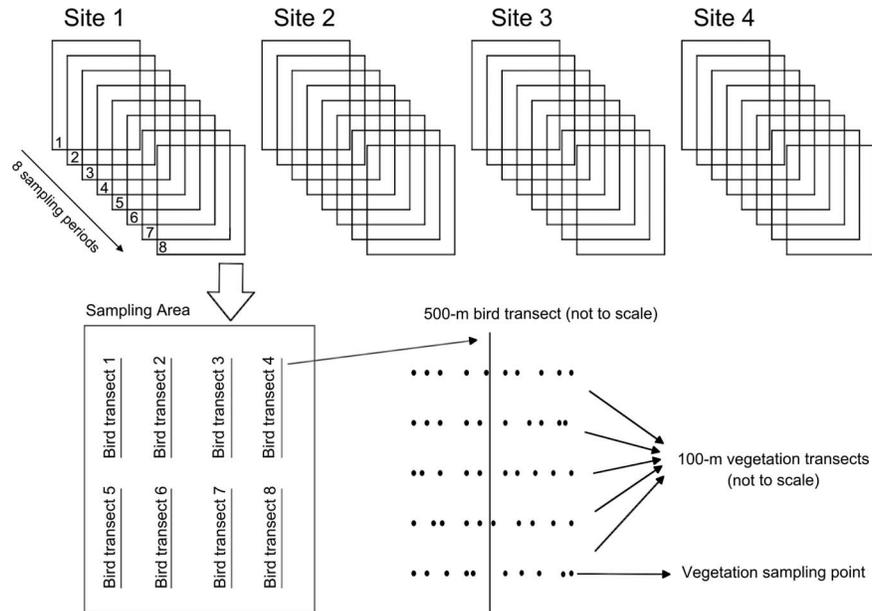


FIGURE 3. Vegetation sampling in the Northern Campos of Uruguay. Vegetation variables were sampled on 50 random points within each of 32 bird transects (distributed among 4 sites) during 8 sampling periods.

selected. Thus, for each bird transect, a total of 50 points were sampled on 5 vegetation transects during each of the 8 sampling periods (12,800 points in total). At each sampling point, a metal rod was placed vertically through the vegetation and the numbers of contacts (hits) by different vegetation types (e.g., grasses, forbs, and standing dead vegetation) in successive 25-cm height intervals were counted, following Rotenberry and Wiens (1980). Also at each sampling point, litter depth and grass and vegetation height were measured to the nearest centimeter. Any plant material lying on the soil was considered litter, and different from standing dead vegetation (Best et al. 1997). With this information, we derived 10 vegetation variables known to influence grassland bird numbers (following Rotenberry and Wiens 1980, Herkert 1994): mean litter depth, mean grass height, mean vegetation height, coefficient of variation of vegetation height, mean number of vegetation contacts (live grass + live forb + dead plant material) between 0 and 25 cm, mean number of vegetation contacts between 25 and 50 cm, mean number of total vegetation contacts, mean percentage grass contacts (grass cover), mean percentage forb contacts (forb cover), and mean percentage dead vegetation contacts (dead vegetation cover). “Forb contacts” refers to hits of vegetation types other than grasses or dead plant material (barley and sunflower contacts were included in this category). Mean values of cover variables (grass, forb, and dead vegetation cover) were obtained from the frequency of occurrence of each of these types at all sampling points ($n = 50$) associated with each bird transect

($n = 64$) and each sampling period ($n = 8$). For example, a 25% mean grass-cover value indicated that a quarter of all vegetation contacts on the metal rod recorded on all 50 sampling points (for a given transect and sampling period) were grasses. In this example, the other 75% would correspond to forb and/or dead vegetation (contacts) cover. Likewise, depth and height, as well as number of vegetation contacts, were also averaged over the 50 sampling points. For example, the height of the tallest grass that hit the rod was measured on each sampling point, and a mean was obtained from the 50 values available for each bird transect during each sampling period. Most of these variables have been identified as important factors for grassland birds (Fisher and Davis 2010). Woody vegetation, which has been found to influence grassland birds, was virtually absent from all sampling areas and, thus, was not measured. The numbers of vegetation contacts at different height intervals were indicative of vegetation density, and the coefficient of variation of vegetation height was used as a surrogate for vegetation patchiness. All bird and vegetation sampling was conducted by the same observer (A.B.A.). All vegetation surveys were conducted within 24 hr of the bird counts.

Data Analysis

Vegetation-structure information was used to determine differences among sites and sampling periods. All data were combined at the transect level for analysis. Thus, for each vegetation variable, the 50 values recorded on the

group of 5 vegetation transects (associated with each bird transect) were averaged to obtain a single mean value. These values were calculated for all bird transects ($n = 64$) and all sampling periods ($n = 8$). Because data did not meet the requirements of parametric analyses, a nonparametric alternative was used. First, a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to test the simultaneous response of multiple vegetation variables to 2 factors, namely site and time. Transect identity was included as a random factor nested in "site" to account for temporal nonindependence of the data (each transect was sampled 8 times during the whole study period). Analyses were performed on a Bray-Curtis similarity matrix with mean values; statistical significance was tested with a permutation procedure (9,999 runs). Estimates of components of variance (E) were used to compare the relative importance of the different terms in the model toward explaining overall variation (Anderson et al. 2008). After this analysis, a series of post hoc pairwise comparisons were conducted to identify differences between specific combinations of sites and sampling periods. These analyses were run with PRIMER version 6 and PERMANOVA+ (Anderson et al. 2008).

Second, canonical correspondence analysis (CCA) was used to identify dominant relationships between grassland-bird-assemblage data and vegetation-structure variables. Among alternative direct gradient analyses, CCA was selected after estimating gradient length through detrended CCA, following the procedure suggested by Lepš and Šmilauer (2003). CCA assumes that species' responses along environmental gradients are unimodal and reduces the species data set to a few orthogonal gradients (i.e. CCA axes), which reflect the influence of the multiple environmental variables included in the analysis (Morey et al. 2005). This is achieved by selecting linear combinations of these explanatory variables that best explain variation in the response variables (ter Braak 1995). The analysis provides a series of eigenvalues related to each of the CCA axes, which are indicative of the explanatory power of each axis with regard to the variation in the species data set. Substantial differences between subsequent eigenvalues suggest the existence of dominant environmental gradients. When results from CCA indicated high correlation among variables ($r \geq 0.80$), a subsequent analysis was run excluding 1 of the variables from correlated pairs. Also, because the removal of rare species generally results in higher eigenvalues and facilitates interpretation of graphical representation of CCA results (Kingston and Waldren 2003), bird taxa with <5 observations were excluded from these analyses. The explanatory power of the vegetation variables was tested by a Monte Carlo randomization procedure (499 runs). The influence of a variable was considered significant if the additional variance explained by it was greater than that

explained by 95% of the permutation tests (Morey et al. 2005). Because the first comprehensive CCA revealed important differences between obligate and facultative birds, a second set of analyses was conducted to determine the proportion of variation explained by the measured variables on each of these 2 groups of species separately.

Results from CCA were visually represented on an ordination graph. In restricted analyses, weighted averaging and linear combination (LC) scores have different properties pertinent to the interpretation of results (Graffelman and Tuft 2004). Given that one of the objectives of the study was to characterize vegetation-structure differences among sites under alternative management conditions, we used LC scores because they enable interpretation of the environmental characteristics of sites. In the resulting ordination diagrams, the environmental variables (i.e. vegetation-structure variables) are represented by arrows and the species scores are represented by symbols. The length of the arrow is proportional to the importance of the variable it represents, and the location of species scores in relation to arrows is informative of the environmental characteristics with which species are associated (Palmer 1993). CANOCO version 4.5 with CANODRAW (ter Braak and Šmilauer 2002) was used to run analyses and construct figures.

Finally, the vegetation variables used in CCA were divided into 2 groups: vegetation cover (grass, forb, and dead vegetation cover) and vegetation structure (litter depth, grass height, vegetation height, and variables related to numbers of vegetation contacts in different height intervals). With each of these groups of variables, partial CCAs were applied to determine the relative contribution of the 2 groups of variables and to establish how redundant their explanatory power was. This analysis, run in CANOCO, allowed designated variables to be treated as covariables and total variation explained by CCA to be partitioned (Wiser 1998). The analysis identifies the amount of explained variation accounted for by each group exclusively, as well as the amount explained jointly by them. If the latter value is small, this is indicative of low redundancy, suggesting that each group of variables explains different aspects of the species dataset. As with CCA, statistical significance was determined by Monte Carlo permutation tests. Sampling periods were not pooled in either CCA or partial CCA analyses.

RESULTS

Vegetation structure varied among sites. Overall, vegetation structure was highly related to site (PERMANOVA, $F_{3,255} = 72.18$, $P = 0.0001$), to time (PERMANOVA, $F_{7,255} = 30.91$, $P = 0.0001$), and, to a lesser degree, to the site \times time interaction (PERMANOVA, $F_{21,255} = 17.9$, $P = 0.0001$). The effect of site was the most important in differentiating vegetation structure among samples. Although a transect

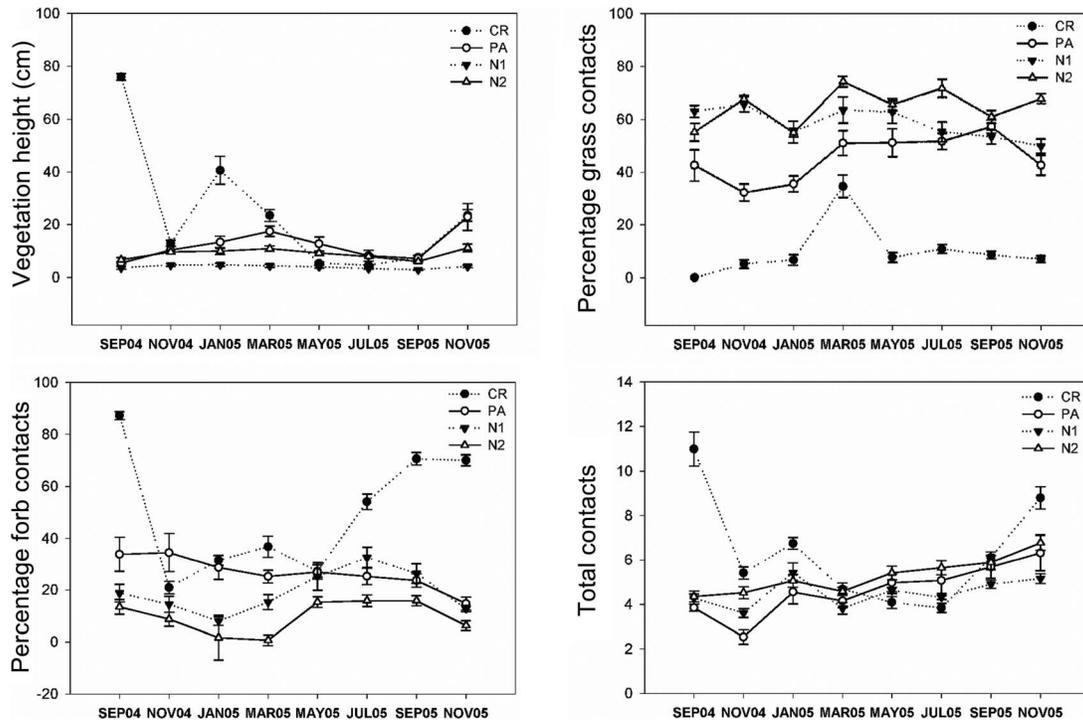


FIGURE 4. Temporal variation of 4 vegetation variables (mean \pm SE) that explained differences among the 4 study sites in the Northern Campos of Uruguay: "Crop" (CR), "Pasture" (PA), "Native 1" (N1), and "Native 2" (N2).

effect was evident (PERMANOVA, $F_{28,255} = 4.26$, $P = 0.0001$), its role in explaining the overall variation ($E = 42.5$) was weaker than that of site ($E = 495.2$), time ($E = 97.8$), or their interaction ($E = 220.9$). Post hoc pairwise comparisons indicated that, with the exception of Pasture compared to Native 1 and Native 2 in period 7 (November 2005), all other site combinations showed significant differences in vegetation structure throughout all sampling periods. Mean vegetation height was shortest in Native 1 (<5 cm), followed by Native 2 (<12 cm) and Pasture (<23 cm) (Figure 4). Vegetation height in Crop showed considerable variation throughout the sampling period, but the opposite was true in Native 1 and Native 2, where mean values were similar throughout the study (Figure 4). Grass cover was, in general, higher in natural grassland sites than in Pasture. In Crop, mean values of grass cover were very low except for in March 2005, shortly before a second crop (sunflower) was harvested (Figure 4). Forb cover showed higher mean values in Crop and Pasture than in natural grassland sites.

The presence and numbers of grassland birds varied according to vegetation-structure features. The 4 CCA axes explained 14.8% of the total variance in the bird dataset and 87.7% of the canonical variance (Table 1). Axis 1 represented a fairly strong gradient (Table 1) that indicated a positive correlation with vegetation height and forb coverage and a negative correlation with grass cover.

Axis 2 was positively correlated with vegetation density (Table 1 and Figure 5). Partial CCA showed that the percentages of variation explained independently by vegetation-structure variables (4.1%) and vegetation-cover variables (8.8%) were larger than the variation explained by the overlap effects of both variable groups (3.9%). Thus, each group explained different aspects of the variation included in the bird dataset.

Among obligate species, 3 main groups were identified. The first included species associated with areas of tall vegetation in which forb cover and dead vegetation were also important features. Species located toward the extreme of the height gradient included Dark-throated Seedeater, Red-winged Tinamou, and White-browed Blackbird, whereas Fork-tailed Flycatcher was associated with high values of forb cover and dead vegetation. A second group was positively correlated with vegetation patchiness. Spotted Nothura, Greater Rhea, Upland Sandpiper, and Southern Lapwing were correlated with intermediate values of patchiness, whereas Burrowing Owl was associated with areas that had higher scores. The third group of obligate birds was positively associated with grass cover. Pampas Meadowlark and Ochre-breasted Pipit occurred in areas with higher grass-cover values than those in which Short-billed Pipit, Hellmayr's Pipit, and South American Snipe occurred (for scientific names of species, see Figure 5).

TABLE 1. Canonical correspondence analysis (CCA) of count data for 36 species of Pampas grassland birds and 10 vegetation-structure variables in the Northern Campos of Uruguay.

(A)	Axis			
	1	2	3	4
Eigenvalue	0.343	0.100	0.062	0.035
Cumulative percentage variance				
Species data	9.4	12.1	13.8	14.8
Species–environment relation	55.6	71.9	82.0	87.7
Sum of all eigenvalues: 3.651				
Sum of all canonical eigenvalues: 0.616				
Test significance of first canonical axis: F -ratio = 25.27, P = 0.002				
Test significance of all canonical axes: F -ratio = 4.95, P = 0.002				
(B)				
Vegetation variable	Weight (first 2 axes)			
Litter depth	−0.0349	0.0337		
Grass height	0.0386	0.2838		
Vegetation height	0.6044	0.2494		
Coefficient of variation_vegetation height	−0.2525	−0.1480		
Total vegetation contacts	0.3264	0.4984		
Vegetation contacts 0–25 cm	0.0369	0.4434		
Vegetation contacts 25–50 cm	0.0032	−0.0084		
Grass cover	−0.7025	0.1944		
Forb cover	0.5086	0.1055		
Dead vegetation cover	0.3555	−0.0760		

Among facultative species, the main group—including several agricultural pests, such as Spot-winged Pigeon, Picazuro Pigeon, Eared Dove, Monk Parakeet, and Shiny Cowbird—showed no strong positive association with any single variable measured. Alternatively, 2 other, smaller groups—represented by Campo Flicker, Firewood-gatherer, and Tawny-headed Swallow; and by Gray-breasted Martin and White-rumped Swallow—were positively correlated with vegetation patchiness and vegetation height, respectively (Figure 5). A second set of analyses in which obligate and facultative species were considered separately revealed that the proportion of variation explained in the case of the obligate species (18.7%) was greater than that for facultative birds (10.2%).

DISCUSSION

Vegetation structure differed among sites, and most of the differences can be linked to specific management activities typical of each. The Crop site included several management phases, which explains the high variability in several vegetation parameters. By contrast, year-round grazing in the Pasture, Native 1, and Native 2 sites resulted in less variable vegetation throughout the study period.

As in other grassland studies, abundances of several species were associated with vegetation height and patchiness. The effects of these variables have been interpreted in terms of foraging, cover, and nesting opportunities (Grzybowski 1976, Isacch and Martínez

2001, Nocera et al. 2007, Codesido et al. 2013, Dias et al. 2014). In the Pampas, specific foraging and nesting requirements determine the strength of associations with either tall-grass or short-grass habitats (Isacch and Martínez 2001, Isacch et al. 2005, Isacch and Cardoni 2011, Dias et al. 2014). For example, the benefits of nest concealment in taller or denser vegetation may need to be balanced with predator-detection efficiency by feeding and nesting birds, which is facilitated in shorter vegetation (Colwell and Dodd 1995, Götmark et al. 1995). In fact, the association of some obligate Pampas grassland birds with patchy vegetation is well known (Isacch and Cardoni 2011). In our study, Greater Rheas and Southern Lapwings were positively associated with intermediate values of patchiness. This supports earlier findings and reported natural-history characteristics of these species. Southern Lapwings were related to patches of short grasslands within plots of taller vegetation in southern Brazil (Dias et al. 2014), whereas Greater Rheas nested in short grass surrounded by taller vegetation (Codesido et al. 2013). With respect to facultative species, as in our study, the Firewood-gatherer was also associated with vegetation patchiness in grasslands of southern Brazil (Dias et al. 2014). Alternatively, other facultative-patchiness-related species (invertebrate-eating passerines) identified by Dias et al. (2014) were not primarily associated with this variable in the Northern Campos of Uruguay.

Grass cover, which was better represented in natural than in cultivated grassland sites, was important for some

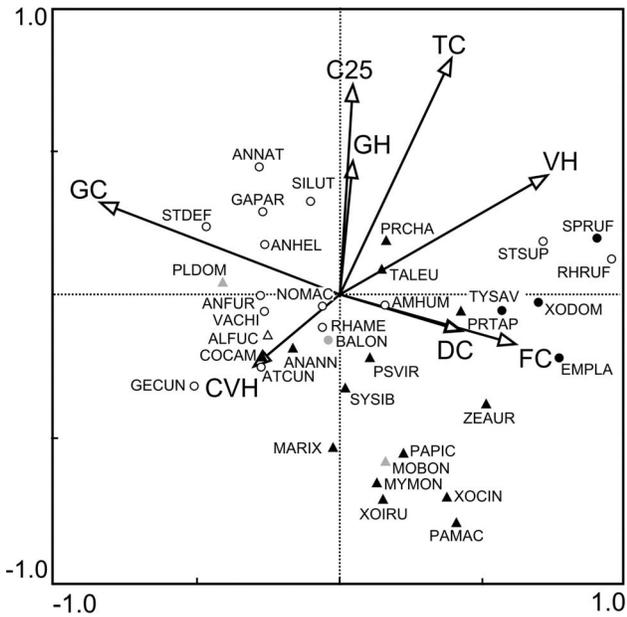


FIGURE 5. Pampas grassland-bird species along a vegetation-structure gradient in the Northern Campos of Uruguay. The ordination diagram from canonical correspondence analysis (CCA) shows vegetation-structure variables (arrows) and 5 grassland-bird categories (circles = obligate; triangles = facultative; open symbols = ground-nesting species; black symbols = species that nest off the ground; and gray symbols = nonbreeders and a generalist brood parasite). The vegetation-structure variables are mean grass height (GH), mean vegetation height (VH), mean contacts under 25 cm (C25), mean total contacts (TC), mean percentage grass contacts (% GC), mean percentage forb contacts (% FC), and mean percentage dead vegetation contacts (% DC). Arrows representing mean litter depth (LD) and mean contacts between 25 and 50 cm (C50) were very short and are not depicted here. The 36 bird species are Greater Rhea (*Rhea americana*; RHAME), Spotted Nothura (*Nothura maculosa*; NOMAC), Red-winged Tinamou (*Rhychochotus rufescens*; RHRUF), Whistling Heron (*Syrigma sibilatrix*; SYSIB), American Golden-Plover (*Pluvialis dominica*; PLDOM), Southern Lapwing (*Vanellus chilensis*; VACHI), Upland Sandpiper (*Bartramia longicauda*; BALON), South American Snipe (*Gallinago paraguaiiae*; GAPAR), Picazuro Pigeon (*Patagioenas picazuro*; PAPIC), Spot-winged Pigeon (*P. maculosa*; PAMAC), Eared Dove (*Zenaida auriculata*; ZEAUR), Burrowing Owl (*Athene cunicularia*; ATCUN), Campo Flicker (*Colaptes campestris*; COCAM), Monk Parakeet (*Myiopsitta monachus*; MYMON), Common Miner (*Geositta cunicularia*; GECUN), Firewood-gatherer (*Anumbius annumbi*; ANANN), Gray Monjita (*Xolmis cinereus*; XOCIN), White Monjita (*Xolmis irupero*; XOIRU), Black-and-white Monjita (*X. dominicanus*; XODOM), Cattle Tyrant (*Machetornis rixosus*; MARIX), Fork-tailed Flycatcher (*Tyrannus savana*; TYSAV), Tawny-headed Swallow (*Alopochelidon fucata*; ALFUC), Brown-chested Martin (*Progne tapera*; PRTAP), Gray-breasted Martin (*P. chalybea*; PRCHA), White-rumped Swallow (*Tachycineta leucorroha*; TALEU), Short-billed Pipit (*Anthus furcatus*; ANFUR), Ochre-breasted Pipit (*A. nattereri*; ANNAT), Hellmayr's Pipit (*A. hellmayri*; ANHEL), Grassland Yellow-Finch (*Sicalis luteola*; SILUT), Great Pampa-Finch (*Embernagra platensis*; EMPLA), Dark-throated Seedeater (*Sporophila ruficollis*; SPRUF), Grassland Sparrow (*Ammodramus humeralis*; AMHUM), Brown-and-yellow Marshbird (*Pseudoleistes virescens*; PSVIR), Shiny Cowbird (*Molothrus bonariensis*; MOBON), White-browed Blackbird (*Sturnella supercilialis*; STSUP), and Pampas Meadowlark (*S. defilippii*; STDEF).

species of conservation concern. This was the case for the Pampas Meadowlark and Ochre-breasted Pipit. In the southern Pampas, a study that focused on the Pampas Meadowlark also revealed its association with features characteristic of natural grasslands (Fernández et al. 2003). The ecology of the Ochre-breasted Pipit is little known, but its association with natural grasslands has also been highlighted (Bencke et al. 2003, Chebez et al. 2008). By contrast, other threatened grassland specialists were associated with forb cover, which tended to be higher in cultivated grasslands. In fact, Black-and-white Monjita and Dark-throated Seedeater were recorded only in cultivated grassland sites. With respect to the former, a similar finding was reported by da Silva et al. (2015), who suggested that the availability of key resources may be a plausible explanation. In our study, Black-and-white Monjitas were recorded only during the breeding season, which may reflect the use of foraging (stubble fields) and nesting (nearby native grassland patches) opportunities in a landscape-complementation fashion (*sensu* Dunning et al. 1992) within areas dominated by croplands during this period (see Codesido et al. 2013, da Silva et al. 2015). Unlike the Black-and-white Monjita, the Dark-throated Seedeater is known to use invasive weeds (which are frequent in crop-dominated landscapes) for nest placement (de la Peña 2005).

As expected, vegetation structure explained more variation in abundance among obligate than among facultative grassland-bird species. Vegetation structure is known to be important to species that nest in open fields (Bradbury and Bradter 2004, and references therein). Thus, differences reported here are most likely related to the fact that, unlike grassland-obligate birds, other grassland species rely on this habitat for feeding but not for breeding purposes (see Batáry et al. 2007). In fact, habitat models for grassland species are correlated with nesting requirements (Fletcher and Koford 2002). Alternatively, facultative species may be influenced by features that were not measured in this study or, because of their generalist nature, may be able to inhabit sites with varying characteristics.

Even though bird distribution and abundance were associated with the vegetation variables considered, the substantial amount of variation in the bird dataset that was unexplained indicated the influence of other important drivers. These may include other unmeasured vegetation-structure variables, floristics, and/or temporal and spatial scale effects. These factors may exert a variety of negative effects on grassland birds, and in some cases these effects may be interrelated. With respect to additional unmeasured structural variables, vegetation volume, for example, is known to be correlated with breeding-bird density. Mills et al. (1991) suggested that the total number of birds in southwestern lowland habitats of North America was

dependent on resources associated with the amounts of vegetation present (insect prey, nest sites, or roosts). Some studies have found that distribution and abundance of grassland birds are associated with floristic variables (e.g., Rotenberry 1985). In the Northern Campos of Uruguay, recent grassland floristic surveys have found a diverse array of plant communities (Lezama et al. 2006); thus, the relationship between this floristic diversity and grassland birds warrants further examination. The scale of spatial resolution is also known to influence the response of birds to key habitat characteristics (Wiens and Rotenberry 1981, Ribic and Sample 2001, Cunningham and Johnson 2006). For example, North American shrub-steppe species can show strong correlations with features of habitat structure at the continental scale, but these associations are much weaker at the regional scale (Wiens and Rotenberry 1981). Also, landscape structural features (e.g., ponds and roads) may influence local grassland-bird communities (Coppedge et al. 2008, Codesido et al. 2013).

The present study is the first to examine how bird distribution and numbers are linked to vegetation structure in the Northern Campos of Uruguay. Our results provide evidence that differences in bird assemblages can be explained, in part, by differences in vegetation structure among alternative agricultural management schemes. Unlike facultative species, many grassland-specialist birds were associated with features (i.e. high grass cover) that are typical of native grasslands used by livestock. Others, however, were associated with features (i.e. taller vegetation) more characteristic of croplands. These findings are in agreement with those of previous studies (e.g., Fernández et al. 2003, Isacch et al. 2005, Azpiroz and Blake 2009, Codesido et al. 2013, Dias et al. 2014, Cardoni et al. 2015, da Silva et al. 2015) that have highlighted the importance of native grasslands for many typical Pampas birds, but our results also show that many species make use of highly modified grasslands. Thus, from a conservation perspective, Pampas grassland-bird populations would benefit from policy strategies focused on the preservation of native grasslands, but also from management guidelines for agriculture sites. For grasslands converted to agriculture, additional studies are needed to better understand grassland-bird resource use. While the presence of some birds may be related to the high resource availability (e.g., seeds) within crop fields themselves (Codesido et al. 2013), others may depend on nearby nesting or foraging opportunities in native habitat patches (da Silva et al. 2015). Different management guidelines would be needed to benefit species under these alternative scenarios.

ACKNOWLEDGMENTS

A.B.A. is grateful to J. T. Rotenberry for useful advice concerning vegetation sampling methods and to M. W.

Palmer for assistance on ordination techniques. We are indebted to M. Bonifacino, who kindly provided his expertise on Uruguayan vegetation topics. For comments and insight on the manuscript, we thank S. Davis, M. Lawes, D. Chamberlain, R. E. Ricklefs, P. Vickery, B. Loiselle, A. Rodríguez-Ferraro, L. Brotons, N. Martínez-Curci, and three anonymous reviewers. A.B.A. is especially grateful to numerous landowners, personnel, and field assistants, who granted access to their property and provided invaluable help in data gathering and in many other ways.

Funding statement: Funds and equipment for this study were provided by Wildlife Conservation Society, The Rufford Foundation, Neotropical Grassland Conservancy, Cleveland Zoological Society, Idea Wild, and Sigma Xi. None of the funders had any influence on the content of the submitted or published manuscript. None of the funders require approval of the final manuscript to be published.

Ethics statement: We followed the protocol of the University of Missouri–St. Louis.

Author contributions: A.B.A. and J.G.B. equally conceived the idea, design, and experiment; A.B.A. collected the data and conducted the research; A.B.A. and J.G.B. wrote the paper; A.B.A. and J.G.B. developed and designed the methods; A.B.A. analyzed the data; and A.B.A. and J.G.B. contributed substantial materials, resources, or funding.

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