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Grassland Birds in Natural and Cultivated Grasslands in the Northern Campos of Uruguay: Diversity Patterns, Responses to Vegetation Structure, and Nest Survival

A Dissertation presented to the Graduate School of the
University of Missouri-St. Louis in partial fulfillment of the requirements for the
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By

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General Abstract

Grassland bird populations are declining in many regions as a consequence of habitat modification and these declines have generated substantial effort to determine how grassland species cope with changes in habitat features, especially in agricultural landscapes. Grassland bird research has been concentrated in North America and Europe where changes in bird community composition and widespread species declines have been documented. In the Neotropical Region, however, many aspects of grassland bird ecology remain virtually unexplored. Avian communities currently associated with habitats that have experienced different land-use practices have not been fully characterized. The objective of this study was to examine the effects of habitat modification on the distribution, abundance, and reproductive success of grassland birds in the Northern Campos of Uruguay. The study focused on birds that inhabit four grassland habitats which differed in terms of agricultural management in the Northern Campos of Uruguay. Bird assemblages in croplands, planted pastures, and two natural grasslands under different grazing regimes were studied. First, distance sampling was used to characterize bird diversity patterns and population densities along the agricultural gradient. Second, nine vegetation structure variables were quantified and the response of birds species to these variables was assessed with multivariate analyses. Finally, systematic nest searching and monitoring activities were conducted during two breeding seasons and this information was used to estimate nest success patterns of both common and globally threatened species.

Overall, a total of 50 species were recorded; cultivated and natural grasslands were dominated by grassland facultative and obligate species, respectively. Some threatened species (*Anthus nattereri*, *Sturnella defilippi*) were largely restricted to natural grasslands. In terms of vegetation structure, grass cover and vegetation height were the two variables to which birds responded most strongly. With respect to nest survival, models that included temporal trends (i.e., seasonal effects) and habitat type effects were the ones best supported by the data. Nest survival of grassland birds was relatively low, but within the range documented in other grassland ecosystems. Contrary to expectation, nest survival of threatened taxa did not differ from that of common congenerics.

This study is the first characterization of grassland bird communities inhabiting an agricultural landscape in the Northern Campos of Uruguay. Using modern sampling techniques and inferential procedures, information on bird diversity patterns and species-habitat relationships was combined with reproductive success data to provide a clear understanding of the effects of habitat alteration on grassland bird populations. The results from this study provide a useful baseline for the development of guidelines targeting bird conservation and land management in the grasslands of the Pampas region.

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CHAPTER 1

AVIAN ASSEMBLAGES IN ALTERED AND NATURAL GRASSLANDS IN THE NORTHERN CAMPOS OF URUGUAY

INTRODUCTION

Grassland bird ecology and conservation have received substantial attention during the last decade. Numerous studies, mostly conducted in Europe and North America, have documented changes in the composition of grassland bird communities, as well as substantial declines of particular species highly dependent on grassland habitats (Zimmerman 1988, Knopf 1994, Tucker and Heath 1994, Patterson and Best 1996, Vickery et al. 1999, Murphy 2003). Declines of grassland birds worldwide have been recognized as a "prominent wildlife conservation crisis of the 21st century" (Brennan and Kuvlesky 2005). Habitat modification, particularly related to agricultural expansion and intensification, has been identified as one of the main causes of such declines (Askins et al. 2007). In the Neotropics, population declines of grassland birds have also been reported, especially in lowland grasslands (Tubaro and Gabelli 1999, Vickery et al. 1999 and references therein), but specific studies on the effects of alternative land-use practices on grassland bird assemblages are still scarce. In fact, there has been a call to extend the current active research effort targeting grassland birds in North America to South America, not only to elucidate the wintering ecology of Nearctic migrants, but also to establish the conservation needs of resident endemic species (Vickery and Herkert 2001). In the Neotropical region, the most important expanse of grasslands is located in south-eastern South America and is known as the Río de la Plata grasslands (Soriano 1992).

This region (ca. 700,000 km^2), which is included within the Pampas biome (*sensu* Stotz et al. 1996), is dominated by temperate sub-humid grasslands that extend from 28 to 38° S and cover the plains of east-central Argentina, Uruguay and southern Brazil (Soriano 1991). The original vegetation was a tall-grass steppe, intermingled with prairies, marshes, and other edaphic communities (Bucher and Nores 1988). These grasslands have, however, been heavily modified by long-term human use (Bucher and Nores 1988). Cattle were introduced to the Pampas in the 16th century (Vickery et al. 1999) and the development of sheep farming in the late 1800s intensified the use of these grasslands, while the building of fences introduced further alterations (Soriano 1991). Agricultural expansion after 1890 has had the most profound effects on this ecosystem. Apart from direct habitat loss, conversion to cropland involved other forms of modification from planting of exotic grasses, succession to shrublands and increased use of agrochemicals and technology (Vickery et al. 1999). In addition, agricultural operations in crop fields are known to negatively affect bird reproduction as a consequence of nest trampling (Wilson et al. 2005 and references therein). Today, in some mesic regions of the Pampas, more than 50% of the land is devoted to agriculture (Vickery et al. 1999).

Pre-settlement information on grassland bird assemblages in the Pampas is limited, but evidence exists that the loss of pristine habitats in the region, as a consequence of expansion of agriculture and livestock grazing, has affected bird populations, producing marked decreases in species abundances and local extinctions (e.g., Bucher and Nores 1988, Soriano 1991, Collar et al. 1992, Tubaro and Gabelli 1999). Recent studies in the Flooded Pampa of eastern Argentina have shown that changes in the structure of grassland habitats due to the effects of fire or grazing result in the replacement of grassland specialists, highly dependent on tall grasslands, by others that prefer short grasslands (Comparatore et al. 1996, Isacch and Martínez 2001). These patterns are similar to those reported in areas of North America where declining grassland endemics have been replaced by more widespread counterparts (Knopf 1994). Studies in the Argentinean Pampas have produced differing results with respect to species richness and abundance. In the Flooded Pampa, species richness and abundance were positively related to the amount of tallgrass cover (Isacch and Martínez 2001), whereas in the West Pampa, grasslands under higher grazing pressure supported more species and individuals than patches of more pristine habitats (Isacch et al. 2003).

In spite of these recent efforts, patterns of avian diversity currently associated with different land-use practices in the Pampas have not been fully characterized and more studies are needed to further assess the role of landscape alteration in shaping bird assemblages in South American grasslands. This is particularly important in Uruguay, located within the "campos" subregion of the Pampas, where agricultural lands are the most extensive wildlife habitat and, thus, represent key habitats for biodiversity; croplands, pastures, and rangelands greatly exceed those areas set aside for wildlife reserves (OEA 1992, World Resource Institute 2007).

Here, I present results of the first study to examine the effects of land-use practices on grassland bird communities in the Northern Campos of Uruguay. A major goal of this study was to determine the relative value for grassland bird conservation of areas that are under different management schemes. First, I characterized the distribution and seasonality of birds associated with croplands, pasturelands, and two types of native grasslands. Second, I compared species richness and abundance of bird communities found in each of these four habitat types. Finally, I examined the findings of this study in the light of data from other subregions of the Pampas and elsewhere. Based on theoretical grounds, and on the results of previous grassland bird research (mostly developed outside the Pampas), I expected natural grasslands to support more species and higher densities of grassland specialists than would cultivated lands, as well as more threatened taxa. Factors, such as habitat loss, that reduce niche availability should represent a particular threat to species that are ecologically specialized (Owens and Bennett 2000). If the degree of habitat specialization is a valid surrogate for ecological specialization, the proportion of grassland specialists (i.e., species that are highly dependant on grassland habitats) should be inversely related to the degree of habitat loss. Thus, obligate grassland species should be less well represented in terms of species numbers and densities in habitats where alteration has been more drastic (i.e., cultivated grasslands).

METHODS

STUDY AREA

This study was conducted in the Northern Campos subregion of the Río de la Plata grasslands (Soriano 1991) within the Pampas biome (*sensu* Stotz et al. 1996; Fig. 1). This subregion extends through most of Rio Grande do Sul, Brazil, southeastern Misiones and eastern Corrientes provinces in Argentina, and northern Uruguay (Bilenca and Miñarro 2004). Within the Northern Campos, the study area was located in southern Salto and northwestern Paysandú departments (31°19’ to 31°44’S and 56° 42’ to 57° 56’W) and it was composed of rolling topography in which low mesas and rocky outcrops are interspersed. The area has mesothermic and humid features (Soriano 1992), with a mean annual temperature of 19°C and mean annual rainfall of 1300 mm (Lezama et al. 2006). Cattle ranching is the major activity, mainly on natural pastures, but also on planted pastures, the latter found especially in the west. Cropland also is widespread in the west, especially fields of wheat and barley. The eastern part of the study region is characterized by large expanses of natural grasslands which have never been plowed and which are used for open-range livestock grazing. The study was conducted on ranches and farms in the surroundings of Chapicuy, in Paysandú department, and San Antonio and Cerros de Vera in Salto department (Fig. 1). Large patches of each habitat type (500 to 1200 ha) were selected within each of these areas.

HABITAT DESCRIPTIONS AND SPECIES DEFINITIONS AND CATEGORIES

The study focused on birds that inhabit four grassland habitats. A grassland habitat is defined as "any extensive area that is dominated by more than 50% grass (Poaceae) or sedge (Cyperaceae) cover and that generally has few scattered shrubs (< 4 m high) and trees" (Vickery et al. 1999). In northern Uruguay, as in other parts of the Pampas, native vertebrate herbivores, especially Pampas Deer (*Ozotoceros bezoarticus*), have been almost completely replaced by domestic livestock; *Rhea americana* is still relatively common throughout the region. Crops and planted pastures have replaced native vegetation in some areas and are considered here as grassland-like habitats. Thus, grasslands were classified into habitat categories on the basis of different cultivation and grazing regimes. A description of each habitat type follows (Fig. 2):

(1) Crop habitat (Crop) was represented by barley fields which were integrated into a livestock grazing system where the crop is rotated with planted pastures that are grazed after the crop is harvested. In fact, this habitat type consisted of three different

management phases: 1) barley fields and stubble, 2) sunflower residual crop fields and stubble, and 3) planted pastures. Barley and pastures were planted in austral winter 2004. By the time bird censuses were initiated (September 2004), barley fields were well developed (> 1m height) and planted pastures were starting to grow beneath the crop. Barley was harvested in late October 2004. From December 2004 to March 2005, a residual crop of sunflower grew on these fields. This second crop developed from seeds that fell to the ground during the sunflower harvest in early 2004 and it was harvested in late March 2005; afterwards, the fields were used for cattle grazing on the planted pastures until the end of the study (November 2005). The management of this cropland is typical of areas in this part of the country.

(2) Planted pastures habitat (Pasture) consisted of grasslands that have been seeded to exotic grasses. These pastures were part of dairy farms and were used for cattle grazing.

(3) Sheep habitat (Sheep) was represented by fields of native grasslands that are grazed by livestock. On these fields cattle and sheep forage on native grasses and forbs. Due to the effects of grazing by sheep, vegetation diversity is lower than that in the following habitat type (Sturm 2001).

(4) Deer habitat (Deer) consisted of fields of native grasslands grazed by cattle and Pampas Deer. The latter are thought to be indicative of distinct grassland habitats (Sturm 2001). Due to the lack of sheep grazing (only about 20-30 sheep were maintained on these fields to supply the ranch), this habitat supports, in general, a more complex and higher vegetation structure than Sheep (Sturm 2001).

Cultivated habitats (Crop and Pasture) and natural grasslands (Sheep and Deer) differ with respect to two important management activities: use of agrochemicals and plowing. These activities are absent from natural grasslands. Additionally, the former habitat types were located within a matrix of croplands and planted pastures. In contrast, Sheep and Deer sites were included in a matrix under similar activities to those found in Sheep. However, because the study was conducted on large patches of each habitat type, any confounding effects related to matrix composition were minimized.

Vickery et al. (1999) defined grassland birds on an ecological basis: “any species that has become adapted to and reliant on some variety of grassland habitat for part or all of its life cycle…”. They also identified two groups of grassland birds, obligate and facultative species. The former are those “exclusively adapted to and entirely dependent on grassland habitats and make little or no use of other habitat types”, while the latter “use grassland as part of a wider array of habitats… [and thus] are not entirely dependant on grasslands but use them commonly and regularly”. Here I have followed Vickery et al.’s (1999) definitions of grassland birds with minor modifications. First, a series of species not included in Vickery et al.’s scheme were classified here as grassland facultative birds. This applies to *Pluvialis dominica* and six species of Hirundinidae. Additionally, three of Vickery et al.’s facultative species were classified as obligate here: *Rhea americana*, *Podager nacunda*, and *Neoxolmis rufiventris*. I believe these adjustments better reflect these species’ dependence on grassland habitats in Uruguay (Azpiroz 2001). Species were classified into four categories reflecting migration patterns: residents (present year-round), summer residents (breeders that move northward during most of austral fall and winter, April-September), Nearctic migrants (non-breeders that are present in Uruguay during the austral spring and summer, September-March) and winter migrants (non-breeders that are present in Uruguay during the austral fall and winter, April-September). Birds were also classified according to five feeding guilds which reflect the main component of their diets: carnivores, granivores, herbivores, insectivores, and omnivores. Information on species migratory status and diet in the Pampas were taken from the literature (e.g., Gore and Gepp 1978, Sick 1985, Canevari et al. 1991, Azpiroz 2001).

GRASSLAND BIRD SURVEYS

I conducted bird counts on eight 500-m variable-width transects on each of four habitat types every two months from September 2004 to November 2005. Thus, each transect was sampled eight times during the whole sampling period. Transects were located at least 400 m apart, far from fencerows (> 400 m), and avoided the intersection of other non-grassland habitats (i.e. gallery forest). Transects were selected randomly after considering these constraints. All bird surveys were conducted by the author who has extensive experience with the birds of the region. I walked transects at a pace of approximately 1km/hour from 0 to 3.5 hours after sunrise and recorded all birds seen or heard on each side with the exception of individuals passing by and making no use of the surveyed area. Swallows feeding on the wing within the surveyed plots were, however, recorded. Coverage of transects and the direction walked on each were rotated systematically. Distances and angles from transects to individuals were estimated with a rangefinder and a compass, to allow calculation of perpendicular distances (see Buckland et al. 2001). These data were used to estimate variables (species richness, composition and density) to describe the avian community structure on each study site.

DATA ANALYSIS

Species richness - I calculated bird species richness in each habitat type as the total number of species encountered in all transects in each habitat across all sampling periods. I also calculated an estimate of species richness using observed species abundance distribution data and program SPECRICH (Hines 1996) which estimates total number of species using methods described in Burnham and Overton (1979). To determine differences in mean number of species and individuals per transect among habitats, I performed one-way analyses of variance (ANOVA); and I used a repeated-measures analyses of variance (rmANOVA) to test for seasonal differences in species richness and number of individuals among habitats. Data were tested for normality and when necessary standard transformations were applied. All analyses of variance were run in SPSS, version 15.0 (SPSS 2006). I compared the rates of species accumulation across habitats through rarefaction analyses based on Monte Carlo simulations run 1000 times using EcoSim 7 (Gotelli and Entsminger 2006). The analyses were based on a sample of 1038 individuals, which was the lowest number of birds recorded for any habitat (Deer).

Community composition - I used species presence/absence data over all sampling periods in each habitat to calculate Bray-Curtis similarity coefficients among habitat types. Data from the similarity matrix were also used to test for differences in species composition among habitats through an analysis of similarity (ANOSIM; described in Clarke and Warwick 2001). ANOSIM determines whether samples (i.e., transects) within each habitat type are more similar to each other than samples taken at random from the whole sample pool (i.e., 32 transects). Thus, ANOSIM compares the level of similarity among transects of a given habitat to that among transects of all habitats and determines if the former is greater than expected by chance. Results from ANOSIM were tested for significance with a Monte Carlo randomization procedure. Afterwards, I used nonmetric multidimensional scaling (MDS) to graphically compare species composition among transects and habitats. ANOSIM and MDS were done with PRIMER version 5.2.9 (Clarke and Gorley 2002) and PC-ORD version 4 (McCune and Mefford 1999), respectively. Across-habitat differences in the proportions of species included in categories of grassland habitat specialization, migration and feeding guild were tested with *G*-tests. In order to identify characteristic species of each habitat type, I used an indicator-species analysis (Dufrêne and Legendre 1997). This analysis, which was conducted in PC-ORD version 4 (McCune and Mefford 1999), calculates an indicator value for species based on their relative frequency and relative abundance in all treatment categories (i.e., habitat types). Indicator values can range from 0 (no indication) to 100 (perfect indication). A species' perfect indication for a given habitat means that it was recorded in all samples (i.e., transects) within that habitat and was not observed in any of the samples of other habitats. Indicator values were tested for significance with a Monte Carlo randomization procedure which compares the observed indicator values to alternative values calculated from the same data and randomly assigned to habitat type. Only species with indicator values that were significant ($P \leq 0.01$) and > 25% are reported.

Population densities - I used program DISTANCE version 5.0 (Thomas et al. 2005) to estimate densities of grassland birds from census data obtained on transects. I constructed detection functions for all species with at least 60 observations. For each species, data were grouped across habitats except when vegetation structure was thought to influence detection probability. For example, census data obtained in fields of barley and sunflower were used separately from data from other habitats where vegetation was significantly lower (Chapter 2). Additionally, in a few cases species with similar morphological and behavioral traits were grouped together in order to increase sample sizes to allow for detection function construction (see Table 4 for details). The probability of detecting each species as a function of perpendicular distance from the transects was determined by using the robust models suggested by Buckland et al. (2001): uniform key function with cosine and simple polynomial expansion series, the half normal key function with cosine and hermite polynomial expansion series, and the hazard rate key function with cosine and simple polynomial expansion series. I evaluated each of these models considering the complete data set (i.e., all observations) or subsets with 5 and 10% truncation of detections at largest distances to reduce errors incurred by outliers, as recommended by Buckland et al. (2001). Model suitability was evaluated through Akaike's Information Criterion (AIC). Density estimates are presented with standard errors and 95% confidence intervals; estimates were considered significantly different for values with non-overlapping intervals.

RESULTS

SPECIES RICHNESS

Throughout the whole 14-month sampling period, 4968 individuals of 50 grassland bird species were recorded on all transects (Appendix). Total observed species richness varied from 24 on Deer to 34 on Sheep (Table 1, Fig. 3). Species richness values estimated with SPECRICH ranged from 26 ± 2.0 for Deer to 38 ± 2.8 for Sheep (Table

1). The lowest number of individuals (1038) was recorded in Deer while the highest (1555) was found in Crop. Species richness estimates corrected through rarefaction analysis resulted in similar patterns (Table 1).

Species richness in transects in Sheep and Crop showed the largest variation (10 to 21 and 11 to 20 species, respectively). Transects in Crop also showed the largest variation in numbers of individuals (95 to 464). In contrast, transects in Deer showed the least variation, both in terms of species (12 to 16) and individuals (104 to 144). However, largely because of this variation, mean number of species (one-way ANOVA, $F_{3,28} = 0.81$, $P = 0.50$) and individuals (one-way ANOVA, $F_{3,28} = 0.42$, $P = 0.74$) per transect for the total sampling period did not differ significantly across habitats.

The mean number of species per habitat varied significantly throughout the sampling period (Fig. 4A), and responded to the effects of time (rmANOVA, $F_{7,196} = 7.46$, $P < 0.001$), habitat (rmANOVA, $F_{3,28} = 10.66$, $P < 0.001$), and time x habitat interaction (rmANOVA, $F_{21,196} = 2.99$, $P < 0.001$). Mean number of individuals per habitat (Fig. 4B), varied as an effect of time (rmANOVA, $F_{7,196} = 2.09$, $P = 0.045$) and time x habitat interaction (rmANOVA, $F_{21,196} = 2.09$, $P = 0.005$); in this case, the effect of habitat was not significant (rmANOVA, $F_{3,28} = 1.12$, $P = 0.359$). During May 2005, a few large flocks (i.e., ≥ 38 individuals, the largest flock size recorded during the whole sampling period) of *Zenaida auriculata* and *Molothrus bonariensis* were observed in Crop (Fig. 4B). When these flocks were excluded from the analysis, the effect of time (rmANOVA, $F_{7,196} = 1.75$, $P = 0.099$) was not significant and the effect of time x habitat interaction (rmANOVA, $F_{21,196} = 1.58$, $P = 0.058$) was only marginally so.

SPECIES COMPOSITION

The 50 species recorded during the study belong to 18 families and include 23 obligate and 27 facultative grassland birds, 14 migrants, and seven globally threatened or near-threatened taxa. In terms of species composition, Crop and Pasture were the most similar habitats, whereas Crop and Deer were the most dissimilar (Table 2). The analysis of similarity indicated that overall differences in species composition among habitats were significant (Global R = 0.79, $P = 0.01$). Additionally, the MDS graphical representation suggests there are important compositional differences between cultivated and natural grassland habitats (Fig. 5).

The indicator species analysis identified 11 species with significant indicator values; four were associated with Crop, three with Sheep, and four with Deer habitat (Table 3). No indicator species were detected for Pasture. Except for *Embernagra platensis*, Crop indicator species were all facultative grassland birds. Conversely, all Deer indicator species were obligate grassland birds. It is noteworthy that all three pipit species showed indicator signals (*Anthus furcatus* for Sheep and *A. hellmayri* and *A. nattereri* for Deer).

The mean number of habitat types used per species was 2.4 ± 0.2. A total of 11 species were recorded in all four habitats and 14 were seen in only a single habitat (Appendix). Species found in all habitats form a diverse group, including two grassland shorebirds, two swallows, two seedeaters, and two blackbirds, among others. Among the group of 14 species found on single habitats, most were observed on few occasions. Two exceptions were *Geositta cunicularia* and *Heteroxolmis dominicana*, both of which were recorded repeatedly throughout the sampling period in Sheep and Crop respectively, but while the former was observed on most transects, most of the latter were found on a single transect. Crop was characterized by several distinct management phases (i.e., barley fields and stubble, sunflower fields and stubble, and pasture fields), each associated with particular vegetation structures. Although 10 species of those found in Crop were recorded during all three different phases, 12 were only observed during particular phases (Appendix).

Bird species differed in terms of habitat specialization, migration status, and diet (Appendix). The total 50-species pool included 23 obligate and 27 facultative grassland species (*sensu* Vickery et al. 1999), respectively. Crop harbored the highest proportion of facultative species and the lowest of obligate species; opposite patterns were found in Deer (Fig. 6A). Bird assemblages were dominated by resident species which represented between 71 to 85% of all species in the four habitat types (Fig. 6B). Among migrants, only summer resident species (present mainly from September to March) were well represented, accounting for 12 to 14% of all species found on each habitat. In terms of feeding guilds, insectivores were the best represented in all habitats, accounting for 42 to 66% of species recorded (Fig. 6C). Proportion of granivores was highest in Crop (30%) and lowest in Deer (8%). Despite these trends, overall proportions of obligate/facultative species ($G = 3.20$, df = 3, $0.50 > P > 0.25$) and of species in different migratory ($G = 6.76$, df = 9, $0.75 > P > 0.50$) and feeding guild ($G = 9.23$, df = 12, $0.75 > P > 0.50$) categories did not differ significantly among habitats.

Conservation-concern species were recorded in all habitat types. *Rhea americana* was the only one found in all four habitats; *Anthus nattereri* and *Sturnella defilippi* were recorded in both Sheep and Deer, whereas *Sporophila ruficollis* was found in Crop and

Pasture. *Tryngites subruficollis*, *Polystictus pectoralis* and *Heteroxolmis dominicana* were recorded only in Sheep, Pasture and Crop, respectively.

POPULATION DENSITIES

Patterns of species densities differed among habitat types. Of the total species pool, 15 had enough observations (or could be combined with other frequently recorded species of similar characteristics) to built detection functions for density estimation (Tables 4 and 5). Of these, five species showed higher densities in Sheep, four species in Crop, and three species in Deer and Pasture, respectively (Table 5). Unlike most species, density estimates of the *Tachycineta leucorrhoa* and *Progne tapera* were similar for all four habitats (Table 5).

Species with the highest densities included *Sturnella superciliaris* and *Zenaida auriculata* in Crop, *Nothura maculosa* and *Sturnella superciliaris* in Pasture, and *Anthus furcatus* and *Nothura maculosa* in both Sheep and Deer. Among the 10 species with the highest densities for each habitat (Table 6), *Nothura maculosa* and *Sicalis luteola* were the only ones shared by all. Additionally, *Vanellus chilensis*, *Tachycineta leucorrhoa*, and *Anthus furcatus* were included in the top ranks of all habitats except Crop. Other common species (within the five most abundant for each habitat) were shared by Crop and Pasture (*Zenaida auriculata*, *Sturnella superciliaris*), and by Pasture, Sheep and Deer (*Vanellus chilensis*, *Anthus furcatus*). In terms of individuals, the five most abundant birds accounted for 67.6% of all birds recorded in Crop, 78% in Pasture, 62.5% in Sheep and 73.0% in Deer (Appendix).

DISCUSSION

Contrary to expectations, natural grasslands did not support more grassland obligate species than did cultivated grasslands, although all but one of the species restricted to natural grasslands were grassland obligates. The hypothesis that grassland specialists should attain higher densities in less modified habitats was, however, supported by the fact that, for those specialist grassland birds for which density estimates could be calculated, seven out of 11 were more abundant in natural grasslands. The value of natural grasslands for grassland specialists is further highlighted by the fact that most generalist indicator species were tied to Crop whereas most specialist indicator species were associated with either Sheep or Deer.

SPECIES RICHNESS

Although mean total number of species and individuals recorded per transect for the total sampling period did not differ significantly among habitats, fewer species were found in Deer than in the other habitat types. The highest number of species was recorded on Sheep, which is also a natural grassland but which has a lower vegetation structure than Deer (Sturm 2001, Chapter 2). A similar pattern in terms of the relationship between pristine conditions and species richness has been documented in the West Pampa, where ungrazed natural grasslands supported fewer species than did those under grazing regimes (Isacch et al. 2003). In this case, higher vegetation structural heterogeneity promoted by grazing activity was hypothesized to be responsible for differences in species richness (Isacch et al. 2003). In contrast, in his study of five North American grassland habitats, Wiens (1974) found it especially intriguing that habitats with higher structural development did not support more species than those with less.

Undoubtedly, the relatively high number of species found in Crop is explained, at least in part, by the fact that this habitat category included several management phases with differing vegetation structures. Out of the total number of species (30) observed in Crop, 24 were recorded during the “crop phase” (September 2004 to March 2005) and 28 during the “pasture phase” (May to Nov 2005). Just as spatial habitat heterogeneity in agricultural landscapes is known to facilitate the co-occurrence of species with diverse habitat requirements (e.g., Verhulst et al. 2004), temporal habitat heterogeneity in Crop probably has a similar effect by allowing species with differing ecological needs to exploit these areas whenever suitable conditions become available (i.e., feeding and/or breeding opportunities). During the “crop phase”, more species were recorded in sunflower fields and stubble than in barley fields and stubble. Similarly, in southeastern Buenos Aires province, sunflower crops sustained higher species richness than did wheat stubble fields (Leveau and Leveau 2004). Also, outside the Pampas, oat and wheat fields were among the habitat types with the fewest species in agricultural landscapes in Iowa, North America (Best et al. 1995).

In general, more species were present during the austral spring and summer than during fall and winter. Similar temporal patterns have been reported for the West and Flooding Pampas (Isacch and Martínez 2001, Isacch et al. 2003), where seasonal variation in species numbers stems from the fact, at least in part, that more migratory birds reach the study area during the summer than during the winter (Isacch and Martínez 2001). This same pattern also applied to my study area in the Northern Campos, where the number of summer migrants (11) was substantially higher than that of their winter counterparts (2).

SPECIES COMPOSITION

The total species pool found in the surveyed habitats represents about 45% of the grassland avifauna of the Pampas biome, including 50% of the Pampas indicator species (Stotz et al. 1996). A relatively low proportion (22%) of all species in the study area was present in all habitat types; most species were restricted to certain subsets of habitats (50%) or single habitats (28%). Few specific ecological characteristics define the former group except that most are common (92%), year-round resident (83%) species (Gore and Gepp 1978, Azpiroz 2001). As for groups of species absent from certain habitat types, some patterns are noteworthy. Species present in all habitats but Deer, nest off the ground (i.e., bushes, trees) and several are insectivores (*Xolmis cinerea*, *X. irupero*, and *Tyrannus savana*) that capture their prey using perch-and-wait techniques. This absence of several tyrant-flycatcher species from Deer is probably related to the lack of suitable perches, a key feature of these species' foraging strategies. In contrast, most of those absent only from Crop are ground-nesting species that feed on insects by gleaning on the ground or probing under its surface (*sensu* Remsen and Robinson 1990). Also, although the proportion of obligate and facultative species did not differ significantly among habitat types, all but one Crop indicator species were facultative, whereas all Deer indicator species were obligate. None of the indicator species for Crop nest on the ground, whereas all of those of Deer do so. These patterns suggest that Crop provides limited opportunities for many ground-nesting species. This is not surprising since management operations in agricultural fields, especially crop harvesting, can have detrimental effects on nesting success (e.g., Müller et al. 2005). For example, barley fields in Crop were harvested at the end of October, a period which coincides with the nesting season for many local species. In fact, harvesting activities in the study area are known to destroy nests of *Rhynchotus rufescens* (G. Battocletti, pers. comm.). The availability of nesting sites is thought to be a key factor shaping bird assemblages in agricultural areas (Söderström et al. 2003).

Several of the species found exclusively in Sheep are birds typically associated with short grass landscapes (e.g., *Oreopholus ruficollis*, *Tryngites subruficollis, Geositta cunicularia*). Similarly, those absent from this habitat type include many species tied to tall grass vegetation (e.g., *Rhynchotus rufescens*, *Polystictus pectoralis*, *Heteroxolmis dominicana*, *Donacospiza albifrons*, *Embernagra platensis*, *Sporophila ruficollis*). All of the latter birds, with the exception of the *Rhynchotus rufescens*, a ground-nesting species, place their nests in tall grass or shrubs, which also suggests that nest site availability plays an important role in determining bird community assemblages in this habitat type.

A number of birds that depend on tall vegetation for nesting, including several conservation-concern species, were only recorded in Crop or Pasture (e.g., *Polystictus pectoralis*, *Heteroxolmis dominicana*, *Sporophila ruficollis*). Most certainly, these species do not nest in Crop and Pasture fields, but probably take advantage of relict tall vegetation patches available within these agricultural landscapes (i.e., vegetation strips along roads and railroads, and non-tilled patches within agricultural fields). For example, no *Polystictus pectoralis* nest was found during thorough nest searches in Pasture habitat (Azpiroz unpubl. data). Also, nesting attempts of *Heteroxolmis dominicana*, and *Sporophila ruficollis* in Crop and Sheep were confirmed in these kind of patches but not within the sampled fields themselves (Azpiroz unpubl. data). Thus, the use that these species make of Crop and Pasture is probably related to the exploitation of feeding opportunities enhanced by the reliance on nearby nesting habitat patches in a landscape complementation fashion (Dunning et al. 1992).

Throughout this study, five of the seven conservation-concern species were recorded repeatedly (≥ 5 times); two were restricted to Sheep and Deer (*Anthus nattereri* and *Sturnella defilippi*), and two others to Crop (*Heteroxolmis dominicana* and *Sporophila ruficollis*). The general habitat requirements and other biological characteristics of the latter two species suggest that they were taking advantage of feeding opportunities (*Heteroxolmis dominicana*) or in transit to more favorable habitat (*Sporophila ruficollis*). Both species nest in patches of tall grassland (Fontana 1997, Azpiroz unpubl. data) which were not available in this habitat type. Such vegetation, however, was present in nearby areas which would facilitate opportunistic use of Crop (see Grzybowski 1982, Best et al. 1995). Additionally, most *Sporophila* seedeaters are stem-gleaning specialists (Remsen and Hunn 1979) which feed exclusively on native grasses (e.g., Bencke et al. 2003, Di Giacomo 2005, Azpiroz unpubl. data). Thus, feeding on seeds from crop species seems unlikely (see Silva 1999). Finally, *Rhea americana*, which was found in all habitat types is not endangered at a national level (Azpiroz 2001).

POPULATION DENSITIES

Except for two swallow species, density estimates among frequently observed birds (i.e., species for whom detection functions were built) differed considerably among habitats. In general, species that showed higher densities in cultivated habitat types are common and widespread throughout the Pampas, while all conservation-concern species for which density estimates are available occurred exclusively or in higher densities in natural grasslands (*Rhea americana*, *Anthus nattereri*, *Sturnella defilippi*). Although detailed information on the diet of Pampas grassland birds is very limited, data from the five most abundant species on each habitat type suggest that bird assemblages in cultivated grasslands were dominated by species that rely heavily on seeds as a feeding resource, while those in natural grasslands were dominated largely by species that regularly take insects.

In the case of *Rhea americana*, density estimates for Sheep were 35 times higher than for Pasture. In contrast, the species' habitat-use patterns in Córdoba province, Argentina, revealed a preference for planted pastures over natural grasslands and avoidance of cropland (Bellis et al. 2004). The effects of poaching, which was recorded in the Pasture sites and is known to severely affect natural populations of *Rhea americana* elsewhere (Bellis et al. 2004 and references therein), might explain the differences observed between these two areas. Poaching was infrequent in the Córdoba study area (Bellis et al. 2004).

Anthus furcatus was the most abundant species in natural grassland habitats. Additionally, differences in pipit densities between cultivated and natural grassland habitat types were very marked. A comparison of pipit species density estimates between Deer and Crop habitats provide a striking example: the former were more than 150 times higher than the latter. Pipit species are also important elements in natural grasslands of other Pampas subregions. In the Flooding Pampa, *Anthus correndera* was one of the most abundant species in short grasslands (Comparatore et al. 1996), while in the West Pampa, *Anthus chacoensis* was the most abundant species during the spring-summer period (Isacch et al. 2003). Similarly, in North America *Anthus spragueii* was the most abundant bird among five species of grassland passerines inhabiting undisturbed natural grasslands in southern Canada (Owens and Myers 1973).

CONSERVATION IMPLICATIONS FOR GRASSLAND BIRDS

Because of its fairly pristine conditions, bird assemblages in Deer probably more closely resemble those typical of pre-settlement times in the Northern Campos of Uruguay. Assuming that this is the case, and considering the diversity patterns established here for alternative land use practices, the effects of such practices on bird assemblages typical of undisturbed Northern Campos seem to have caused both an increase in species richness, and substantial shifts in species composition.

Deer sustained fewer species than all other habitats. Additionally, the only species exclusive to Deer was *Ciconia maguari*, a grassland facultative species whose primary habitat is wetlands. Of those species recorded on Deer and for which density estimates are available, 11 were more abundant on other habitat types. *Anthus hellmayri*, *A. nattereri*, and *Ammodramus humeralis* were, however, characterized by higher densities in Deer. Thus, agricultural development over the last several hundred years has presumably benefited the former group of species while negatively affecting the latter.

Perhaps more informative with respect to future predictions based on trends of current land use are differences between bird assemblages associated with natural grasslands and those found in cultivated grasslands. Among the five species restricted to both cultivated habitat types, most are fairly common birds throughout Uruguay, including two species (*Zenaida auriculata*, *Myiopsitta monachus*) which are considered agricultural pests (Arballo and Cravino 1999). The exception is *Sporophila ruficollis* a globally near-threatened species which is nonetheless considered locally common in northeastern Uruguay (Gore and Gepp 1978). In contrast, the four species restricted to natural grassland habitat types include a fairly common Nearctic migrant (*Pluvialis dominica*), two globally-threatened species (*Anthus nattereri* and *Sturnella defilippi*) and a Patagonian winter migrant (*Neoxolmis rufiventris*), which may be declining not only in Uruguay (Azpiroz and Menéndez 2008) but throughout its whole range (Fitzpatrick 2004). In general, habitat use and abundance patterns of all these species are consistent with general descriptions of habitat and relative abundance reported elsewhere (e.g., Gore and Gepp 1978, Canevari et al. 1991, Tubaro and Gabelli 1999, Narosky and Yzurieta 2003, Gabelli et al. 2004).

The presence of *Anthus nattereri* in Uruguay was first confirmed during this study. It is unclear if the species is a recent arrival to Uruguayan Northern Campos, or whether the lack of previous reports stems from the inability to distinguish it from other co-occurring congenerics. Density estimates of *Anthus nattereri* for Deer were 20-fold higher than those for Sheep, which suggest that the species' population trends will be affected by the availability of areas with similar characteristics to those found in Deer. In other parts of its range, it has been reported to inhabit burnt areas with regenerating short grass and lightly grazed grasslands (Tyler 2004). It is worth noting that a few individuals were recorded from early October to early November 2005 in Pasture (i.e., between sampling periods). Breeding attempts were not successful (nests were predated or abandoned; unpubl. data).

On the basis of available information, which suggested high sensitivity to habitat change (Fernández et al. 2003), a tight association of *Sturnella defilippi* with Deer was expected. This was not the case, however, since the species was only regularly found along a single transect in Sheep and density estimates were one order of magnitude higher in Sheep than in Deer. The bird was once a widespread species throughout the Pampas, but its range has shrunk 90% in the last 100 years (Tubaro and Gabelli 1999). In southern Buenos Aires province, where the largest remaining populations are located, the species prefers ungrazed natural grasslands or fields with low grazing pressure as breeding sites (Fernández et al. 2003, Gabelli et al. 2004). Here, most of the reproductive groups were found in natural grasslands with high vegetation cover (Fernández et al. 2003). In terms of habitat structure, *Sturnella defilippi* sites in southern Buenos Aires province differ markedly from inhabited areas in the Northern Campos (R. Sánchez pers. comm., Azpiroz unpubl. data). It is intriguing that *Sturnella defilippi* was largely confined to a specific area of Sheep and mostly absent from Deer, even though, in terms of grazing pressure and vegetation cover, the latter habitat better resembles the species' preferences in its southern distributional range (Fernández et al. 2003). Interestingly, in southern Buenos Aires, planted pastures were occupied by a few reproductive groups while many fields with adequate vegetation characteristics remained unused (Fernández et al. 2003). It has been suggested that factors such as limited food resources and presence of predators may deter the species from occupying what seem to be adequate nesting sites (Fernández et al. 2003). Data to test such hypotheses are currently unavailable, either for Buenos Aires or the northern Uruguay populations.

Cultivated and natural grasslands sites differed not only in terms of agricultural management practices (local characteristics), but also in terms of the composition of the matrix in which the different types of grasslands were embedded (regional characteristics). Cultivated grasslands were located within a similar matrix of crops and planted pastures, whereas natural grasslands were located within a matrix characterized by conditions resembling Sheep habitat. This reflected a logistic constraint, since there is currently no region in Uruguay that contains habitat patches with the characteristics of those studied here within a single type of matrix. Because of this mismatch in matrix characteristics, bird community differences between habitats in cultivated and natural grasslands may be influenced by this variable. But the fact that a substantial proportion of species was restricted to a single habitat within each matrix type indicates that management practices (i.e., local conditions) do play an important role in determining species richness in the region (Crop and Pasture did not share 33% of the species found in either habitat and, similarly, Sheep and Deer did not share 49% of the species). Information from the southern Pampas supports this conclusion; the presence of *Sturnella defilippi* reproductive groups could be predicted by local variables (e.g., local habitat-specific characteristics) but not by landscape variables (Fernández et al. 2003). A study of grassland bird assemblages in farmlands of southern Portugal, however, found that species richness was primarily influenced by landscape context (Moreira et al. 2005). This pattern is supported in my study area by Crop and Pasture's similar species richness values, but not by those of Sheep and Deer, which differed markedly.

Here I presented the first characterization of grassland bird communities inhabiting an agricultural landscape in the Northern Campos of Uruguay. I found that cultivated grasslands seem to provide suitable habitat requirements for a substantial proportion of grassland birds, including some of the Pampas conservation-concern species. Threatened species, however, only attained relatively high densities (i.e., included within the top 10 rank of most abundant species) in natural grasslands. The availability of feeding and breeding opportunities seem to have been an important factor shaping bird community structure in this region, something that has also been reported for avian communities in other farmland ecosystems (e.g., Söderström et al. 2003, Whittingham et al. 2006). Because these patterns are based solely on presence/absence data and species' density estimates, the question of whether each habitat type can support viable populations of those species recorded on them has not been fully addressed. To do so, information on demographic parameters, such as species survival rates and breeding success on each habitat type need to be considered. Also, the availability of more detailed ecological information (e.g., species diets, nesting requirements, dispersal capabilities) will provide additional insight with respect to the mechanisms driving the bird assemblage patterns found here. There is still a great need of further research on the grassland birds of South America (Vickery et al. 1999, Vickery and Herkert 2001). Hopefully, the information presented will promote future studies of grassland bird ecology in the threatened Pampas region.

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Table 1. Observed numbers of individuals and species and expected number of species (see Methods) on each of four habitats types in the Northern Campos of Uruguay.

	Crop	**Pasture**	**Sheep**	**Deer**
Total number transects	8	8	8	8
Total survey periods	8	8	8	8
Individuals observed	1,555	1,150	1,225	1,038
Observed species richness	33	30	34	24
Rarified species richness (± 95 CI)	31.4	29.7	33.2	24.0
	(29.0-33.0)	(29.0-30.0)	(31.0-34.0)	(24.0-24.0)
Estimated species richness (± SE)	36 ± 2.5	33 ± 2.5	38 ± 2.8	26 ± 2.0

Table 2. Bray-Curtis similarity among habitats located in the Northern Campos of Uruguay. Similarity based on species presence-absence.

Habitat	**Crop**	**Pasture**	**Sheep**
Pastures	0.729		
Sheep	0.589	0.666	
Deer	0.461	0.644	0.634

Table 3. Indicator values (as % of perfect indication) and values of Monte Carlo test of significance of observed maximum indicator values. Only species indicator values significant at least at $P < 0.01$ are shown.

Species	**Indicator values based on habitats**				
	Crop	**Pasture**	**Sheep**	**Deer**	***P***
Gallinago paraguaiae	0	6	9	61	0.002
Columba maculosa	63	0	0	0	0.003
Zenaida auriculata	87	13	0	0	0.001
Geositta cunicularia	0	0	63	0	0.001
Xolmis cinerea	68	0	1	0	0.001
Alopochelidon fucata	1	0	56	0	0.002
Anthus furcatus	0	19	47	30	0.003
Anthus hellmayri	2	0	19	55	0.006
Anthus nattereri	0	0	1	83	0.001
Sicalis luteola	3	2	10	75	0.007
Embernagra platensis	54	2	0	0	0.003

Table 4. Number of observations and model selection of detection functions of grassland birds in four habitats in northern Uruguay. *Pluvialis dominica*, *Bartramia longicauda*, *Progne chalybea*, and *Sturnella defilippi* had fewer than 60 observations each, so detection functions for these species included additional observations of species of similar characteristics and behavior (*Vanellus chilensis* for *P. dominica* and *B. longicauda*, *Tachycineta leucorrhoa* for *P. tapera*, and *Sturnella superciliaris* for *S. defilippi*)

Species	*n*[a]	Model selected	m[b]
Rhea americana	81	HR[c] + cosine	2
Nothura maculosa	131	HR + cosine	2
Vanellus chilensis	351	HN[d] + cosine	3
Pluvialis dominica	367	HN + cosine	3
Bartramia longicauda	377	HN + cosine	3
Zenaida auriculata [e]	71	HN + cosine	2
Zenaida auriculata [f]	62	HR + cosine	2
Tachycineta leucorrhoa	80	HN + cosine	1
Progne tapera	116	HN + cosine	1
Anthus furcatus	498	HR + cosine	5
Anthus hellmayri	63	UN[g] + polynomial	1
Anthus nattereri	83	HN + cosine	1
Ammodramus humeralis	68	HR + cosine	3
Sicalis luteola	131	UN + cosine	1
Sturnella defilippi	266	HR + polynomial	5
Sturnella superciliaris [e]	89	HR + cosine	4
Sturnella superciliaris [f]	264	UN + cosine	4

[a] Number of observations.

[b] Number of parameters in detection function.

[c] Hazard-rate base function.

[d] Half-normal base function.

[e] Detection function was built exclusively with data collected from September 2004 to March 2005, which corresponded to the "crop phase" (barley and sunflower fields) of crop habitat.

[f] Detection function was built with data collected from May to November 2005, which corresponded to the "crop phase" (barley and sunflower fields) of crop habitat, as well as with data from other habitats for the total sampling period.

[g] Uniform base function.

Table 5. Density (ind per 100 ha), SE, and 95% CI calculated with program DISTANCE for species with at least 60 visual observations. The highest density value for each species is shown in bold.

Species/Habitat		**Crop**	**Pasture**	**Sheep**	**Deer**
Rhea americana	Mean	5.5	0.3	**10.7**	7.0
	SE	2.1	0.3	3.1	2.3
	95% CI	2.6-11.6	<0.1-1.6	6.2-18.7	3.7-13.2
Nothura maculosa	Mean	20.7	**126.7**	98.3	93.1
	SE	9.6	41.2	32.5	29.4
	95% CI	8.6-49.5	67.8-236.8	52.0-185.7	50.6-171.2
Vanellus chilensis	Mean	5.6	28.1	**49.3**	31.7
	SE	2.1	6.9	5.9	4.2
	95% CI	2.7-11.5	17.3-45.6	39.0-62.4	24.4-41.1
Pluvialis dominica	Mean	0.0	0.0	**4.8**	1.1
	SE			1.9	0.8
	95% CI			2.2-10.4	0.3-4.2
Bartramia longicauda	Mean	1.3	**4.0**	3.0	1.3
	SE	1.0	1.7	1.2	0.8
	95% CI	0.3-5.3	1.7-9.1	1.4-6.3	0.4-4.1
Zenaida auriculata [a]	Mean	**134.4**	N/A	N/A	N/A
	SE	43.7			
	95% CI	70.8-255.3			
Zenaida auriculata [b]	Mean	25.4	66.1	0.0	0.0
	SE	15.0	29.0		
	95% CI	8.5-75.6	29.0-151.2		
Tachycineta leucorrhoa	Mean	**18.4**	14.1	11.7	4.9
	SE	5.3	3.8	3.4	1.9
	95% CI	10.4-32.4	8.3-23.9	6.6-20.7	2.3-10.4
Progne tapera	Mean	**7.7**	5.1	2.6	3.1
	SE	2.1	2.1	1.7	1.2
	95% CI	4.5-13.2	2.3-11.5	0.8-8.6	1.4-6.7
Anthus furcatus	Mean	0.0	94.3	**321.2**	219.2
	SE		32.7	78.5	56.9
	95% CI		48.5-183.3	200.0-515.6	132.7-362.0
Anthus hellmayri	Mean	1.5	0.0	5.8	**11.8**
	SE	0.7		1.7	3.2
	95% CI	0.7-3.5		3.2-10.4	6.9-20.1

Table 5. Continued

Species/Habitat		**Crop**	**Pasture**	**Sheep**	**Deer**
Anthus nattereri	Mean	0.0	0.0	1.1	**21.1**
	SE			0.8	4.2
	95% CI			0.3-4.3	14.2-31.1
Ammodramus humeralis	Mean	20.2	**27.3**	9.7	2.6
	SE	6.9	14.0	4.3	2.1
	95% CI	10.5-39.0	10.4-71.1	4.2-22.3	0.7-10.5
Sicalis luteola	Mean	3.2	3.2	5.0	**47.9**
	SE	1.5	2.0	1.7	10.4
	95% CI	1.3-7.7	1.0-9.9	2.6-9.6	31.2-73.5
Sturnella defilippi	Mean	0.0	0.0	**13.6**	1.5
	SE			6.7	1.1
	95% CI			5.4-34.3	0.4-5.8
Sturnella superciliaris [a]	Mean	**242.4**	N/A	N/A	N/A
	SE	83.7			
	95% CI	124.8-470.8			
Sturnella superciliaris [b]	Mean	91.7	**95.1**	0.0	11.3
	SE	27.0	21.4		4.1
	95% CI	51.3-164.1	61.2-147.7		5.6-22.6

[a] Detection function was built exclusively with data collected from September 2004 to March 2005, which corresponded to the “crop phase” (barley and sunflower fields) of crop habitat

[b] Detection function was built with data collected from May to November 2005, which corresponded to the “crop phase” (barley and sunflower fields) of crop habitat, as well as with data from other habitats for the total sampling period

Table 6. Ranks of species with the 10 highest density estimates in each of four grassland habitat types in Northern Campos of Uruguay. Only *Nothura maculosa*, *Vanellus chilensis*, *Tachycineta leucorrhoa*, and *Sicalis luteola* are included in the ranks of all four habitat types.

	HABITAT TYPE			
Species	**Crop**	**Pasture**	**Sheep**	**Deer**
Rhea americana	8		6	8
Nothura maculosa	3	1	2	2
Vanellus chilensis	7	5	3	4
Bartramia longicauda		9		
Pluvialis dominica			10	
Zenaida auriculata	2	4		
Tachycineta leucorrhoa	5	7	5	9
Progne tapera	6	8		10
Anthus furcatus		3	1	1
Anthus hellmayri	10		8	6
Anthus nattereri				5
Ammodramus humeralis	4	6	7	
Sicalis luteola	9	10	9	3
Sturnella defilippi			4	
Sturnella superciliaris	1	2		7

Figure 1. Location of the study area in the Northern Campos subregion of southeastern South American Pampas. Large patches of four habitat types were selected in northern Paysandú and southern Salto departments in northern Uruguay.

Figure 2. Habitat types in which bird assemblages were studied. A) Crop habitat; B) Planted Pastures habitat; C) Sheep habitat, and D) Deer habitat. Crop habitat included three different phases (barley fields, sunflower fields, and planted pastures); figure 2A illustrates the first of these.

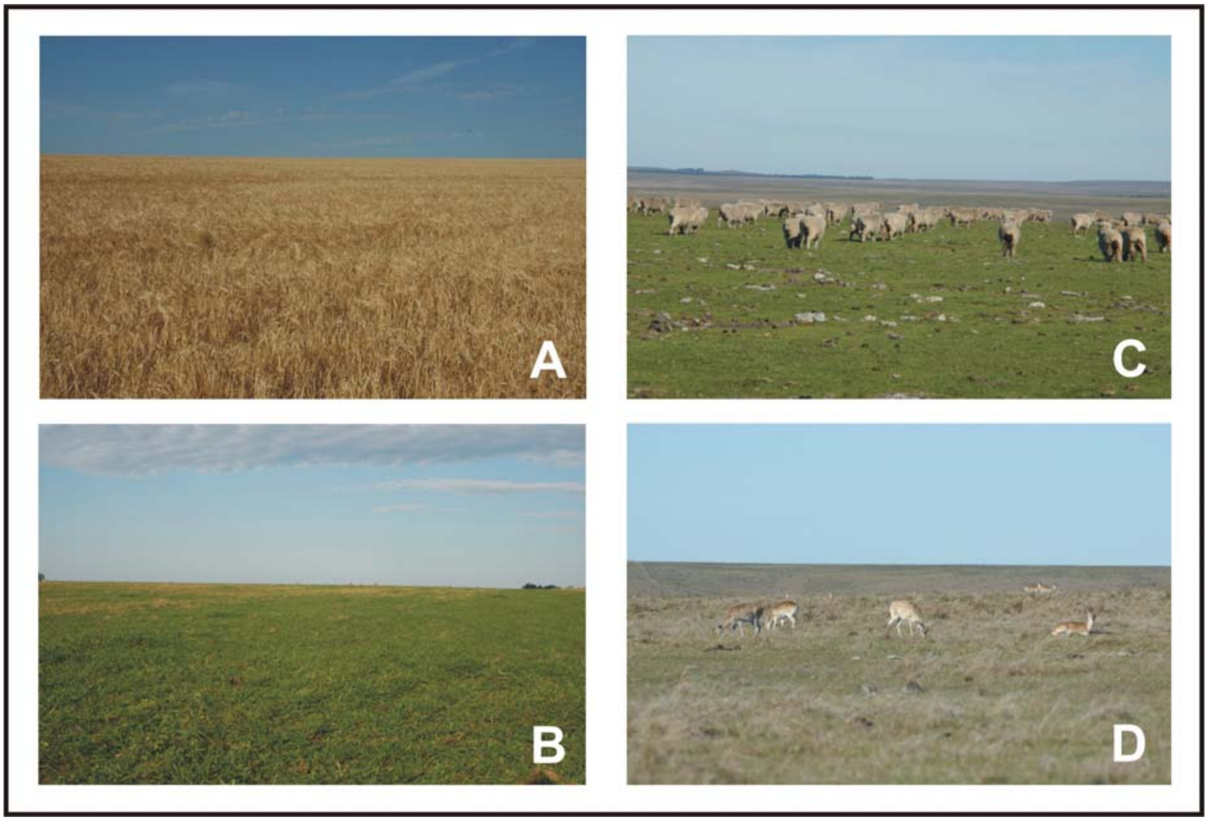


Figure 3. Species-accumulation curves for each of the four studied habitats, based on visual and aural detections from September 2004 to November 2005.

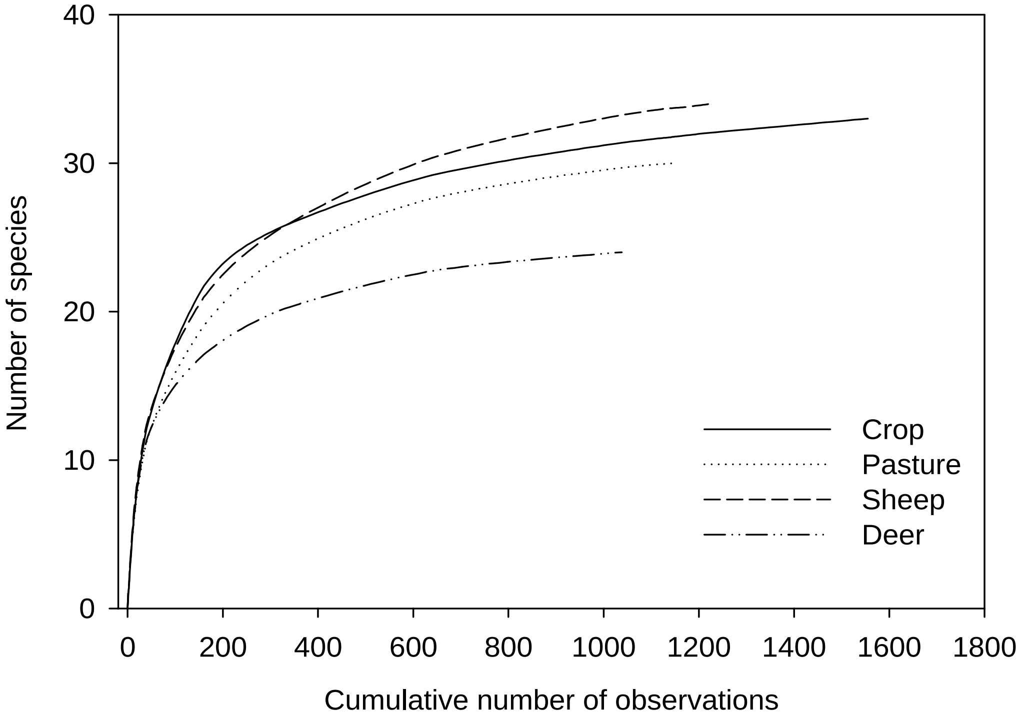


Figure 4. Temporal variation in mean species richness (A) and mean number of individuals (B) for each habitat type from September 2004 to November 2005 in the northern campos of Uruguay.

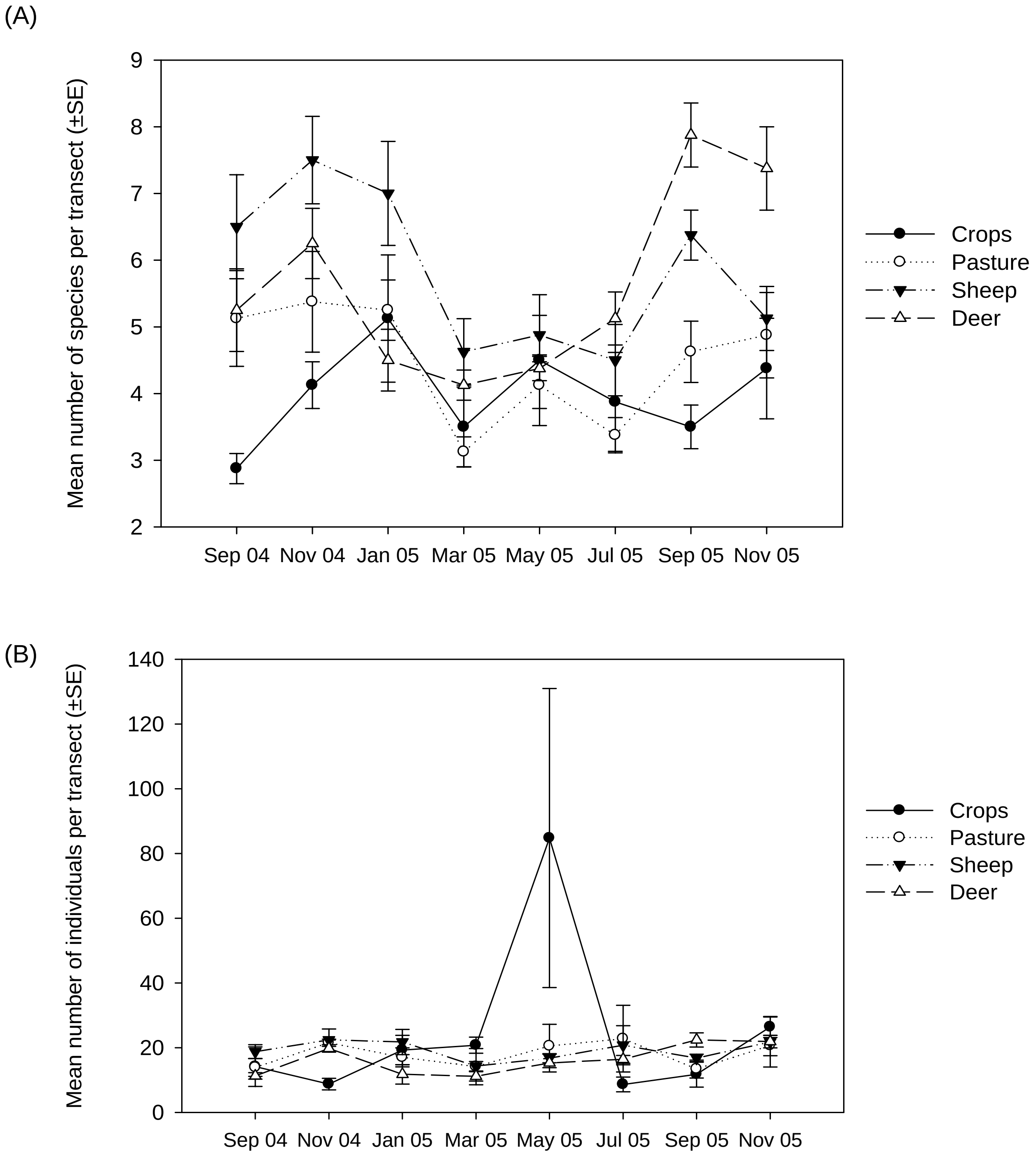


Figure 5. Nonmetric multidimensional scaling based on species presence/absence per transect during the total sampling period (September 2004-November 2005). Symbols represent individual transects in Crop (filled circles), Pasture (open circles), Sheep (open squares), and Deer (filled squares) habitats. The dashed line separates transects on cultivated grasslands from those on natural grasslands. Species showing high correlations with the horizontal axis are indicated.

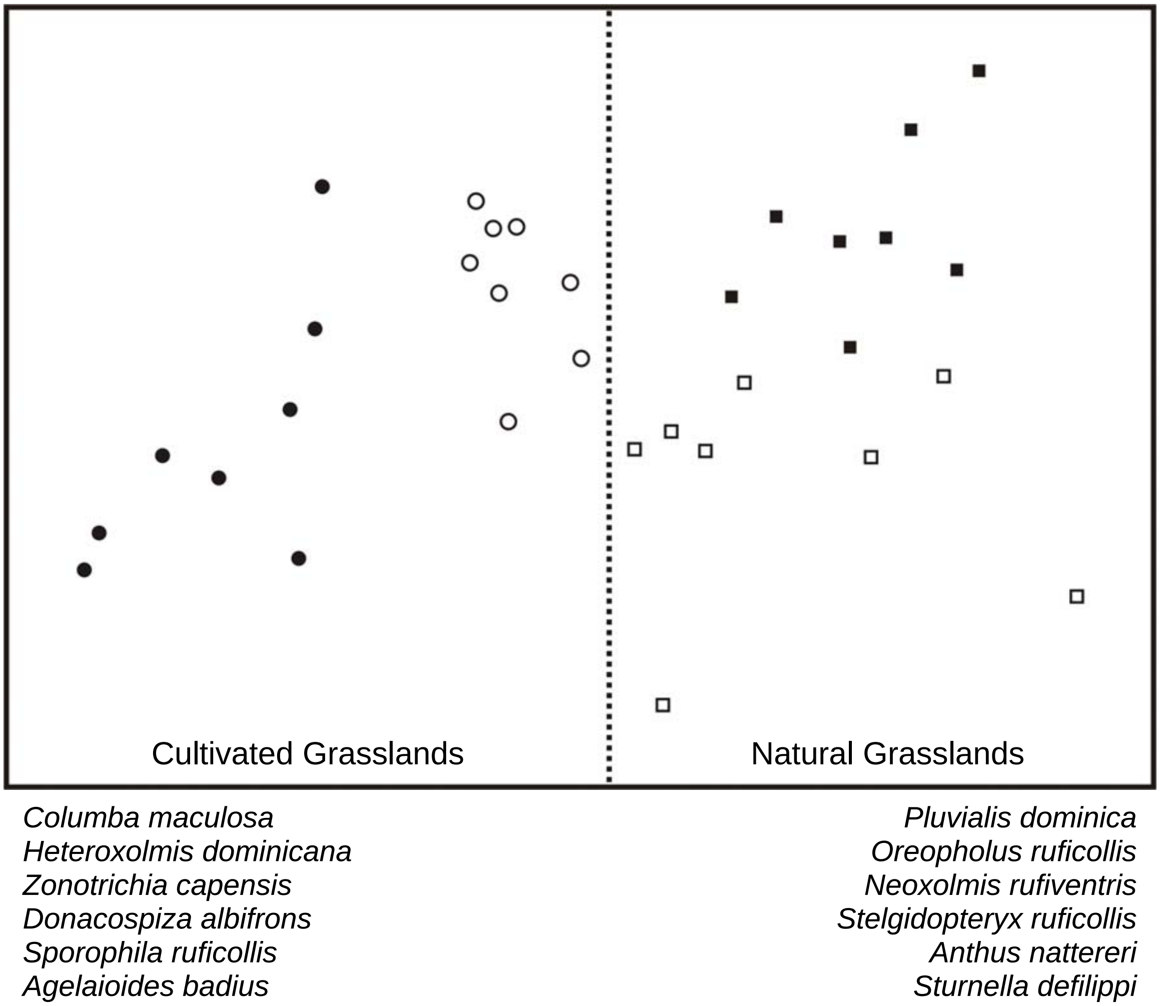
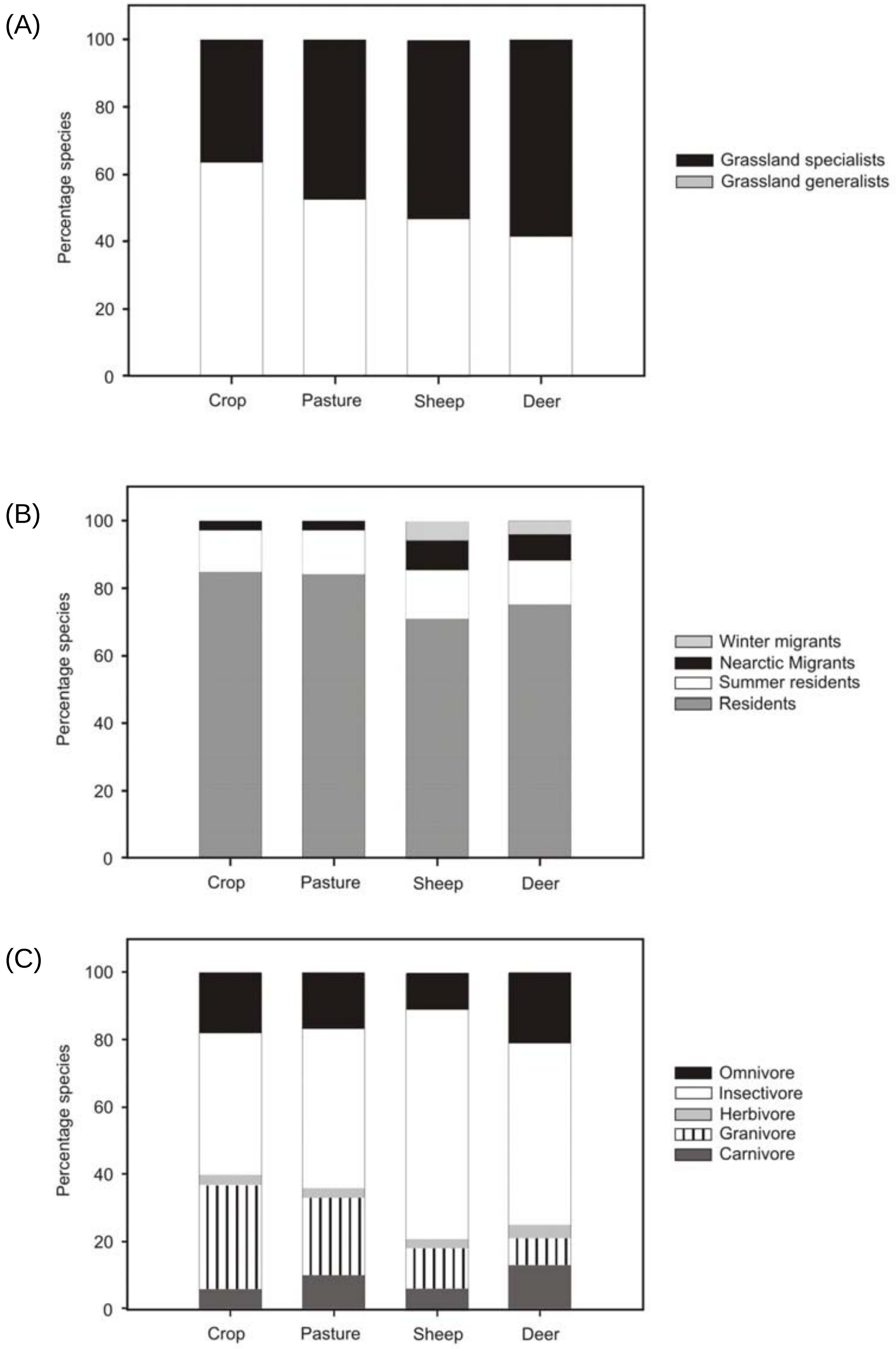


Figure 6. Proportion of species in each habitat that belong to alternative ecological categories. (A) Level of dependence on grassland habitats (*sensu* Vickery et al. 1999); (B) Migratory status; and (C) Trophic guilds.



Appendix. Number of individuals and species found in four grassland habitats (Crop [CR], Pastures [PA], Sheep [SH], and Deer [DE]). For the Crop column superscripts denote species recorded only on specific management phase (^{a} = barley, ^{b} = sunflower, ^{c} = pastures). Each species is also classified (+) within one of different habitat specialization, migration status and feeding guild categories. Habitat Specialization: obligate (OB) and facultative (FA) species *sensu* Vickery et al. 1999. Migration status: year-round resident (RE), summer resident (SR), Nearctic migrant (NM), winter migrant (WM). Feeding guild: carnivore (CA), granivore (GR), herbivore (HE), insectivore (IN), omnivore (OM).

FAMILY/SPECIES	**HABITAT TYPE**				**HAB. SPE.**		**MIGRATION**				**FEEDING GUILD**				
	CR	**PA**	**SH**	**DE**	**OB**	**FA**	**RE**	**SR**	**NM**	**WM**	**CA**	**GR**	**HE**	**IN**	**OM**
RHEIDAE															
Greater Rhea															
Rhea americana	41	4	69	50	+		+						+		
TINAMIDAE															
Red-winged Tinamou															
Rhynchotus rufescens	15	9	0	0	+		+								+
Spotted Nothura															
Nothura maculosa	38	143	142	116	+		+								+
ARDEIDAE															
Whistling Heron															
Syrigma sibilatrix	2^{p}	4	1	0		+	+				+				
CICONIIDAE															
Maguari Stork															
Ciconia maguari	0	0	0	3		+	+				+				
ACCIPITRIDAE															
White-tailed Kite															
Elanus leucurus	1	0	0	0		+	+				+				
Cinereous Harrier															
Circus cinereus	0	1	0	2	+	+	+				+				

Appendix Continued.

FAMILY/SPECIES	**HABITAT TYPE**				**HAB. SPE.**		**MIGRATION**				**FEEDING GUILD**				
	CR	**PA**	**SH**	**DE**	**OB**	**FA**	**RE**	**SR**	**NM**	**WM**	**CA**	**GR**	**HE**	**IN**	**OM**
CHARADRIIDAE															
Southern Lapwing															
Vanellus chilensis	29^{p}	146	278	186	+		+							+	
American Golden-Plover															
Pluvialis dominica	0	0	130	16		+			+					+	
Tawny-throated Dotterel															
Oreopholus ruficollis	0	0	1	0	+					+				+	
SCOLOPACIDAE															
Upland Sandpiper															
Bartramia longicauda	6^{p}	20	27	15	+				+					+	
South American Snipe															
Gallinago paraguaiae	0	6	9	34	+		+							+	
Buff-breasted Sandpiper															
Tryngites subruficollis	0	0	4	0	+				+					+	
COLUMBIDAE															
Spot-winged Pigeon															
Columba maculosa	19	0	0	0		+	+					+			
Picazuro Pigeon															
Columba picazuro	23^{c}	10	2	0		+	+					+			
Eared Dove															
Zenaida auriculata	481	74	0	0		+	+					+			
PSITTACIDAE															
Monk Parakeet															
Myiopsitta monachus	61^{c}	12	0	0		+	+					+			

Appendix Continued.

FAMILY/SPECIES	HABITAT TYPE				HAB. SPE.		MIGRATION				FEEDING GUILD				
	CR	PA	SH	DE	OB	FA	RE	SR	NM	WM	CA	GR	HE	IN	OM
STRIGIDAE															
Burrowing Owl															
Athene cunicularia	0	5	3	4	+		+				+				
CAPRIMULGIDAE															
Nacunda Nighthawk															
Podager nacunda	0	0	2	0	+			+						+	
PICIDAE															
Field Flicker															
Colaptes campestris	1^{c}	25	20	1		+	+							+	
FURNARIIDAE															
Common Miner															
Geositta cunicularia	0	0	18	0	+		+							+	
Rufous Hornero															
Furnarius rufus	2	0	0	0		+	+							+	
Firewood-Gatherer															
Anumbius annumbi	0	5	5	4		+	+							+	
TYRANNIDAE															
Bearded Tachuri															
Polystictus pectoralis	0	3	0	0	+			+						+	
Grey Monjita															
Xolmis cinerea	29	1	2	0		+	+							+	
White Monjita															
Xolmis irupero	3^{c}	2	1	0		+	+							+	

Appendix Continued.

FAMILY/SPECIES	HABITAT TYPE				HAB. SPE.		MIGRATION				FEEDING GUILD				
	CR	**PA**	**SH**	**DE**	**OB**	**FA**	**RE**	**SR**	**NM**	**WM**	**CA**	**GR**	**HE**	**IN**	**OM**
Black-and-white Monjita															
Heteroxolmis dominicana	20	0	0	0		+	+							+	
Chocolate-vented Tyrant															
Neoxolmis rufiventris	0	0	2	1	+					+				+	
Cattle Tyrant															
Machetornis rixosus	4	1	5	0		+	+							+	
Fork-tailed Flycatcher															
Tyrannus savana	14	12	5	0	+			+						+	
HIRUNDINIDAE															
White-rumped Swallow															
Tachycineta leucorrhoa	43	45	21	13		+	+							+	
Gray-breasted Martin															
Progne chalybea	4[a]	3	0	6		+		+						+	
Brown-chested Martin															
Progne tapera	22	22	7	6		+	+							+	
Blue-and-white Swallow															
Notiochelidon cyanoleuca	0	0	2	0		+		+						+	
Tawny-headed Swallow															
Alopochelidon fucata	1[a]	0	8	0		+		+						+	
Rough-winged Swallow															
Stelgidopteryx ruficollis	0	0	2	0		+		+						+	

Appendix Continued.

FAMILY/SPECIES	**HABITAT TYPE**				**HAB. SPE.**		**MIGRATION**				**FEEDING GUILD**				
	CR	**PA**	**SH**	**DE**	**OB**	**FA**	**RE**	**SR**	**NM**	**WM**	**CA**	**GR**	**HE**	**IN**	**OM**
MOTACILLIDAE															
Short-billed Pipit															
Anthus furcatus	0	118	292	216	+		+							+	
Hellmayr's Pipit															
Anthus hellmayri	5	0	23	48	+		+							+	
Ochre-breasted Pipit															
Anthus nattereri	0	0	5	92	+		+							+	
EMBERIZIDAE															
Rufous-collared Sparrow															
Zonotrichia capensis	6[b]	0	1	0		+	+					+			
Grassland Sparrow															
Ammodramus humeralis	29	43	32	13	+		+					+			
Long-tailed Reed-Finch															
Donacospiza albifrons	1[b]	0	0	0		+	+					+			
Grassland Yellow-Finch															
Sicalis luteola	15	9	26	148	+		+					+			
Great Pampa-Finch															
Embernagra platensis	12	2	0	0	+		+					+			
Dark-throated Seedeater															
Sporophila ruficollis	3	4	0	0	+			+				+			
ICTERIDAE															
Pampas Meadowlark															
Sturnella defilippi	0	0	33	4	+		+							+	

Appendix Continued.

FAMILY/SPECIES	**HABITAT TYPE**				**HAB. SPE.**		**MIGRATION**				**FEEDING GUILD**				
	CR	**PA**	**SH**	**DE**	**OB**	**FA**	**RE**	**SR**	**NM**	**WM**	**CA**	**GR**	**HE**	**IN**	**OM**
White-browed Blackbird															
Sturnella superciliaris	460	416	0	55	+		+								+
Brown-and-Yellow Marshbird															
Pseudoleistes virescens	23	2	43	3		+	+								+
Bay-winged Cowbird															
Agelaioides badius	15	0	0	0		+	+								+
Shiny Cowbird															
Molothrus bonariensis	127[c]	3	4	2		+	+								+
TOTAL INDIVIDUALS	1555	1150	1225	1038											
TOTAL SPECIES	33	30	34	24	23	27	37	8	3	2	5	10	1	28	6

CHAPTER 2

RESPONSES OF GRASSLAND BIRDS TO VARIATION IN VEGETATION STRUCTURE IN THE NORTHERN CAMPOS OF URUGUAY

INTRODUCTION

Vegetation composition and structure can directly affect bird survival and reproduction and, thus, are thought to be important influences on avian assemblages and bird-habitat relationships (e.g., Rotenberry 1985, Skowno and Bond 2003, Suárez et al. 2003, Whittingham et al. 2006). For grassland birds in particular, empirical evidence indicates that species can respond strongly to 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 it provides protection from the elements and predators (e.g., Rotenberry and Wiens 1980, Grzybowski 1983, Cody 1985). In terms of foraging, vegetation structure may influence both prey availability and detectability. Mills et al. (1991), for example, found a relationship between vegetation volume and bird density and suggested that vegetation volume is a proxy for available resources. With respect to nesting resources, vegetation structure can assist in nest relocation, influence nest microclimate, provide thermoregulation advantages to incubating individuals, and probably most important for grassland birds, reduce nest predation risks by increasing nest concealment (Walsberg 1985, Hoekman et al. 2002, Davis 2005). Finally, vegetation structure not only influences predation risk for nests, but also for individuals themselves (Grzybowski 1983, Lima 1993, Whittingham et al. 2006).

The Pampas biome of southeastern South America is dominated by grassland ecosystems that extend from southern Brazil into Uruguay and eastern Argentina. The region's extraordinary conditions for agriculture have resulted in a drastic modification of its native vegetation since European settlement (Vervoorst 1967, León et al. 1984, Bilenca and Miñarro 2004, Di Giacomo and Krapovickas 2005). Most of the Pampas have now been converted either to rangelands or croplands. The role of fire and grazing as major ecological drivers shaping grassland structure have been largely altered because of changes in natural fire regimes and the replacement of populations of native herbivores (i.e., Pampas Deer *Ozotoceros bezoarticus* and Greater Rhea *Rhea americana*) by large stocks of cattle, sheep and other domestic animals (Vervoorst 1967, Sala et al. 1986, Soriano 1992, Sarmiento 1996, González et al. 2002). Agricultural activities have also resulted in the replacement of tall grass by short grass species, the establishment of exotic plants, succession to shrublands, and increased use of agrochemicals and technology (Vervoorst 1967, Bucher and Nores 1988, Vickery et al. 1999, Di Giacomo and Krapovickas 2005).

Habitat modification has been identified as the most likely factor behind declines of populations of Pampas grassland birds (Collar et al. 1992, Soriano 1992, Stotz et al. 1996, BirdLife International 2000, Vickery et al. 1999). Even though information on population trends is limited, there is evidence that many species have suffered substantial reductions, coupled with important range contractions (Fraga et al. 1998, Krapovickas and Di Giacomo 1998, Tubaro and Gabelli 1999, Gabelli et al. 2004). Eight Pampas grassland birds are currently considered globally threatened and five additional ones are classified as near-threatened (IUCN 2007). Despite the need for relevant ecological information, the region has received little attention in terms of research activity, especially when compared to other grassland biomes and agricultural landscapes in the Northern Hemisphere.

The identification of habitat attributes that influence bird numbers can guide the design of sound management strategies (Davis et al. 1999, Rotenberry and Knick 1999). In the Pampas, there are limited data on the vegetation structure of fields under alternative management practices and habitat requirements for virtually all Pampas grassland birds remain largely unknown (Vickery and Herkert 2001). The available information suggests contrasting responses of bird species to agriculture-related activities. For example, whereas Pampas Meadowlarks (*Sturnella defilippi*) prefer ungrazed or lightly grazed natural grasslands as breeding grounds (Fernández et al. 2003), Buff-breasted Sandpipers (*Tryngites subruficollis*) seem to depend on intensive livestock grazing pressure for the maintenance of suitable wintering habitat conditions (Lanctot et al. 2002).

This study aimed to identify features of vegetation structure that influence avian assemblage organization within Pampas grassland habitat types that are under different agricultural management. To do this, I quantified vegetation structure variables and sampled bird populations in four habitat types. First, I used this information to test for differences in vegetation structure among habitats. Then, I used ordination analyses to explain bird distribution and numbers in terms of the vegetation variables considered. A series of analyses targeted the entire grassland assemblage as well as more specific groups of birds of ecological and conservation interest. Considering the known variation in vegetation structure of grasslands under different management regimes (Fletcher and

Koford 2002), I expected larger vegetation-structure differences between cultivated (crops and planted pastures) and natural grasslands (grasslands used to raise free-ranging livestock) than between habitat types within these two categories. Previous studies have identified several vegetation features that are especially important to grassland birds (e.g., Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Patterson and Best 1996, Delisle and Savidge 1997, Davis 2004). Based on such findings, I expected litter depth, vegetation height and vegetation density to have a major influence on bird distribution and abundance. I also expected habitat specialist and generalist grassland birds to show different responses to vegetation structure because grassland bird specialists have been found to show stronger correlations to grassland habitat features when compared to grassland generalists (Wiens and Rotenberry 1981, Patterson and Best 1996). Finally, since the conservation status of Pampas grassland birds has been linked to habitat modification (Tubaro and Gabelli 1999, Vickery et al. 1999), I expected threatened species (following IUCN 2007) to show a stronger association to vegetation features typical of natural sites as opposed to those characteristic of altered areas.

METHODS

STUDY AREA AND GRASSLAND HABITATS

The study was conducted in northwestern Paysandú department and southern Salto department, northwestern Uruguay (31°19’ to 31°44’S and 56° 42’ to 57° 56’W). This area is located in the Northern Campos of Uruguay within the Río de la Plata grasslands (Soriano 1992) and the Pampas biome (Stotz et al. 1996). In terms of climate, the area has humid and mesothermic features with mean annual temperature and rainfall of 19°C and 1300 mm, respectively (Lezama et al. 2006). The Northern Campos are a vast plain with few areas of relief and the general landscape is a mixture of flat and gently rolling areas, further characterized by a rich fluvial network (Soriano 1992). Within the study area, open-range livestock grazing is the major economic activity. Planted pastures and croplands are common in the western part of the region, while the eastern part is characterized by large expanses of unplowed natural grasslands. The latter are characterized by species in the families Poaceae and Asteraceae, with genera such as *Stipa*, *Paspalum*, *Aristidsa*, *Conyza* and *Piptochetium* being well represented (Lezama et al. 2006). This study was conducted in several ranches and farms in the surroundings of Chapicuy, in Paysandú department, and San Antonio and Cerros de Vera in Salto department. Within each of these regions large patches (500 to 1200 ha) of the following four habitat types were selected:

1) Croplands (Crop) - This was defined as cultivated land that was plowed and seeded to annual crops (barley, sunflower) which grew during spring and summer of the first half of the sampling period and that later included a phase of planted pastures (through the second half of the sampling period) after crops were harvested.

2) Planted pastures (Pasture) – These lands were plowed and seeded with non-native species and used for cattle grazing.

3) Sheep rangelands (Sheep) – These native grasslands, which have never been plowed, were grazed by free-ranging sheep and cattle. Due to the effects of grazing by sheep, vegetation diversity is lower than that in the following habitat type (Sturm 2001).

4) Deer rangelands (Deer) – These were also native grasslands which have never been plowed, and which were grazed by cattle and Pampas Deer *Ozotoceros bezoarticus* (a few sheep were maintained on these fields for consumption at the ranch).

More specific information about each habitat type has been described elsewhere (see Chapter 1).

SAMPLING OF BIRD POPULATIONS

Birds were sampled every two months from September 2004 to November 2005 (i.e., six sampling periods). Eight replicates (i.e., transects) per treatment were established. On each 500-m variable-width transect, grassland bird species were counted using distance sampling (Buckland et al. 2001). Transects were placed randomly after considering certain constraints such as a minimum inter-transect distance of 400 m and the avoidance of fencerows or other non-grassland habitats. Sampling of each 500-m transect took approximately 25-30 min and was conducted within 3.5 hours after sunrise during rainless mornings. The direction and order in which transects were surveyed were rotated systematically throughout the whole sampling period to control for biases in detection related to varying degrees of bird activity throughout the morning. Except for transient individuals flying over the surveyed area, all other birds detected visually and aurally within the sampled plot were recorded, including birds feeding on the wing (i.e., swallows).

SAMPLING OF VEGETATION STRUCTURE

On the same bird transects and during the same periods, vegetation was sampled using a measuring tape and a cylindrical (6 mm diameter) metal rod. Five 100-m transects were placed at 100-m intervals; the first 100-m vegetation transect crossed the bird transect perpendicularly at 50 m from its starting point and the last one at 450m from the starting point. In this way, half of each 100-m vegetation transect lay to the right of the bird transect and the other half to the left. Each 100-m transect was divided in 10 10-m sections, and within each section a sampling point was randomly selected. Thus, on each bird transect, a total of 50 points were sampled during each of the six sampling periods. On each sampling point, the metal rod was placed through the vegetation and the number 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 within 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, whereas dead plant material above the soil and still attached in the ground was classified as standing dead vegetation (Best et al. 1997). With this information I calculated nine vegetation variables known to influence grassland bird numbers (following Rotenberry and Wiens 1980 and Herkert 1994): mean litter depth, mean grass height, mean vegetation height, mean number of vegetation contacts (live grass + live forb + dead plant material) between 0-25 cm, mean number of vegetation contacts between 25-50 cm, mean number of total vegetation contacts, mean percentage grass contacts (grass cover), mean percentage forb contacts (forb cover), and mean percentage live vegetation contacts (live vegetation cover). Variables related to numbers of vegetation contacts in different height intervals were considered to be indicative of vegetation density. Forb contacts refer to hits of vegetation types other than grasses or dead plant material; contacts from crop species were included in this category. All bird and vegetation sampling were conducted by the same observer during the whole sampling period, aided by one or two assistants. All vegetation surveys were conducted within a 24-hour period concurrent with the bird counts.

DATA ANALYSIS

Vegetation structure information first was used to determine differences among habitat types and sampling periods. All data were combined at the transect level for analysis. Thus, for each vegetation variable, the 50 values recorded within a given transect on each sampling period were averaged to obtain a transect mean for that period. Because variables were not normally distributed, even after transformation, non-parametric analyses of variance were used. A Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2001) was used to test the simultaneous response of multiple vegetation variables to two factors, namely habitat type and time. Statistical significance was tested with a permutation procedure (9999 runs). After performing the analysis, a series of *post hoc* pairwise comparisons were conducted to identify differences between specific combinations of habitat types and sampling periods. These analyses were run with the program PERMANOVA (Anderson 2005).

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 Canonical Correspondence Analysis 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 into 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 of 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 in terms of 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 one 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 (e.g., Kingston and Waldren 2003), bird taxa with less than five 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). Since the first comprehensive CCA revealed important differences between obligate and facultative species, additional analyses were conducted for each of these groups of species independently. Similarly, data from other subgroups of species of special interest (e.g., common and threatened species) were also re-analyzed to facilitate the interpretation of the effects of vegetation structure on such groups. Results from CCA were visually represented with ordination graphs. In restricted analyses, weighted averaging (WA) and linear combinations of variables (LC) scores have different properties pertinent to the interpretation of results (Graffelman and Tuft 2004). Because one of the objectives of the study was to characterize vegetation structure differences among habitat types, LC scores were used since these enable the 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 site and 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 site and species scores relative to arrows is informative of the environmental characteristics of sites and of the environmental preferences of species, respectively (Palmer 1993). CANOCO 4.5 (ter Braak and Šmilauer 2002) was used to run analyses and construct figures.

Finally, the vegetation variables used in CCA were divided in two groups: those related to vegetation cover (grass, forb, and live vegetation cover) and alternative ones (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 two groups of variables and to establish how redundant their explanatory power was. This analysis, run in CANOCO 4.5, 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 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 is explaining alternative aspects of the species dataset. As with CCA, statistical significance is determined by Monte Carlo permutation tests.

RESULTS

BIRD ASSEMBLAGES AND VEGETATION FEATURES

A total of 4968 individuals of 50 grassland bird species were observed on all transects during the whole sampling period; 36 species were recorded on five or more occasions. Overall, *Nothura maculosa*, *Vanellus chilensis*, *Zenaida auriculata*, *Anthus furcatus*, and *Sturnella superciliaris* were the five most common species (i.e. highest number of individuals recorded). Although about 22% of the total bird species pool was shared by all habitats, 28% were restricted to a single habitat type. Additionally, several species were restricted to either cultivated or natural grasslands (18%).

The structure of the vegetation also varied among habitats. For example, mean vegetation height was shortest in Sheep (< 5 cm), followed by Deer (< 12 cm), and Pasture (< 23 cm) (Appendix, Fig. 1). Whereas vegetation height in Crop showed considerable variation throughout the sampling period, the opposite was true in Deer and Sheep, where mean values were similar throughout the study (Appendix, Fig. 1). Grass cover was, in general, higher in natural grasslands than in Pasture. In Crop, mean values were very low except for March 2005, shortly before a second crop (sunflower) was harvested (Fig. 1). Forb cover showed higher mean values in Pasture than in natural grasslands. The highest values, however, were recorded in Crop during the first crop phase (Sep 2004) and during the planted pasture phase after broad-leaf pastures were well developed (Jul-Nov 2005). In contrast to other habitat types, mean live vegetation cover was low in Deer (Appendix). Overall, vegetation structure responded to the effects of habitat (PERMANOVA, $F_{3, 255} = 17.05$, $P = 0.0001$), time (PERMANOVA, $F_{7, 255} = 10.50$, $P = 0.0001$) and habitat x time interaction (PERMANOVA, $F_{21, 255} = 4.75$, $P =$

0.0001). *Post hoc* pairwise comparisons indicated that, with the exception of Pasture and Deer, all other habitat combinations showed significant differences in vegetation structure. Even when data from Crop were removed from the original analysis, the effects of both factors and their interaction were still significant (as well as the results of the relevant pairwise comparisons).

BIRD-VEGETATION RELATIONSHIPS

For the whole dataset (nine vegetation variables and 36 bird species; species recorded < 5 times excluded), the four CCA axes explained 11% of the total variance in the bird dataset and 82% of the canonical variance (Table 1). A first relatively high eigenvalue, coupled with a much weaker second eigenvalue implies that axis 1 represents a fairly strong gradient (Table 1), primarily reflecting a negative association of axis 1 with grass cover (Fig. 2). Axis 2 reflected a negative relationship with grass height and vegetation density. Results from partial CCA showed that the variation explained independently by vegetation cover variables (6.43%) and by a group of alternative vegetation variables more related to structure *per se* (4.94%), was larger than the variation jointly explained by both groups (2.36%). This pattern indicates that the explanatory power of the two groups of variables is not very redundant and, thus, that each group is explaining different aspects of the species dataset.

The relative position of samples (i.e. transects) in the ordination diagram indicates a segregation of natural grasslands from cultivated grasslands (Fig. 2). In addition, samples from Sheep and Deer were more clumped and showed less dispersion than samples from either Pasture or Crop. These patterns highlight the higher spatio-temporal variability of samples from cultivated grasslands in terms of vegetation structure, which was especially evident for Crop transects. Most transects with the highest number of bird species were concentrated towards the left side of the diagram and, thus, evidenced a positive association with grass cover and a negative one with vegetation height and forb cover. The location of transects with low number of species was more variable, but several were positively associated with vegetation height and forb cover. Most were positioned to the right of the diagram which indicated a negative relationship to grass and live vegetation cover (Fig. 2).

The positions of species scores in the ordination diagram showed an association of most obligate grassland birds with sites with an important grass component. This group was also negatively associated with vegetation height (Fig. 3). In contrast, a smaller group of obligate species (in the lower right corner in Fig. 3) were linked to tall non-grass vegetation. Among facultative species, birds that are considered as agricultural pests (*Columba maculosa*, *C. picazuro*, *Zenaida auriculata*, *Myiopsitta monachus*, *Molothrus bonariensis*) grouped close together (upper right corner in Fig. 3) and were negatively associated to most measured variables. With regard to breeding species, ground-nesters and burrowers (most of which are obligate grassland species), responded positively to grass cover, whereas birds that nest off-the-ground (i.e., in marshy vegetation, or on shrubs and trees) showed no specific association patterns (Fig. 3).

When obligate and facultative species were analyzed independently, a few contrasting patterns were highlighted. Even though the first eigenvalue was fairly high in both analyses (suggesting relatively strong gradients), the proportion of variation explained in the case of the obligate species was greater than in the case of the facultative species (Table 2). In the first of these analyses, axis 1 was positively related to vegetation height and negatively to live vegetation cover, whereas axis 2 showed an association to grass height and vegetation density in the 0-25 cm layer (Fig. 4A). Among obligate species, birds such as *Rhynchotus rufescens* and *Sporophila ruficollis* were positioned to the right of the graph, an indication of their association with high vegetation. Towards the upper left area of the ordination, a second group of species, including *Sturnella defilippi* and *Anthus nattereri*, responded positively to grass cover and negatively to forb cover. Finally, several species located within the lower left quadrant showed a preference for short, sparse vegetation, as evidenced by their negative association with variables related to vegetation height and density. Among the latter, *Geositta cunicularia* showed the strongest response (Fig. 4A). In the ordination diagram for facultative birds, most scores lay outside the center region and the scattered pattern of the points suggested that there was a high variability in the way facultative species respond to vegetation structure (Fig. 4B). Overall, the comparison of arrow lengths in both ordinations indicated that, while grass cover was an important variable for both obligate and facultative species, live vegetation cover, vegetation height and density had contrasting contributions in the two groups (Fig. 4).

An analysis limited to threatened taxa showed a high first eigenvalue followed by a second relatively high value, indicating that the first gradient was not very strong. Overall, vegetation variables explained 29% of the variation of these species' distribution and abundance (Table 3). Species with the strongest response were *Heteroxolmis dominicana* and *Sporophila ruficollis*, which were positively affected by vegetation density in the 25-50 cm height interval and by vegetation height. *Anthus nattereri* and *Sturnella defilippi* showed relatively weak positive responses to litter depth and grass cover, whereas *Rhea americana* was also weakly associated with forb cover and responded negatively to variables related to vegetation density (Fig. 5).

A final analysis focused exclusively on the distribution of common bird species (i.e., those with 10 or more observations) on natural grasslands (i.e., Sheep and Deer habitats). Only birds and vegetation data restricted to Sheep and Deer were considered. The first axis explained 53% of the canonical variation but overall, the amount of variation in the bird data explained by all axes was low (12%, Table 4). The distribution of species along the first two axes resulted in three main groups: one comprising species related to higher vegetation (positioned to the right), one with species associated with short and sparse vegetation (located to left), and a third group whose species responded negatively to most variables, except litter depth (situated at the lower center, Fig. 6). The first two groups involved only obligate species, while the latter included both obligate and facultative birds.

DISCUSSION

Grassland birds in the Northern Campos of Uruguay are strongly influenced by vegetation structure. Most differences in vegetation structure among habitats can be linked to the specific management activities on each habitat type. Crop included several management phases, which explained the high variability in several of the vegetation parameters, such as mean vegetation height. In contrast, year-round grazing in Pasture, Sheep and Deer resulted in a less variable vegetation height throughout the sampling period. Vegetation height was shortest in Sheep habitat, in agreement with previous studies in this area which documented the relationship between sheep grazing and low vegetation height (Sturm 2001).

In this study vegetation height was among the structural variables that had the strongest influences on bird species richness and abundance. A similar result has been highlighted in other studies of grassland birds where the effects of this variable have been interpreted in terms of foraging and nesting opportunities (Grzybowski 1976, Isacch and Martínez 2001, Nocera et al. 2007 and references therein). Despite the general importance of vegetation height, not all bird species responded in the same manner to this variable. As in other major grassland ecosystems, some species are specialized in tall grass and others in short grass, as a consequence of specific foraging and nesting requirements.

Vegetation height had an effect on distribution of common species even in habitats that did not differ in overall grass cover (i.e., Sheep and Deer). Here, however, vegetation density was also identified as an important factor. For grassland birds in North America, vertical vegetation density has also been reported as one of the most important explanatory variables for distribution and density of grassland birds (Renfrew and Ribic 2001, Fletcher and Koford 2002, Nocera et al. 2007). Other studies have found positive correlations between grassland bird densities and litter depth (Wiens 1973, Grzybowski 1976, Rotenberry and Wiens 1980, Renfrew and Ribic 2001). Litter depth, however, was not indicated as an important factor in this study. Only *Anthus hellmayri* and *A. nattereri* were positively associated to this variable in some of the analyses. Arthropod abundance has been shown to be positively related to the presence of litter (Facelli 1994) and this might explain the observed pattern for these two insectivorous birds.

Some of the most common birds were associated with short and sparse vegetation. This was the case of *Nothura maculosa*, *Vanellus chilensis* and *Anthus furcatus*, which were among the most abundant species in all three non-crop habitat types. The link between common grassland birds and short vegetation has been reported in other studies. *Vanellus chilensis*, *Nothura darwini* and *Anthus correndera* are thought to benefit from the effects of cattle grazing in the pampas of Argentina (Isacch and Martínez 2001, Isacch et al. 2005). Colwell and Dodd (1995, 1997) also found an inverse relationship between vegetation height and diversity and density of bird assemblages, especially shorebirds, feeding in pastures in the surroundings of Humboldt Bay, California. Species' densities were greater in actively grazed pastures and this pattern was hypothesized to be a response to increased prey availability (Colwell and Dodd 1995). In fact, in another study conducted in the Great Plains of Texas, arthropod abundance was found to be higher in native shortgrass prairie than in several grasslands characterized by taller vegetation (McIntyre and Thompson 2003). Additionally, species that pick prey from the ground or snatch them from the air should benefit from access to the ground such as in areas with short vegetation (Clarke et al 1997, Bradbury and Bradter 2004). It has also been argued that foraging in short vegetation may reduce physiological costs in comparison to feeding in dense vegetation, since the latter is wetter and harder to move in (Moorcroft et al. 2002). Finally, a trade-off involving vegetation structure and nesting and predator detection advantages has also been proposed; 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 short vegetation (Colwell and Dodd 1995, Gotmark et al. 1995).

In the analysis based on the complete dataset, all three *Anthus* species showed a similar positive response to grass cover. Within natural grasslands, however, *Anthus nattereri* occupied sites with relatively higher and denser vegetation and *A. furcatus* was found in sites with relatively short and sparse vegetation; *A. hellmayri* tended to be in intermediate sites. These patterns suggest resource partitioning among closely related species with similar morphologies. Vegetation height has been identified as one of the most important variables responsible for interspecific habitat differences among grassland birds (Cody 1968). In the case of three co-occurring species of *Calcarius* (Emberizidae), these distributed themselves in different parts of the vegetation height gradient in grasslands of Oklahoma (Grzybowski 1976).

As expected, vegetation structure explained more variation among obligate than among facultative grassland bird species. The importance of specific variables also differed between the two groups. 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 probably related to the fact that, unlike grassland specialist birds, virtually all grassland species rely on this habitat for feeding but not for breeding purposes (Batáry et al. 2007). In fact, habitat models for grassland species have been shown to correlate with nesting requirements (Fletcher and Koford 2002). Among migrants, species that are grassland specialists during the breeding season also show stronger associations to specific habitat features even during the non-breeding season (Igl and Ballard 1999).

Taxa of conservation-concern showed diverse responses to vegetation structure, with some favoring taller vegetation in cultivated grasslands (*Heteroxolmis dominicana*, *Sporophila ruficollis*), others preferring short vegetation in natural grasslands (*Anthus nattereri*, *Sturnella defilippi*), and some with no strong association to any particular variable (*Rhea americana*). In agreement with the results from studies in the southern Pampas (Fernández et al. 2003), *Sturnella defilippi* was found to be largely restricted to natural grasslands and absent from cultivated lands in the Northern Campos. The species, however, showed contrasting patterns in relation to vegetation height in the two regions. In the Northern Campos, *S. defilippi* was not positively associated with vegetation height, but in the southern Pampas, this variable was among the most reliable predictors of meadowlark occurrence (Fernández et al. 2003). Comparison of results from both studies indicates that this species occupies fields with higher vegetation in the southern Pampas. Among the pipits, the response of *Anthus nattereri* to vegetation structure was more similar to that of more geographically restricted and less common congenerics (*A. chacoensis*, *A spragueii*), which seem to avoid short vegetation (Davis et al. 1999, Isacch et al. 2005), than to other common and more widely distributed pipits (*A. correndera*, *A. furcatus*, Isaach and Martinez 2001 and this study).

In grassland ecosystems, land management practices can be especially important for species that feed and nest on the ground (Bradbury and Bradter 2004), such as most of the obligate grassland birds of the Pampas. The positive response of many obligate species to short and sparse vegetation indicates that they can successfully use areas grazed by sheep. This might not be the case for other species such as *Anthus nattereri*. Thus, management of natural grasslands to conserve obligate grassland birds should consider the different habitat needs of each species.

Even though bird distribution and abundance were associated with the vegetation variables considered, the substantial amount of variation in the bird dataset that remained unexplained indicated the influence of other important drivers. The high diversity of plant species in grasslands of the Pampas region (Soriano 1992), as well as the recent identification of several characteristic plant communities within the native grasslands of the Northern Campos (Lezama et al. 2006), suggest that floristics may be an additional aspect that warrants further examination. It has been suggested that, at local scales, vegetation composition may have important effects on bird communities because of specific resources that different plant species may provide (Rotenberry 1985). This is the first study to relate bird distribution and abundance to vegetation structure in the Northern Campos of Uruguay. My results support previous knowledge based on natural history data, and present new information on more specific bird responses to vegetation structure. It also provides evidence that population declines of grassland birds in the Pampas are the result, at least in part, of the negative effects of agriculture-related habitat modification on vegetation structure variables important to birds. Future studies should focus on determining the influence of vegetation structure on bird foraging and nesting requirements and on the investigation of additional factors responsible for grassland bird assemblage organization, such as vegetation composition.

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Table 1. Canonical Correspondence Analysis of 36 species of Pampas' grassland birds and nine vegetation structure variables.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.362	0.150	0.087	0.063
Cumulative percentage variance:				
Species data	6.1	8.7	10.2	11.2
Species-environment relation	44.7	63.3	74.0	81.8
Sum of all eigenvalues: 5.893				
Sum of all canonical eigenvalues: 0.809				
Test of significance of first canonical axis: *F*-ratio=16.02, *P*=0.002				
Test of significance of all canonical axes: *F*-ratio=4.33, *P*=0.002				

Table 2. Canonical Correspondence Analysis of obligate (17 species) and facultative (18 species) Pampas' grassland birds and nine vegetation structure variables.

GRASSLAND OBLIGATES

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.344	0.087	0.071	0.016
Cumulative percentage variance:				
Species data	13.6	17.0	19.8	20.5
Species-environment relation	61.5	77.2	89.8	92.7

Sum of all eigenvalues: 2.529

Sum of all canonical eigenvalues: 0.558

Test of significance of first canonical axis: *F*-ratio=38.35, *P*=0.002

Test of significance of all canonical axes: *F*-ratio=7.68, *P*=0.002

GRASSLAND FACULTATIVES

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.344	0.177	0.157	0.106
Cumulative percentage variance:				
Species data	4.0	6.1	8.0	9.2
Species-environment relation	35.8	54.2	70.5	81.6

Sum of all eigenvalues: 8.500

Sum of all canonical eigenvalues: 0.961

Test of significance of first canonical axis: *F*-ratio=6.49, *P*=0.002

Test of significance of all canonical axes: *F*-ratio=2.18, *P*=0.002

Table 3. Canonical Correspondence Analysis of five conservation-concern Pampas grassland birds and nine vegetation structure variables.

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Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.527	0.273	0.111	0.045
Cumulative percentage variance:				
Species data	16.1	24.4	27.8	29.2
Species-environment relation	55.1	83.7	95.3	100.0
Sum of all eigenvalues: 3.279				
Sum of all canonical eigenvalues: 0.957				
Test of significance of first canonical axis: *F*-ratio=15.90, *P*=0.002				
Test of significance of all canonical axes: *F*-ratio=3.80, *P*=0.002				

Table 4. Canonical Correspondence Analysis of seven vegetation structure variables and 17 common species of birds that inhabit natural grasslands in the Northern Campos.

Axes	**1**	**2**	**3**	**4**
Eigenvalues	0.134	0.051	0.035	0.021
Cumulative percentage variance:				
Species data	6.7	9.3	11.0	12.1
Species-environment relation	53.0	73.1	87.0	95.5
Sum of all eigenvalues: 1.994				
Sum of all canonical eigenvalues: 0.252				
Test of significance of first canonical axis: *F*-ratio=8.697, *P*=0.002				
Test of significance of all canonical axes: *F*-ratio=2.923, *P*=0.002				

Figure 1. Temporal variation of four of the vegetation variables (mean ± SE) that explained differences among the four habitat types in the Northern Campos: CR (Crop), PA (Pasture), SH (Sheep), and DE (Deer).

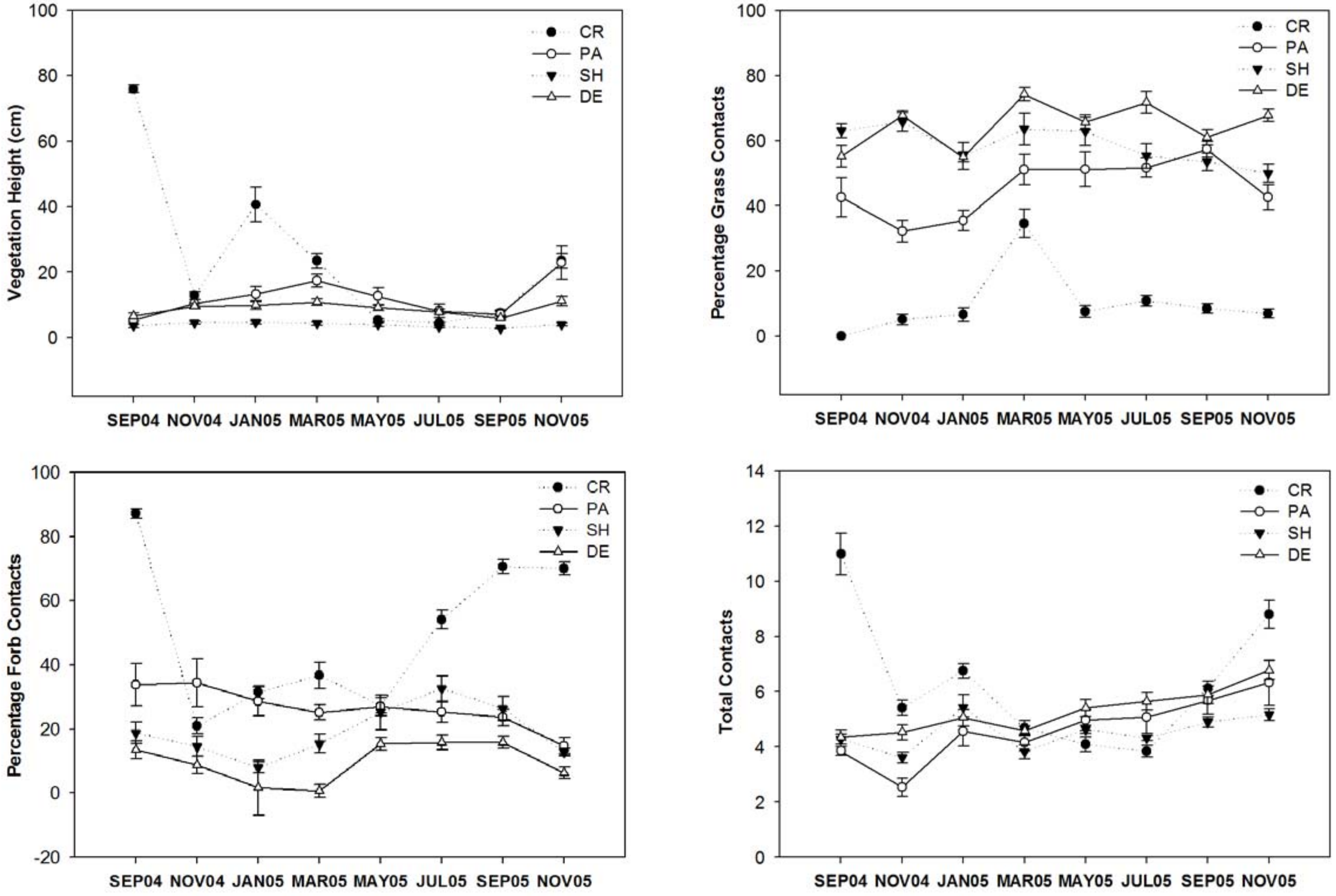


Figure 2. Grassland samples (i.e. transects) along a vegetation structure gradient in the Northern Campos of Uruguay. CCA ordination diagram with LC scores shows vegetation structure variables (arrows) and transects (symbols) of four grassland habitat types: Crop (circles), Pastures (squares), Sheep (triangles), and Deer (diamonds). Filled symbols show transects in which the highest number of species (9-11) were recorded (black), and those transects in which the lowest number of species (2) were recorded (gray). The vegetation structure variables are: GH (mean grass height), VH (mean vegetation height), C25 (mean contacts under 25 cm), TC (mean total contacts), % GC (mean percentage grass contacts), % FC (mean percentage forb contacts), and % LC (mean percentage live vegetation contacts). Arrows representing LD (mean litter depth) and C50 (mean contacts between 25 and 50 cm) were very short and are not depicted here. One outlier (Crop transect 5/May 2005) is also excluded from the diagram.

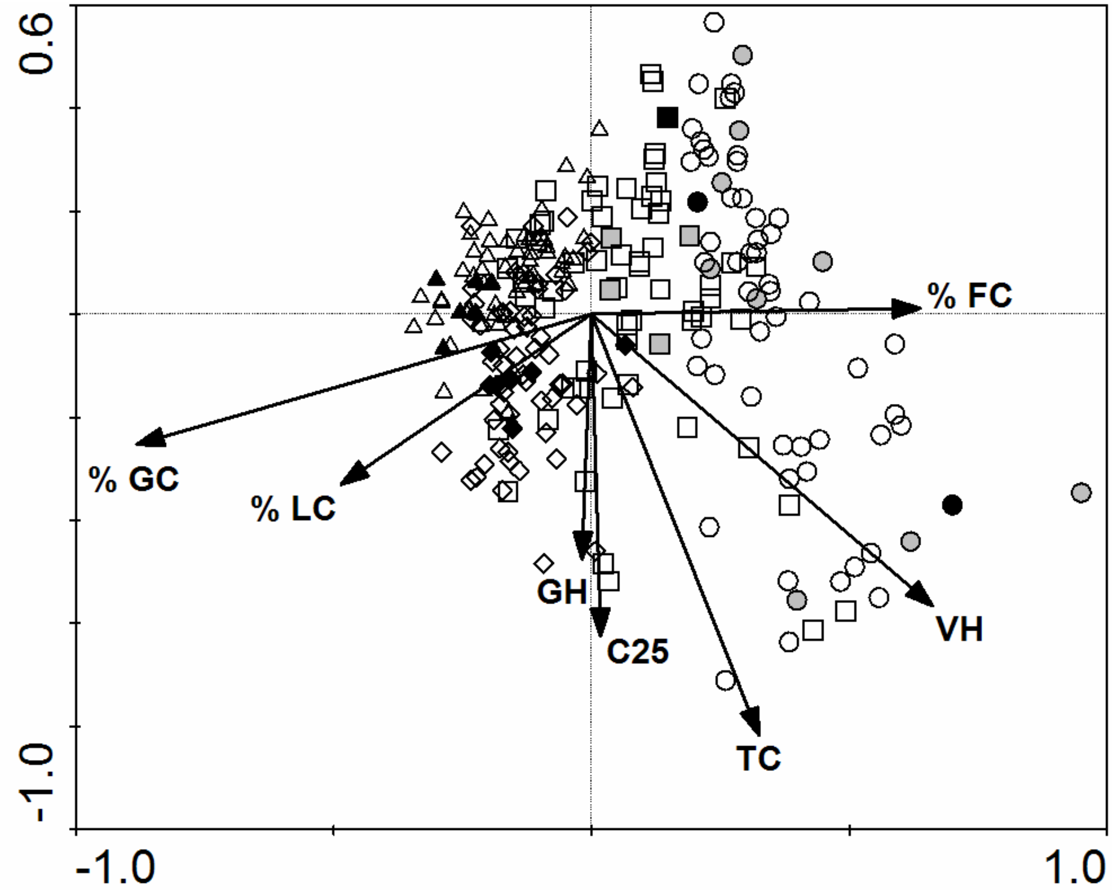


Figure 3. Pampas' grassland bird species along a vegetation structure gradient in the Northern Campos. The CCA ordination diagram shows vegetation structure variables (arrows) and five grassland bird categories: obligate (circles), facultative (triangles), and ground-nesting species (open symbols), as well as species that nest off-the-ground (black symbols), and non-breeders and a generalist brood parasite (gray symbols). The 36 species are: RHAME (*Rhea americana*), RHRUF (*Rhynchotus rufescens*), NOMAC (*Nothura maculosa*), SYSIB (*Sirigma sibilatrix*), VACHI (*Vanellus chilensis*), PLDOM (*Pluvialis dominica*), BALON (*Bartramia longicauda*), GAPAR (*Gallinago paraguaiae*), ATCUN (*Athene cunicularia*), COMAC (*Columba maculosa*), COPIC (*Columba picazuro*), ZEAUR (*Zenaida auriculata*), MYMON (*Myiopsitta monachus*), COCAM (*Colaptes campestris*), GECUN (*Geositta cunicularia*), ANANN (*Anumbius annumbi*), XOCIN (*Xolmis cinerea*), XOIRU (*Xolmis irupero*), HEDOM (*Heteroxolmis dominicana*) MARIX (*Machetornis rixosus*), TYSAV (*Tyrannus savanna*), TALEU (*Tachycineta leucorrhoa*), PRCHA (*Progne chalybea*), PRTAP (*Progne tapera*), ALFUC (*Alopochelidon fucata*), ANFUR (*Anthus furcatus*), ANHEL (*Anthus hellmayri*), ANNAT (*Anthus nattereri*), AMHUM (*Ammodramus humeralis*), SILUT (*Sicalis luteola*), EMPLA (*Embernagra platensis*), SPRUF (*Sporophila ruficollis*), STDEF (*Sturnella defilippi*), STSUP (*Sturnella superciliaris*), PSVIR (*Pseudoleistes virescens*), MOBON (*Molothrus bonariensis*). For details of the nine vegetation structure variables see legend in Fig. 2 (a very short arrow representing C50 is not shown).

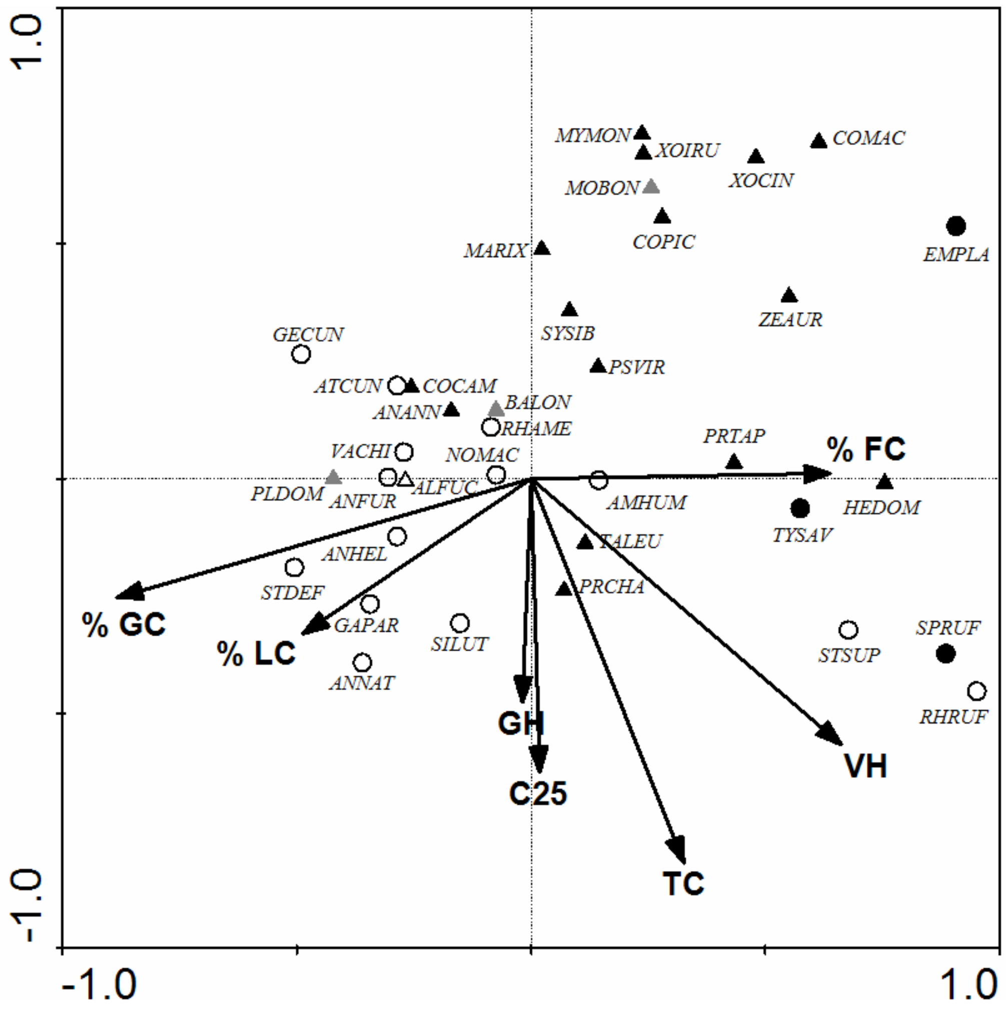


Figure 4. Patterns of distribution of obligate (A) and facultative (B) grassland bird species (circles) in CCA ordination diagrams with nine vegetation structure variables (arrows). One vegetation variable represented by a very short arrow (C50) and one outlier (*Embernagra platensis*) are not depicted in (A). For details of vegetation structure variables and bird species see legends in Figs. 2 and 3.

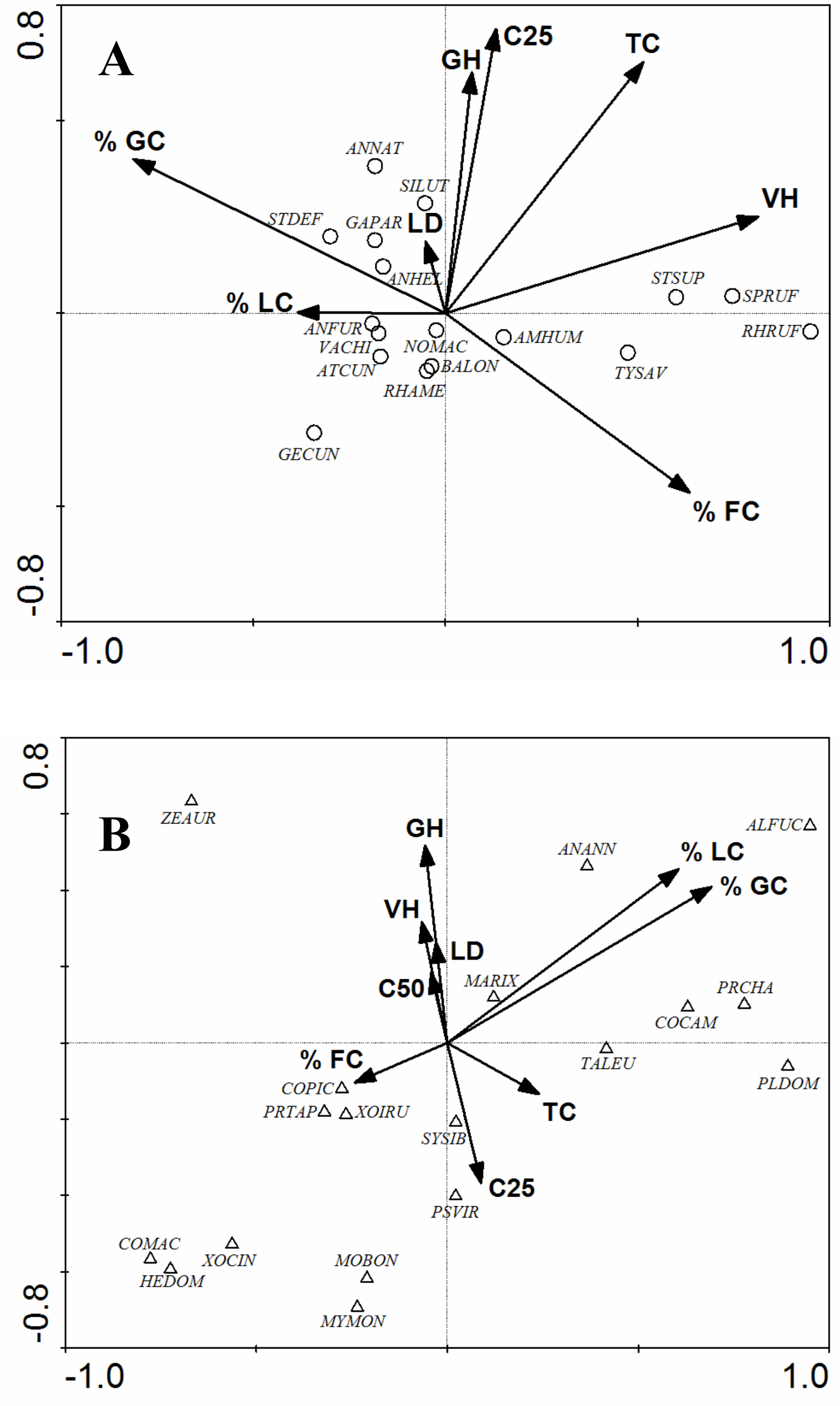


Figure 5. Conservation-concern grassland bird species along a vegetation structure gradient in the Northern Campos of Uruguay. The CCA ordination diagram shows vegetation structure variables (arrows) and conservation-concern obligate (circles) and facultative (triangle) species: *Rhea americana* (near-threatened), *Heteroxolmis dominicana* (vulnerable), *Anthus nattereri* (vulnerable), *Sporophila ruficollis* (near-threatened), and *Sturnella defilippi* (vulnerable). Vegetation structure variables are described in Fig. 2.

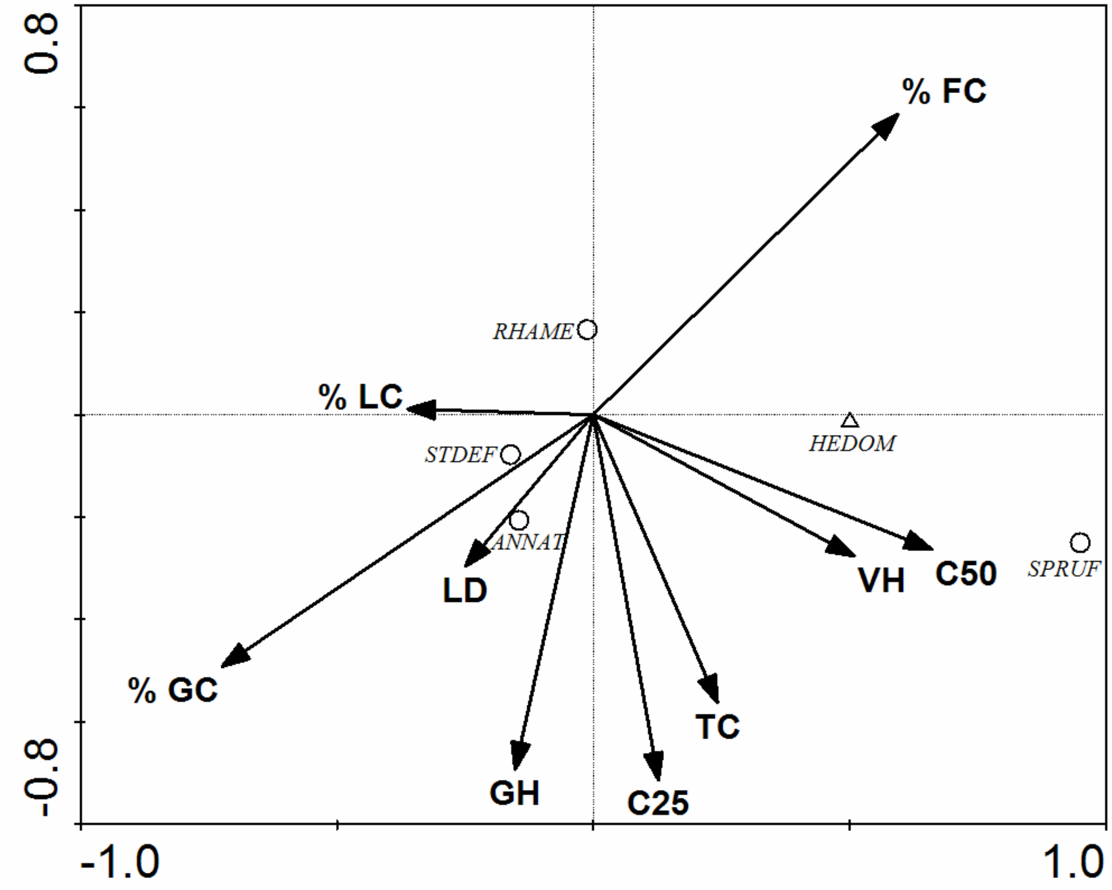
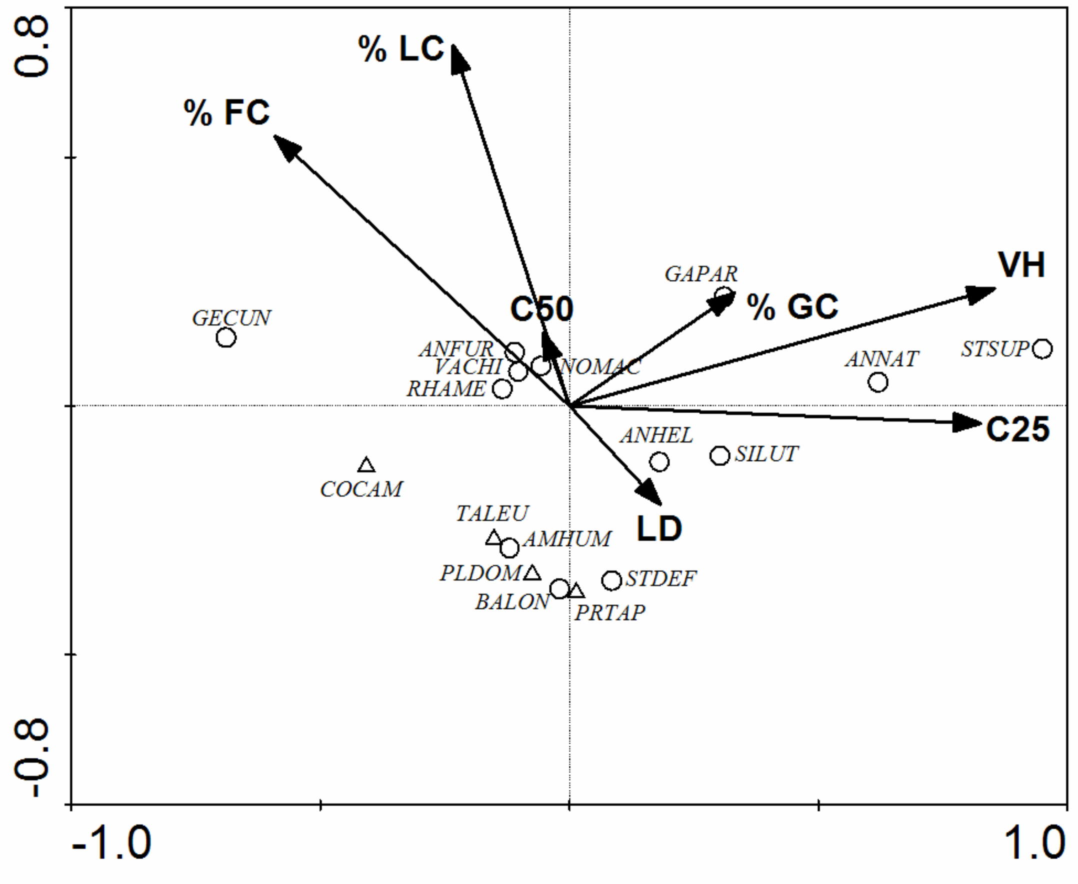


Figure 6. CCA ordination diagram of grassland bird species along a vegetation structure gradient in natural grasslands (i.e., Sheep and Deer) of the Northern Campos of Uruguay. The plot includes seven vegetation structure variables (arrows) and 17 common obligate (circles) and facultative (triangles) species (i.e., 10 or more observations). GH and TC were removed because of their high correlation with other variables. Acronyms for bird species and vegetation structure variables are specified in legends in Figs. 2 and 3.



Appendix. Mean values (± SE) of vegetation structure variables for each habitat type (CR: Crop; PA: Pasture; SH: Sheep; DE: Deer) and sampling period in the Northern Campos of Uruguay. LD: litter depth; GH: grass height; VH: vegetation height; TC: total contacts; C25: contacts under 25 cm; C50: contacts between 25 and 50 cm; %GC: percentage grass contacts; %FC: percentage forb contacts; %LC: percentage live vegetation contacts. Non-percentage values are in cm.

		SAMPLING PERIODS							
Habitat	**Variables**	**SEP 04**	**NOV 04**	**JAN 05**	**MAR 05**	**MAY 05**	**JUL 05**	**SEP 05**	**NOV 05**
CR	LD	0.00	0.26±0.12	0.43±0.04	0.77±0.09	0.00	0.00	0.07±0.01	0.09±0.02
PA	LD	4.28±0.89	0.61±0.09	0.26±0.08	0.09±0.03	0.04±0.02	0.09±0.02	0.10±0.03	0.06±0.03
SH	LD	0.59±0.12	0.43±0.12	0.30±0.10	0.31±0.09	0.24±0.08	0.09±0.03	0.03±0.01	0.04±0.02
DE	LD	1.22±0.19	1.04±0.16	0.82±0.09	0.83±0.12	0.51±0.07	0.27±0.07	0.17±0.04	0.28±0.04
CR	GH	0.00	1.15±0.24	2.62±0.62	9.31±1.10	1.23±0.48	1.02±0.17	1.49±0.24	3.07±0.38
PA	GH	4.27±0.65	6.39±1.32	7.93±2.15	11.93±2.19	9.93±2.50	6.42±1.70	6.38±1.07	21.21±5.20
SH	GH	3.11±0.42	4.29±0.49	4.28±0.60	3.83±0.57	3.50±0.47	2.91±0.27	2.38±0.17	3.76±0.42
DE	GH	47.48±0.82	75.02±0.76	77.52±1.35	84.22±1.03	70.54±0.94	61.44±0.74	46.28±0.67	87.00±1.50
CR	VH	75.92±1.20	12.86±1.17	40.61±5.29	23.41±2.25	5.28±0.50	4.53±0.21	7.47±0.66	23.43±2.21
PA	VH	5.39±0.36	10.30±1.42	13.26±2.32	17.41±1.95	12.62±2.68	8.13±2.08	7.13±1.26	22.84±5.09
SH	VH	3.58±0.55	4.61±0.47	4.70±0.56	4.30±0.58	3.94±0.48	3.25±0.26	2.82±0.19	4.07±0.43
DE	VH	6.60±0.88	9.56±0.75	9.91±1.36	10.81±1.03	9.14±0.91	7.89±0.70	5.96±0.65	11.15±1.46
CR	TC	10.99±0.76	5.41±0.27	6.75±0.26	4.68±0.27	4.09±0.27	3.83±0.21	6.11±0.26	8.80±0.50
PA	TC	3.85±0.15	2.53±0.33	4.55±0.53	4.15±0.31	4.97±0.39	5.07±0.58	5.68±0.51	6.32±0.81
SH	TC	4.28±0.18	3.61±0.19	5.43±0.44	3.82±0.26	4.62±0.14	4.31±0.09	4.90±0.18	5.15±0.22
DE	TC	4.35±0.25	4.52±0.27	5.05±0.29	4.58±0.18	5.41±0.31	5.65±0.32	5.89±0.32	6.78±0.34
CR	C25	2.39±0.17	5.28±0.29	5.74±0.19	3.95±0.26	4.08±0.27	3.83±0.21	6.11±0.26	7.57±0.29
PA	C25	3.85±0.15	2.33±0.24	4.36±0.43	3.69±0.23	4.66±0.27	4.99±0.53	5.64±0.49	5.12±0.34
SH	C25	4.22±0.14	3.44±0.14	5.42±0.44	3.80±0.25	4.60±0.14	4.31±0.09	4.89±0.18	5.14±0.22
DE	C25	4.35±0.25	4.32±0.23	4.90±0.28	4.44±0.17	5.34±0.30	5.62±0.32	5.87±0.32	6.57±0.30
CR	C50	1.25±0.09	0.11±0.03	0.57±0.11	0.49±0.10	0.01±0.01	0.00	0.00	1.19±0.30
PA	C50	0.00	0.20±0.09	0.19±0.11	0.43±0.12	0.30±0.13	0.08±0.06	0.04±0.04	0.86±0.31
SH	C50	0.01±0.01	0.15±0.13	0.01±0.01	0.02±0.01	0.02±0.01	0.00	0.01±0.00	0.01±0.01
DE	C50	0.00	0.16±0.03	0.13±0.04	10.06±9.94	0.06±0.02	0.03±0.01	0.02±0.02	0.20±0.04
CR	%GC	0.00	5.13±1.60	6.64±2.05	34.64±4.31	7.65±1.85	10.82±1.67	8.51±1.37	6.97±1.29
PA	%GC	42.64±5.93	32.25±3.29	35.49±3.08	51.04±4.67	51.16±5.28	51.68±3.01	57.30±2.47	42.65±3.84
SH	%GC	62.98±2.25	65.69±2.89	55.24±4.10	63.51±4.84	62.79±4.28	55.27±3.76	53.41±2.76	49.89±2.77
DE	%GC	55.21±3.34	67.70±1.33	54.93±1.59	74.23±2.04	65.62±2.22	71.70±3.36	60.98±2.35	67.76±1.84

Appendix Continued

		SAMPLING PERIODS							
Habitat	**Variables**	**SEP 04**	**NOV 04**	**JAN 05**	**MAR 05**	**MAY 05**	**JUL 05**	**SEP 05**	**NOV 05**
CR	%FC	87.23±1.52	20.96±2.42	31.43±1.92	36.77±4.12	27.28±2.38	54.12±2.97	70.63±2.34	70.10±2.06
PA	%FC	33.83±6.62	34.48±7.40	28.68±4.63	25.20±2.45	26.93±2.75	25.28±3.15	23.67±2.57	14.78±2.55
SH	%FC	18.79±3.40	14.52±3.08	8.00±1.66	15.33±2.93	25.23±5.38	32.59±3.92	26.39±3.77	12.80±1.18
DE	%FC	13.51±2.79	8.77±2.69	1.68±8.55	0.70±2.02	15.32±2.02	15.85±2.25	15.84±1.94	6.30±1.87
CR	%LC	87.24±1.52	26.10±2.96	39.41±2.40	75.37±4.06	34.93±2.90	64.94±2.59	79.14±1.32	77.06±1.30
PA	%LC	76.47±2.46	66.73±6.05	64.17±2.58	76.24±2.68	78.09±4.33	76.96±1.71	80.97±1.66	57.43±4.83
SH	%LC	81.78±2.27	80.20±2.19	63.25±2.78	78.85±2.64	88.01±2.04	87.86±2.25	79.80±2.84	62.69±2.33
DE	%LC	10.99±0.76	5.41±0.27	6.75±0.26	4.68±0.27	4.09±0.27	3.83±0.21	6.11±0.26	8.80±0.50

CHAPTER 3

NEST SURVIVAL GRASSLAND BIRD IN CULTIVATED AND NATURAL GRASSLANDS OF THE NORTHERN CAMPOS OF URUGUAY

INTRODUCTION

Many populations of grassland birds are declining widely as a consequence of habitat modification (Askins 1993, Vickery et al. 1999, Herkert et al. 2003, Murphy 2003, Brennan and Kuvlesky 2005). This has resulted in much effort devoted to determining how grassland species respond to changes in habitat features, especially with respect to those generated by agricultural activities (e.g., Herkert 1994, Knopf 1994, Best et al. 1995, Fletcher and Koford 2002, Filloy and Bellocq 2007). In general, population density has been traditionally used as a surrogate for habitat quality (Van Horne 1983) and under this premise the same resources that sustain high population densities also are assumed to positively affect indices of fitness, such as reproductive success (Vickery et al. 1992a). The relationship between density and nesting habitat quality, however, is variable, and it has been shown that the former it is not necessarily a reliable surrogate of the latter (Fretwell 1969, Maurer 1986, Vickery et al. 1992a, Hughes et al. 1999, Winter and Faaborg 1999).

Population declines of grassland birds in North America have been related to low quality of breeding habitat (Askins 1993). Habitat modifications imposed by agriculture can reduce the availability of foraging and nesting resources through effects on vegetation structure and, thus, may force birds to breed in unfavorable areas (Evans

2004). For example, in the case of ground-nesting birds, livestock grazing may decrease vegetation density and heterogeneity which can, in turn, negatively affect nest microclimate and concealment (With and Webb 1993, Gregg et al. 1994, Beck and Mitchell 2000, Hoekman et al. 2002, Evans 2004). Brood parasitism poses an additional threat as brood parasites are thought to benefit from conditions provided by agriculture (Rodenhouse et al. 1993, Best et al. 1997, Davis and Sealy 2000). In the Neotropics in particular, the expansion of the Shiny Cowbird (*Molothrus bonariensis*) has been associated with habitat alterations related to agricultural development (Post and Wiley 1977, Cavalcanti and Martins Pimentel 1988).

Testing hypotheses about survival processes and determining survival estimates are fundamental steps towards a thorough understanding of animal population dynamics (Lebreton et al. 1992). The nesting season can be critical for bird populations (Martin 1993a), and understanding patterns of nest survival is a key aspect for the management of declining birds (Grand et al. 2006). Agricultural landscapes include diverse management practices which probably affect birds' reproductive success differentially. For example, some activities can result in the replacement of native vegetation by introduced species and grazing may involve different types of domestic and native animals. Given the importance of breeding ecology for bird population persistence and the diversity of agricultural habitats, there is a need for more studies that focus on species' reproductive biology (Davis 2003, Thompson 2004), especially those that provide habitat-specific demographic measures (Johnson 2007).

The Pampas biome of south-eastern South America comprises a region dominated by temperate sub-humid grasslands (Soriano 1992). The original vegetation, which included a mixture of tallgrass steppe, prairies, and marshlands, has been extensively modified by agriculture (León et al. 1984, Bucher and Nores 1988, Vickery et al. 1999, Bilenca and Miñarro 2004). Most of the Pampas has now been converted either to croplands or to rangelands (Krapovickas and Di Giacomo 1998, Vickery et al. 1999). Within the latter, livestock has largely replaced native grazers (i.e., Pampas Deer *Ozotoceros bezoarticus* and Greater Rhea *Rhea americana*; Soriano 1992, González et al. 2002), and a variety of grazing practices result in habitats of diverse vegetation structure that are used by grassland birds (e.g., Lanctot et al. 2002, Fernández et al. 2003). These agricultural habitats are key for grassland bird conservation because they greatly exceed the area set aside for wildlife reserves in the region (Di Giacomo and Krapovickas 2005, World Resource Institute 2007). The region's conservation status has triggered new efforts focused on grassland research, most of which have been directed towards the characterization of bird assemblages in agricultural settings (e.g., Isacch and Martínez 2001, Isacch et al. 2003) and the identification of bird-habitat relationships (Fernández et al. 2003; Isacch et al. 2005). Studies of nest success have also received some attention (e.g., Mermoz and Reboreda 1998), but not with the aim to contrast patterns among habitats with differing degrees of alteration.

In this study, nest-survival patterns of ground-nesting birds breeding in cultivated and natural grasslands in the Northern Campos of Uruguay were investigated. After a general characterization of the breeding biology of ground-nesting species of the Northern Campos, nest-survival models were used to test hypotheses dealing with possible factors underlying avian nest-success patterns, including temporal, habitat type, and vegetation structure effects. In general, nest-survival rates were predicted to be higher in native grasslands and in habitats with higher and denser vegetation, based on the positive effects these features can have on nest success (Davis 2005). Given the association of *Molothrus bonariensis* with cultivated lands, brood parasitism was predicted to be higher in cultivated rather than in natural grasslands. Among congeneric species with contrasting conservation status, patterns of nest survival were also predicted to reflect such differences (i.e., threatened species should have lower nest survival).

METHODS

Study area

Research was conducted in southern Salto department, northwestern Uruguay (31°19' to 31°44'S and 56° 42' to 57° 56'W), a region within the Northern Campos of the Río de la Plata grasslands (Soriano 1992). The general landscape of the study area is composed of rolling topography in which low mesas and rocky outcrops are interspersed. The climate is considered temperate humid with mean annual temperature of 19°C and 1300 mm annual rainfall (Lezama et al. 2006). Agricultural activity is primarily represented by open-range livestock grazing on natural and cultivated grasslands. Planted pastures and croplands are common in the western part of the region, whereas the eastern part is characterized by large expanses of natural grasslands which have never been plowed. These natural grasslands harbor many species in the families Poaceae and Asteraceae; *Stipa*, *Paspalum*, *Aristidsa*, *Conyza* and *Piptochetium* are all well represented (Lezama et al. 2006). Large patches of grasslands (800 to 1200 ha) were selected within ranches and farms in the surroundings of San Antonio and Cerros de Vera in Salto department.

Field work was conducted in three grassland types: 1) planted pastures (Pasture), represented by lands that were plowed and seeded with non-native species and used for cattle grazing; 2) sheep rangelands (Sheep), native grasslands that had not been previously plowed and were grazed by free-ranging sheep and cattle; and 3) deer rangelands (Deer), unplowed native grasslands which were grazed by cattle and Pampas Deer. The lack of sheep grazing (although a few animals were present in these fields to supply the ranch) in this type of grassland resulted in higher vegetation height and diversity than in Sheep (Sturm 2001, Chapter 2). Additional details about each habitat type are provided elsewhere (see Chapter 1).

Nest searching and monitoring

From September 2004 to November 2005 grassland bird populations were sampled on eight 500-m transects on each of the three grassland types. Four transects were chosen among the eight available (after considering constraints imposed by landowners' and other logistic issues) and 15-ha plots (500 x 300 m) were established along them (i.e., four plots per habitat type). On these plots, the nests of the following ground-nesting species were targeted: *Rhea americana*, *Nothura maculosa*, *Vanellus chilensis*, *Gallinago paraguaiae*, *Podager nacunda*, *Anthus furcatus*, *A. hellmayri*, *A. nattereri*, *Ammodramus humeralis*, *Sicalis luteola*, *Sturnella defilippi*, and *S. superciliaris*. To locate nests, an adaptation of the rope-dragging method (Wiens 1969, Klute 1994) was used on each plot. This consisted of a 30-m length rope with 1-m pieces of rope suspended at 1-m intervals. Two observers walked parallel to each other while pulling the rope through the vegetation. At the same time, one or two additional observers walked 10-20 m behind the rope and spotted birds as they were flushed. After each flushing event the area was carefully checked to locate a potential nest. This method performed poorly for *Vanellus chilensis* and *Sturnella defilippi*, because these species tend to abandon the nest in advance, as soon as a threat is perceived by the attending adult. Most nests of these species were located using behavioral clues. During the first breeding season (Sep 19-Dec 3, 2004), all plots were surveyed approximately every 25 days. During the second breeding season (Sep 26-Dec 12, 2005) more assistants were available, and plots were surveyed approximately every 15 days. Despite differences in effort between the two consecutive breeding seasons, nest finding methods used were the same and, thus, nests monitored were assumed to be a random subset of all nesting attempts. Once a nest was found, its geographic coordinates were recorded into a GPS receiver and two marks (located ≥ 2.5 m from the nest) were placed forming a straight line with the nest in the middle. These marks consisted of small pieces of flagging attached to vegetation or small piles of natural materials such as dry cattle dung. The GPS receiver was very reliable in terms of relocating the general spot where the nest was located, whereas the marks provided cues regarding the specific nest placement. Nests were checked every 2-3 days until their final fate (e. g., predation, abandonment, young fledged) was established. Nest fate was determined following guidelines described by Martin (1993) and Martin and Geupel (1993). Potential nest predators sighted during field work included several snakes (e.g., *Philodryas patagoniensis*), birds (*Cariama cristata*, *Circus cinereus*), and mammals (*Dasypus novemcinctus, D. hybridus, Conepatus chinga*). Field assistants were trained in nest searching techniques and on how to minimize nest disturbance during marking and monitoring activities. In addition to nests located during the systematic searches on the designated plots, several nests of target species were found incidentally while conducting other research activities. Whenever possible these nests were also monitored and were included in the analyses to increase sample sizes.

Data Analysis

G-tests were used to examine across-habitat patterns in numbers of nests of different species as well as proportions of nests within several fate categories. These analyses were conducted in SPSS ver. 15 (SPSS 2006).

Recent advances in analytical techniques and accompanying software allow sound nest-survival estimates to be computed (White and Burnham 1999, Dinsmore et al. 2002, Shaffer 2004). Program MARK (White and Burnham 1999, hereafter MARK) was used to model daily nest survival (DNS) as a function of several variables of interest. These analyses were restricted to species represented by five or more nests of known fate. DNS is defined as “the probability that a nest will survive a single day”, and nest survival as “the probability that a nest will be successful”, that is, will produce at least one young (Dinsmore et al. 2002). On the basis of encounter histories of individual nests, MARK uses likelihood-based procedures to estimate regression coefficients for those explanatory variables included in the analysis (Shaffer 2004). The nest survival model in MARK provides several advantages over classical approaches to true nest survival estimation (e.g., Mayfield 1961, 1975, Johnson 1979, Bart and Robson 1982). Some of the most important features include the ability to accommodate non-constant daily survival rates (i.e., nest survival can be modeled as a function of time-specific variables) and the consideration of multiple variables simultaneously (which can be either categorical or continuous), without the need to divide the data into discrete groups for testing

(Dinsmore et al. 2002, Jehle et al. 2004). The latter is especially useful when small sample sizes are involved. Thus, the program is particularly well suited for the consideration of specific biologically meaningful questions (Dinsmore et al. 2002, Shaffer 2004). Here, MARK was used with two objectives in mind: a) to identify factors driving nest survival patterns of grassland birds and, b) to estimate nest survival rates of grassland species, including closely-related pairs of common and threatened taxa.

A total of 83 models were considered for different subsets of the data. The complete dataset included 259 known-fate nests which were monitored for a total of 1977 exposure days across 76- (2004) and 78-day (2005) periods during the two-year study. A hierarchical approach based on a step-down procedure (Lebreton et al. 1992) was used. First, the fully parameterized model, one that included all variables of interest was run. Second, different variables were systematically excluded through a series of subsequent analyses. Considering the information available for each nest and based on results from previous research on nest survival of grassland birds, *a priori* models included linear and quadratic effects of date (i.e., seasonal effects) and year (2004, 2005), habitat type (Pasture, Sheep, Deer), and vegetation structure effects (mean vegetation height and vegetation density in the 0-25 cm height interval; Chapter 2). The latter referred to fields in which the nests were placed. Each model set also included a null model in which DNS was constrained to be constant across all nests and all days in the sample, and global models which included all the variables under consideration. These were incorporated as covariates with the use of a logit link function which constrains estimates between 0 and 1. Analyses of the complete dataset were used to test for general effects on the grassland bird community. Apart from the factors mentioned above, the general analyses also included the effect of species. Afterwards, specific nest survival patterns of species with relatively large sample sizes (i.e., ≥ 20 nests) were examined.

Model selection was based on Akaike's information criterion corrected for small sample sizes (AIC_c, Anderson and Burnham 2002); in each analysis sample size reflected the total number of days all nests in the sample were monitored (Dinsmore et al. 2002, Shaffer 2004). Apart from AIC_c values, MARK computes several other metrics: ΔAIC_c is the difference in AIC_c between a given model and the model with the lowest AIC_c; normalized Akaike weights (*w*) provide a measure of relative likelihood of each model given the candidate set of models and the data (Blums et al. 2005); deviance values represent a measure of discrepancy between observed and fitted values (Shaffer 2004). Models with $\Delta AIC_c \leq 2$ were considered to have substantial support while those with $\Delta AIC_c \geq 4$ were thought to have little support (following Burnham and Anderson 2001 and Anderson and Burnham 2002).

Through consideration of these metrics the ultimate objective was to select the most parsimonious model, defined as the one which is consistent with the data while using the fewest number of parameters (Cooch and White 2008). To obtain nest survival estimates of species over the entire nest period, DSR was raised to the power equivalent to the average number of days of the species' nesting cycle (Cooch and White 2008). On the basis of information available in the literature (Saunders 1932, Cabot 1992, Lanyon 1995, Davis 2003, Cozzani et al. 2004, Tyler 2004) and on that obtained during this study, nesting cycle lengths of 16 days (*Nothura maculosa*), 26 days (*Anthus* spp.), and 24 days (*Sturnella* spp.) were used to determine nest survival estimates. Estimates are reported as means ± SE or 95% upper and lower confidence intervals (95% CI) unless otherwise stated.

RESULTS

General nesting patterns

A total of 315 nests from 12 grassland species were found during the study (Table 1). Numbers of nests found in 2005 (224) more than doubled those found in 2004 (91), reflecting differences in searching effort. The greatest number of nests was found in Sheep, followed by Pasture and Deer (Table 1). The largest number of breeding species was recorded in Deer (11), followed by Sheep (10) and Pasture (8). All birds nested in two or more habitat types except for *Sturnella defilippi*, which bred only Sheep; the mean number of habitats used per species was 2.4 ± 0.2. There were differences among species in terms of habitat use, as indicated by the number of nests found in each habitat. Of those species with relatively large samples sizes (i.e, $\geq$ 20 nests), three (*Nothura maculosa*, *Anthus furcatus*, *Sicalis luteola*) nested in all three habitats, and two (*Anthus nattereri* and *Sturnella superciliaris*) nested in both Pasture and Deer. Proportions of nests in each habitat type were significantly different for both the first ($G = 84.1$, df = 4, $P < 0.001$) and second group of species ($G = 50.7$, df = 1, $P < 0.001$).

Among nests of known fate ($n = 283$), 26% were successful, whereas predation, abandonment, and flooding accounted for 53%, 11%, and 4% of nest fates, respectively; 6% of all unsuccessful nests could not be attributed to a specific category. Fate proportions were significantly different among species ($G = 59.8$, df = 33, $0.005 > P > 0.001$, Figure 1). Considering nests of known fate and species represented by 10 or more nests, the proportion of successful nests ranged from 14% for *Sicalis luteola* to 40% for

Vanellus chilensis (Figure 1). The incidence of brood parasitism was minimal; only two out of 170 passerine nests of known fate were affected. Single eggs of *Molothrus bonariensis* were found in one nest of *Anthus furcatus* and in one nest of *Sturnella superciliaris* in Sheep and Deer, respectively.

Within the timeframe in which nest searching and monitoring was conducted (mid September to early December), the overall peak of the nest activity occurred from mid October to late November (Figure 2). Nesting activity patterns, however, varied among species, with some concentrated during the first (*Vanellus chilensis*), mid (*Sturnella defilippi*), or second half (*Sicalis luteola* and *Sturnella superciliaris*) periods. The nesting activity of two common species, *Nothura maculosa* and *Anthus furcatus* extended throughout the whole period, with peaks in October and early November (Figure 3).

Nest survival patterns

In the analyses of nest survival (all species combined), the best models included a quadratic seasonal trend (Tables 2 and 3) which indicated that nest survival increased during the first part of the nesting season and then decreased toward the late season; nest survival rates were highest during the midseason and lowest during the late season. In the first of these analyses, in which vegetation structure variables were not considered, the best model also included habitat and year effects. The weight of support for the latter was high (67%) in comparison to other models, all of which had ΔAIC_c values > 2 and $w \leq 0.22$ (Table 2). The second analysis was restricted to 199 nests for which information on vegetation structure data were available. In this case, there were five equally-supported models (i.e., ΔAIC_c values < 2), all of which included habitat type effects apart from the quadratic trend for calendar day. In addition, effects of year, vegetation height and density also were incorporated in some of the models. The summed weight of support for these five best-fitting models was 68%; none of the other models considered had more than 9% support (Table 3). Also, in the two analyses, neither the global nor the null models had much support (ΔAIC_c values > 9, $w \leq 0.01$; Tables 2 and 3).

Analyses that focused on *Nothura maculosa* revealed similar patterns. Habitat type was incorporated in all best-fitting models together with seasonal trends (included either as a linear or quadratic effects) in most cases; year and vegetation structure effects were also included in some of the best supported models. For the analysis that included all nests (n = 78), the five best models had a summed weight of support of 89% (Table 4), whereas in the analysis of nests for which additional vegetation structure data were available (n = 60), the top four models comprised 60% of the support in the data (Table 5). Considering both analyses, habitat type was the only variable among those investigated for which direct effects were supported (Tables 4 and 5). In general, patterns of model support were similar in both analyses. The exceptions were the models that included habitat and year effects and habitat effects alone, which were among the best fitting models only in the analysis corresponding to the complete nest data set. Conversely, when considering nests with vegetation structure data, these models were weakly supported (ΔAIC_c values > 3, w $\leq$ 0.04). This suggests that there was an additional effect of vegetation structure variables on DNS irrespective of habitat type. The best supported model in the analysis without vegetation structure variables (habitat type + year effects) yielded higher nest success estimates for 2004 (0.26 [0.07-0.53, 95% CI] to 0.61 [0.38-0.82]) than for 2005 (0.07 [0.01-0.22] to 0.44 [0.23-0.59]). Estimates were higher for Pasture (0.44 [0.23-0.59] to 0.61[0.38-0.82]), than for Sheep (0.11 [0.03-

0.27] to 0.31 [0.08-0.62]) or Deer (0.07 [0.01-0.22] to 0.26 [0.07-0.53]). Nest success estimates from the best supported model in the analysis that included vegetation structure data (quadratic trend in calendar day + habitat effects) were congruent with the latter results. The estimated values for the middle of the nesting season (when nest success was hypothesized to be at its highest) were: 0.58 (0.36-0.75, 95% CI), 0.27 (0.06-0.55) and 0.14 (0.02-0.38) for Pasture, Sheep, and Deer, respectively.

Two additional analyses focused on the pairs of closely-related birds with differing conservation statuses. In the case of *Anthus* species (*A. furcatus* is common whereas *A. nattereri* is threatened), all of the models considered had approximately equal weight in the data (ΔAIC_c values < 2), including the one that assumed constant DNS. In terms of Akaike weights, the model that considered differences in DNS among species was the only one to have more support than the null model (30% vs. 21%, Table 6). On the basis of the model considering species differences, the nest survival estimates were of 0.11 and 0.03 for *Anthus furcatus* and *Anthus nattereri*, respectively.

The analysis of nest data from *Sturnella* species revealed little support for the existence of time effects or difference between species in DNS. The model that included species as a sole factor received considerably less support than the others. Models that combined effects of species and time had approximately equal weight in the data (Table 7). The model with the highest Akaike weight (0.39, linear trend of calendar date + species effects) provided early-season nest success estimates (which decreased linearly during the nesting season as a consequence of the hypothesized calendar date effects) of 0.25 (0.07-0.50, 95% CI) and 0.51 (0.12-0.81) for *Sturnella defilippi* and *S. superciliaris*, respectively. It is worth noting, however, that on the basis of differences in AIC_c, the latter model had approximately the same weight in the data (ΔAIC_c values < 2) as did the null model (constant nest success).

DISCUSSION

General nesting patterns

Most grassland birds in the study area nested in more than one habitat type, but numbers of nests varied significantly across habitats. For a given species, the greatest number of nests was found in the habitat in which the species attained its highest density (Chapter 1). *Nothura maculosa* was the only relatively common breeder (i.e., > 20 nests on each habitat type) in all three habitats. Nest success was greater in Pasture, where population density was greatest as well (Chapter 1). Thus, for this species, population density might be indicative of nesting habitat quality.

Sturnella defilippi was the only species that bred in only one habitat (Sheep). The species' absence from Pasture is in agreement with its strong association with natural grasslands (Fernández et al. 2003, Chapter 2). In terms of vegetation structure, however, Deer more closely resembled the characteristics of breeding sites in southern Buenos Aires province (Fernández et al. 2003, R. Sánchez pers. comm.), where vegetation height seems to be one important element driving *Sturnella defilippi*'s selection of breeding habitat (Fernández et al. 2003; Cozzani et al. 2004). In the Northern Campos, the presence of this species in areas with relatively short vegetation (Sheep) suggests that other factors, such as breeding-site fidelity, also influence breeding habitat use patterns. In Argentina, nesting areas tend to be reoccupied except when land use changes occur; some reproductive groups even reoccupied sites after they had been transformed from natural grassland to agricultural lands (Fernández et al. 2003). In the Northern Campos, *Sturnella defilippi* occupied the same nesting areas for at least three consecutive breeding seasons. Site-fidelity, however, can not fully account for the lack of breeding activity in Deer.

Predation accounted for most nest losses. The overall predation rate estimated in this study (53%) is similar to that reported for North American grassland birds (48.8% ± 2.7; reviewed by Martin 1993b). Comparisons restricted to obligate grassland passerine species (*sensu* Vickery et al. 1999), however, showed higher predation rates in the Northern Campos sites (63.2-77.3%) than in North America (22.3-64.4%), whereas abandonment rates were similar in these two regions (Martin 1993b, Martin 1995, Best et al. 1997, Davis 2003, Winter et al. 2004). Given the disproportionate impact of nest predation on avian nest fate (Ricklefs 1969, Martin 1993a), rates of successful nests were, accordingly, higher in North America (25.8-62.8% vs. 11.5-22.2% in this study). Unfortunately, additional data for temperate South American grassland species are limited. For one well-studied species, *Pseudoleistes virescens*, predation and desertion rates were 61.2% and 15.8% (Mermoz and Reboreda 1998). Although these figures are similar to the ones reported here, this should be viewed with caution since *P. virescens* is an above-ground nester (Mermoz and Reboreda 1998). For one ground-nesting species, *Sturnella defilippi*, a study of a small sample of nests revealed a predation rate of 46.7% (Cozzani et al. 2004).

Contrary to expectations, rate of brood parasitism was not higher in cultivated grasslands and, in fact, instances of parasitism were particularly infrequent overall. All of the studied species are known or suspected to be hosts of *Molothrus bonariensis* (Friedmann et al. 1977, Fraga 2002). Although the incidence of brood parasitism tends to be lower in grasslands than in shrublands or forested habitats, the low proportions of parasitized nests in the Northern Campos contrast with those reported for North American grassland regions (from 10% to more than 20%; Peer et al. 2000 and references therein). Relatively lower brood parasitism rates may reflect either the effects of high levels of egg rejection behavior or low cowbird densities (Peer et al. 2000, Herkert et al. 2003). In the Northern Campos, the latter seems a more plausible explanation given the fact that *Molothrus bonariensis* was recorded in small numbers in all three habitat types (Chapter 1), and that egg rejection was not observed in the few parasitized nests found. Another explanation for the low incidence of brood parasitism in the study sites could be the general lack of elevated perches and wooded edges, two factors that are thought to facilitate cowbird activity (Johnson and Temple 1990).

Nest survival patterns

Overall, quadratic temporal trends and habitat type effects were the two most frequent variables included in best-supported models of nest survival. These effects were particularly evident in the general analyses that included nests of all species and in those restricted to *Nothura maculosa*. Seasonal effects on nest survival have been identified in other studies of grassland birds (e.g., Dinsmore et al. 2002, Davis 2005, Wilson et al. 2007). A higher nest survival during midseason, such as the one reported here, was also found for *Pseudoleistes virescens*, a tallgrass nesting species. The pattern may have been related to higher nest defense levels due to the presence of more nesting conspecifics during the midseason (Mermoz and Reboreda 1998). This factor cannot, however, apply to *Nothura maculosa* because, unlike *Pseudoleistes*, it does not nest colonially or provide active nest defense. An alternative explanation is that nest survival could be highest during the peak of the breeding season because of the satiated predator effect (Ims 1990), but this is not supported by available evidence. *Nothura maculosa* does not display reproductive synchrony (despite a peak of activity in October and November its breeding extends through several months; De la Peña 2007, pers. obs.), and species that commonly depredate avian nests are incidental, not specialized predators (Vickery et al. 1992b, Herkert et al. 2003, Renfrew and Ribic 2003). In addition, other studies of open habitat birds suggest that predators may prey on nests when the latter are most abundant (Wilson et al. 2007). A higher nest survival during midseason may also be explained by a change in the abundance of preferred prey for nest predators, which may switch to nests when preferred prey becomes scarce or unavailable.

Both in the case of the general analyses that included nest data sets of all species, and those that focused on *Nothura maculosa*, habitat effects revealed higher nest survival rates in Pasture, followed by Sheep and Deer. One factor responsible for this result could be among-habitat differences in conditions affecting nest concealment. Vegetation structure differed among habitats (Chapter 2) and some studies have shown that vegetation height and density, in particular, can influence nest survival of grassland birds, with species tending to place nests in taller vegetation than that randomly available on nesting grounds (Davis 2005). Nest survival, however, was higher in Sheep than in Deer, despite vegetation being shorter and sparser in the latter (Chapter 2). However, vegetation structure data available for the study sites refer to nesting fields, not nesting sites (i.e., specific sites where nests were placed). Grassland birds that nest in areas with short and sparse vegetation can still select nest sites with taller and denser vegetation (Davis 2005). It has also been suggested that there is a trade-off between nest concealment and predation detection efficiency (Gotmark et al. 1995). Whereas taller and denser vegetation may provide more concealment, these conditions also limit predator detection capabilities of nesting birds. The latter may drive birds to nest in short and sparse vegetation (Gotmark et al. 1995). In any case, vegetation structure through its effect on nest concealment cannot explain all observed nest survival patterns; Pasture and Deer were similar in terms of vegetation structure characteristics (Chapter 2), but nest survival was highest in the former and lowest in the latter. In addition, vegetation variables were contained in few of the best-supported models in this study and, in fact, few studies have found strong effects of vegetation on nest success of grassland passerines (Winter et al. 2005). Differences in predator communities among habitats may provide additional insight. Pasture habitat was imbedded in a more altered landscape than that of Sheep and Deer (see Chapter 1); if predator communities in the former are depauperate they may exert lower nest predation pressure on grassland birds. Another subject that merits further investigation relates to recent evidence that livestock and cervids can act as grassland nest predators (Pietz and Granfors 2000a, Renfrew and Ribic 2003, Nack and Ribic 2005, Walsberg 2005), and whether this may be related to relatively lower nest survival of grassland birds in Deer habitat.

Although nest survival estimates for threatened species were lower than those of congenerics, models failed to identify any strong “species” effects. Models that tested for differences between species had levels of support similar to that of null models (i.e., ΔAIC_c values < 2). Thus, with respect to nest survival, common taxa seem to have no advantage over their globally threatened counterparts. These results suggest that nest survival may not be the main factor behind declines of grassland bird populations in the

Northern Campos. A lack of association between reproductive success and population decline has been reported for other ground-nesting birds in North America (Aldridge and Bridham 2001).

In general, nest survival estimates were low but within the range of those reported for other North American and South American grassland species (Mermoz and Reboreda 1998, Jehle et al. 2004, Shriver et al. 2007). *Anthus nattereri* had a particularly low nest survival (0.03), despite a relatively high population density in Deer (Chapter 1). It is important to note that nest success metrics do not necessarily equate to annual reproductive output (Thompson et al. 2001). Re-nesting and multiple brooding attempts can have substantial influence on productivity and, in the case of ground nesters, may counteract the effects of heavy predation pressure (Beitiema and Müskens 1987, Winter 1999). Little information on this topic is available for South American grassland birds, but replacement clutches and re-nesting are known or suspected in at least some species (e.g., *Ammodramus humeralis*, *Sturnella defilippi*; Di Giacomo 2005, pers. obs.). Also, high nest predation tends to be associated with production of more broods (Martin 1995).

Here, the breeding biology of grassland birds in the Northern Campos was characterized for the first time. Apart from new natural history data, patterns of nest survival were documented and the factors responsible for these patterns were tested using modern inferential procedures. Additional work is much needed and results from this study should provide a useful baseline for future research efforts. First, there is a need for more natural history information. Basic data such as nesting cycle lengths and incidence of multiple nesting are poorly documented among many Pampas grassland birds. This type of information is crucial for rigorous assessments of nest survival and annual productivity (e.g., Thompson et al. 2001). Given the pervasive effects of predation on nest survival, the general characterization of the predator community and precise identification of predator species may also provide valuable information, especially for management activities (Ammon and Stacey 1997, Pietz and Granfors 2000b, Renfrew and Ribic 2003). These efforts may be especially useful in combination with experimental manipulations of grazing regimes given the potential direct and indirect influences of native and domestic grazers on the breeding activity of populations of grassland birds (i.e., predation, vegetation modification). In this context, the inclusion of livestock-free sites could provide new insight. Finally, the highly variable nature of grassland ecosystems calls for more studies at large spatial and temporal scales (Winter et al. 2005) which could provide broad application of results within the threatened Pampas region.

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Table 1. Number of nests found for each of 12 grassland bird species during 2004 and 2005 in three habitat types in the Northern Campos of Uruguay. The last column specifies the number of nests used for nest survival analyses (NSA).

Species	**Habitat Type**				
	Pasture	**Sheep**	**Deer**	**Total**	**NSA**
Rhea americana	1	4	3	**8**	
Nothura maculosa	36	21	26	**83**	**78**
Vanellus chilensis	5	3	2	**10**	**6**
Gallinago paraguaiae	0	2	4	**6**	**5**
Podager nacunda	0	5	1	**6**	
Anthus furcatus	1	44	8	**53**	**42**
Anthus hellmayri	0	4	2	**6**	**6**
Anthus nattereri	4	0	19	**23**	**21**
Ammodramus humeralis	4	1	1	**6**	
Sicalis luteola	3	2	21	**26**	**20**
Sturnella defilippi	0	36	0	**36**	**33**
Sturnella superciliaris	50	0	2	**52**	**48**
Total	**104**	**122**	**89**	**315**	**259**

Table 2. Comparison of the models used to assess the combined effects of season (modeled as linear [SS] and quadratic [SS^2] time trends in the most parameterized models), year (YR), habitat (HAB), and species (SPE) on daily survival rates (DNS) of nests ($n = 259$) in the Northern Campos of Uruguay. A "+" indicates an additive effect of variables. Models are ranked by the difference in Akaike's information criterion corrected for small sample size (AIC_c); *w* reflects the relative support for the model in question given the model set and the data; *K* is the number of parameters estimated by the model; deviance is a measure of model fit. Treatments within factors are: 2004 and 2005 for YR; Pasture, Sheep, and Deer for HAB; and *Nothura maculosa*, *Vanellus chilensis*, *Gallinago paraguaiae*, *Anthus furcatus*, *A. hellmayri*, *A. nattereri*, *Sicalis luteola*, *Sturnella defilippi*, and *S. superciliaris* for SPE. The original set included 12 models of which the top-10 (which include the global models indicated with a "*") and a null models (constant DNS) are shown. Effective sample size = 1977.

Model	**ΔAIC_c**	***w***	***K***	**Deviance**
SS^2 + HAB + YR	0.00	0.67	6	898.36
SS^2 + HAB	2.19	0.22	5	902.56
SS^2 + YR	4.20	0.08	4	906.58
SS^2	7.51	0.02	3	911.90
SS^2 + HAB + Year + SPE *	9.21	0.01	14	891.40
SS^2 + YR + SPE	11.37	<0.00	12	897.61
SS + HAB + YR + SPE *	11.88	<0.00	13	896.10
SS^2 + HAB + SPE	13.27	<0.00	13	897.49
HAB + YR	13.84	<0.00	4	916.22
HAB	14.59	<0.00	3	918.98
Constant DNS	15.40	<0.00	1	923.80

Table 3. Model set used to assess the combined effects of season (modeled as linear [SS] and quadratic [SS^2] time trends in the most parameterized models), year (YR), habitat (HAB), species (SPE), vegetation density (C25), and vegetation height (VH) on daily survival rates (DNS) of nests (*n* = 194) in the Northern Campos of Uruguay. Models included additive effects of variables of interest. Models are ranked by the difference in Akaike's information criterion corrected for small sample size (AIC_c); *w* reflects the relative support for the model in question given the model set and the data; *K* is the number of parameters estimated by the model; deviance is a measure of model fit. For treatments within factors see legend in Table 1. The original set included 26 models of which the top-10, two global (indicated with a "*") and null models (constant DNS) are shown. Effective sample size = 1541.

Model	**ΔAIC_c**	***w***	***K***	**Deviance**
SS^2 + HAB	0.00	0.23	5	680.11
SS^2 + HAB + YR	0.54	0.17	6	678.64
SS^2 + HAB + YR + VH	1.71	0.10	7	677.76
SS^2 + HAB + VH	1.76	0.09	6	679.86
SS^2 + HAB + C25	1.79	0.09	6	679.89
SS^2 + HAB + YR + C25	2.02	0.08	7	678.10
SS^2 + HAB + VH + C25	2.08	0.08	7	678.16
SS^2 + HAB + YR + VH + C25	3.71	0.04	8	677.77
SS + HAB	3.99	0.03	4	686.12
SS^2 + C25 + VH	4.82	0.02	5	684.93
Constant DNS	12.27	<0.00	1	700.42
SS^2 + HAB + YR + SPE + VH + C25 *	15.20	<0.00	16	673.00
SS + HAB + YR + SPE + VH + C25 *	16.78	<0.00	15	676.62

Table 4. Model set used to assess the combined effects of season (modeled as linear [SS] and quadratic [SS^2] time trends in the most parameterized models), year (YR), and habitat (HAB), on daily survival rates (DNS) of *Nothura maculosa* nests (*n* = 78) in the Northern Campos of Uruguay. Variables are modeled as additive effects and models are ranked by the difference in Akaike's information criterion corrected for small sample size (AIC_c); *w* reflects the relative support for the model in question given the model set and the data; *K* is the number of parameters estimated by the model; deviance is a measure of model fit. Treatments within factors are specified in Table 1.The model set included two global models (*) and a null model (constant DNS). Effective sample size = 575.

Model	**ΔAIC_c**	***w***	***K***	**Deviance**
HAB + YR	0.00	0.27	4	227.66
SS + HAB + YR *	0.34	0.23	5	225.96
SS^2 + HAB + YR *	1.30	0.14	6	224.88
SS + HAB	1.52	0.13	4	229.18
HAB	1.69	0.12	3	231.37
SS + YR	3.49	0.05	3	233.17
SS	3.60	0.05	2	235.30
YR	7.27	0.01	2	238.98
Constant DNS	8.78	<0.00	1	242.50

Table 5. Comparison of the models used to assess the combined effects of season (modeled as linear [SS] and quadratic [SS^2] time trends in the most parameterized models), year (YR), and habitat (HAB), vegetation density (C25), and vegetation height (VH) on daily survival rates (DNS) of *Nothura maculosa* nests (*n* = 60) in the Northern Campos of Uruguay. Variables are modeled as additive effects and models are ranked by the difference in Akaike's information criterion corrected for small sample size (AIC_c); *w* reflects the relative support for the model in question given the model set and the data; *K* is the number of parameters estimated by the model; deviance is a measure of model fit. Treatments within factors are specified in Table 1. The original set included 26 models of which the top-10, and the global (indicated with a "*") and null models (constant DNS) are shown. Effective sample size = 428.

Model	**ΔAIC_c**	***w***	***K***	**Deviance**
SS^2 + HAB	0.00	0.24	5	166.00
SS^2 + HAB + YR	1.08	0.14	6	165.02
SS^2 + HAB + C25	1.28	0.12	6	165.22
SS^2 + HAB + VH	1.81	0.10	6	165.75
SS^2 + HAB + YR + VH	3.00	0.05	7	164.88
SS^2 + HAB + YR + C25	3.05	0.05	7	164.93
SS^2 + HAB + VH + C25	3.24	0.05	7	165.11
Year + HAB	3.70	0.04	4	171.75
HAB	4.24	0.03	3	174.33
HAB + C25	4.47	0.03	4	172.52
SS^2 + HAB + YR + VH + C25 *	5.05	0.019	8	164.85
SS + HAB + YR + VH + C25 *	5.88	0.012	7	167.76
Constant DNS	9.73	<0.00	1.	183.87

Table 6. Model set used to assess the combined effects of season (modeled as linear [SS] and quadratic [SS^2] time trends), year (YR), and habitat (HAB), on daily survival rates (DNS) of *Anthus furcatus* and *A. nattereri* nests (*n* = 41 and n = 21, respectively) in the Northern Campos of Uruguay. Variables are modeled as additive effects and models are ranked by the difference in Akaike's information criterion corrected for small sample size (AIC_c); *w* reflects the relative support for the model in question given the model set and the data; *K* is the number of parameters estimated by the model; deviance is a measure of model fit. Treatments within factors are specified in Table 1.The model set included a null model (constant DNS). Effective sample size = 514.

Model	**ΔAIC_c**	***w***	***K***	**Deviance**
SPE	0.00	0.30	2	241.06
Constant DNS	0.68	0.21	1	243.76
SS^2	0.72	0.21	3	239.76
SS^2 + SPE *	1.09	0.17	4	239.10
SS + SPE *	1.99	0.11	3	241.03

Table 7. Model set used to assess the combined effects of season (modeled as linear [SS] and quadratic [SS^2] time trends), year (YR), and habitat (HAB), on daily survival rates (DNS) of *Sturnella defilippi* and *S. superciliaris* nests (*n* = 33 and n = 47, respectively) in the Northern Campos of Uruguay. Variables are modeled as additive effects and models are ranked by the difference in Akaike's information criterion corrected for small sample size (AIC_c); *w* reflects the relative support for the model in question given the model set and the data; *K* is the number of parameters estimated by the model; deviance is a measure of model fit. Treatments within factors are specified in Table 1. The model set included a null model (constant DNS). Effective sample size = 622.

Model	**ΔAIC_c**	***w***	***K***	**Deviance**
SS + SPE *	0.00	0.39	3	294.16
SS	1.41	0.19	2	297.59
SS^2 + SPE *	1.49	0.18	4	293.62
Constant DNS	1.63	0.17	1	299.82
SPE	3.55	0.06	2	299.73

Figure 1. Fates of nests from 12 grassland birds breeding in the Northern Campos of Uruguay in 2004 and 2005. Species: *Rhea americana* (RAM), *Nothura maculosa* (NMA), *Vanellus chilensis* (VCH), *Gallinago paraguaiae* (GPA), *Podager nacunda* (PNA), *Anthus furcatus* (AFU), *Anthus hellmayri* (AHE), *Anthus nattereri* (ANA), *Ammodramus humeralis* (AHU), *Sicalis luteola* (SLU), *Sturnella defilippi* (SDE), *Sturnella superciliaris* (SSU). Numbers on top of each column refer to samples sizes.

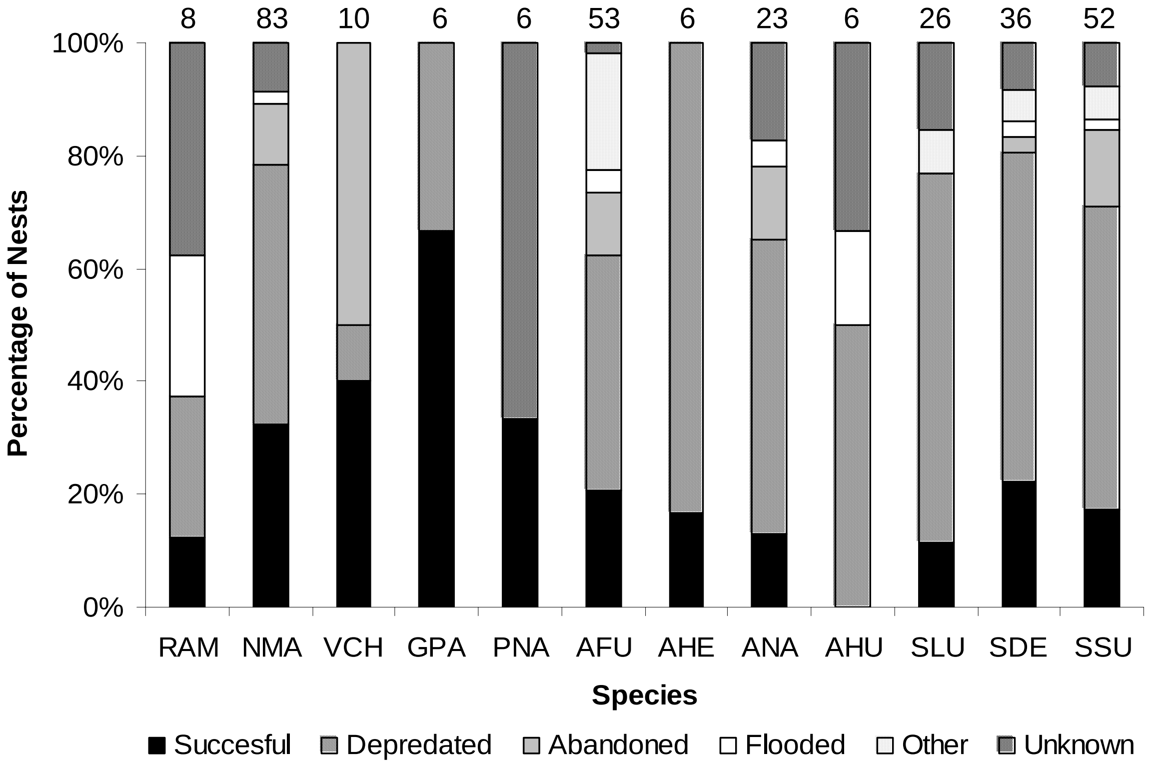

Figure 2. Overall nesting activity of 12 grassland birds in three habitat types in the Northern Campos of Uruguay in 2004 and 2005.

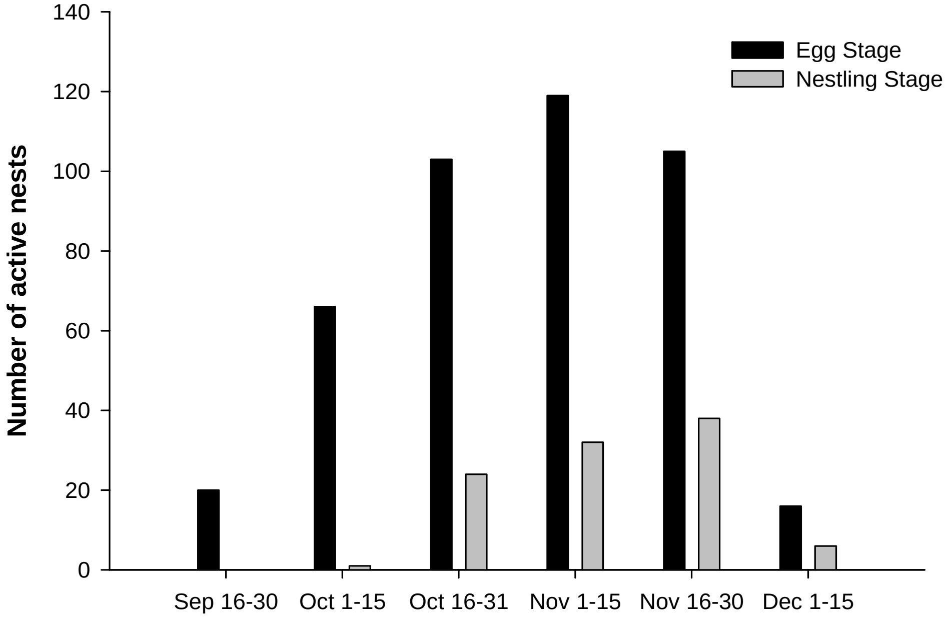

Figure 3. Number of active nests discriminated by egg (black columns) and nestling (gray columns) stages of eight grassland birds in the Northern Campos of Uruguay (*Rhea americana*, *Nothura maculosa* and *Vanellus chilensis* are precocial species).