AVIAN CONSERVATION
& ECOLOGY

VOLUME 14, ISSUE 2, ARTICLE 18

Alfaro, M., L. Liguori, B. K. Sandercock, M. Berazategui, and M. Arim. 2019. Habitat selection and space use of Upland Sandpipers at nonbreeding grounds. *Avian Conservation and Ecology* 14(2):18. https://doi.org/10.5751/ACE-01461-140218

Research Paper

Habitat selection and space use of Upland Sandpipers at nonbreeding grounds

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ABSTRACT. Habitat requirements of migratory birds can be dynamic during the annual cycle, and understanding habitat use during the nonbreeding season is important for conservation planning. In grassland birds, habitat selection is often determined by features of vegetative structure that are associated with predation risk, food resources, or thermal environments. And, these habitats are affected by anthropogenic influences such as agriculture conversion and production of livestock. In our four-year field study, we examined the space use and habitat selection of Upland Sandpipers (*Bartramia longicauda*) during the nonbreeding season in an area of private grasslands managed for livestock production within the Northern Campos ecoregion of Uruguay. We radio-tracked sandpipers during the nonbreeding season to test the hypothesis that space use, habitat selection, and flock size were determined by vegetative structure in managed grasslands with different grazing and agricultural management regimes. We captured and tagged 62 sandpipers during the nonbreeding season in the austral summer, and recorded a total of 506 locations for our sample of radio-marked birds. Foraging Upland Sandpipers primarily selected two types of native grasslands associated with shallow, rocky soils. The vegetation configuration of disturbed pastures were open landscapes that were good for detection of arthropod prey but offered little cover for avoidance of predators. Sandpipers were usually found in small groups of 2–20 birds, and the largest flocks of 40–50 birds were found in pastures with relatively short grass cover (20 to 40% tall grass cover). Low to moderate stocking densities of domestic livestock created variation in vegetation height and cover in large areas and allowed for coexistence of grassland birds with different habitat requirements. Upland Sandpipers preferred disturbed areas, which may not support the needs of other species of grasslands birds. Our results emphasize the need for habitat heterogeneity and disturbance forces such as grazing in grassland systems. Our research contributes new information on the ecology of migratory grassland birds and provides insights for biodiversity conservation on private lands used for livestock production.

Sélection de l'habitat et utilisation de l'espace par les maubèches des champs sur les lieux d'hivernage

RÉSUMÉ. Les besoins des oiseaux migrateurs en termes d'habitat peuvent évoluer en cours d'année. Il est donc important de comprendre l'utilisation de l'habitat pendant la saison d'hivernage pour élaborer des programmes de conservation. Chez les oiseaux des prairies, la sélection de l'habitat est souvent déterminée par des caractéristiques de la structure végétale en termes de risques de prédation, de ressources alimentaires ou d'environnement thermique. Or, ces habitats sont affectés par certaines influences anthropiques telles que la conversion agricole et l'élevage de bétail. Au cours de notre étude de quatre ans sur le terrain, nous avons examiné l'utilisation de l'espace et la sélection de l'habitat par les maubèches des champs (*Bartramia longicauda*) au cours de la saison d'hivernage, dans une zone de prairies privées consacrées à l'élevage dans l'écorégion des Campos du nord, en Uruguay. Nous avons suivi des maubèches baguées au cours de la saison d'hivernage afin de tester l'hypothèse selon laquelle l'utilisation de l'espace, la sélection de l'habitat et la taille des volées étaient déterminées par la structure végétale dans les régions de prairies cultivées où coexistaient différents systèmes de gestion de l'élevage et de l'agriculture. Nous avons capturé et bagué 62 maubèches au cours de la saison d'hivernage pendant l'été austral et enregistré en tout 506 emplacements de nos oiseaux radiomarqués. Les maubèches des champs fourragères sélectionnaient principalement deux types de prairies natives associées à des sols rocheux et peu profonds. La configuration de la végétation de pâturages piétinés se composait de paysages ouverts, propices à la détection des arthropodes. En revanche, ces zones offraient un abri limité contre les prédateurs. Les maubèches se rassemblaient généralement par petits groupes de 2 à 20 individus, tandis que les volées plus nombreuses de 40 à 50 oiseaux choisissaient des pâturages où la couverture herbeuse était relativement courte (hautes herbes représentant 20 à 40 % de leur taille). Les densités faibles à modérées des troupeaux de bétail engendraient une végétation de hauteur variable offrant différents degrés de protection dans des zones étendues et permettaient la coexistence d'oiseaux des prairies présentant des besoins différents en termes d'habitat. Les maubèches des champs préféraient les espaces piétinés, lesquels peuvent ne pas suffire aux besoins d'autres espèces d'oiseaux des prairies. Nos résultats soulignent la nécessité d'habitats hétérogènes et de différents niveaux de perturbation, par exemple de l'aménagement de zones de pâturage dans des prairies. Notre recherche a apporté de nouvelles informations sur l'écologie des oiseaux des prairies migrateurs et fournit des données sur la conservation de la biodiversité sur les terres privées consacrées à l'élevage.

Key Words: *group size; habitat selection; land management; migratory bird; vegetation height*

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INTRODUCTION

Key ecological factors that determine the distribution and abundance of migratory birds include habitat resources such as food availability, vegetative structure, soil quality, and climatic conditions, as well as trophic interactions such as predation risk and competition (Rosenzweig 1981, Masse et al. 2014, Leclerc et al. 2016). Animals use environments with varying degrees of heterogeneity at a range of spatial scales, from the geographic range of a species to the level of an individual's home range (Aebischer et al. 1993, Mysterud and Ims 1998, Jedlikowski et al. 2016). Consequently, a complete understanding of habitat use should consider the evaluation of patterns and processes at multiple ecological and spatial scales (Johnson 1980, Mysterud and Ims 1998, Ribic et al. 2009). Moreover, human activities related to land use, such as livestock grazing, agricultural production and forestry, and urbanization, have produced large changes in many features of landscape structure (Brennan and Kuvlesky 2005, Baldi and Paruelo 2008, Isacch and Cardoni 2011, Azpiroz et al. 2012, Fedy et al. 2018). Land-use and land-cover change likely impact migratory species that use features of the landscape to orient and find specific sites during migration and at breeding and nonbreeding grounds (Huston 1998, Lindström 2007).

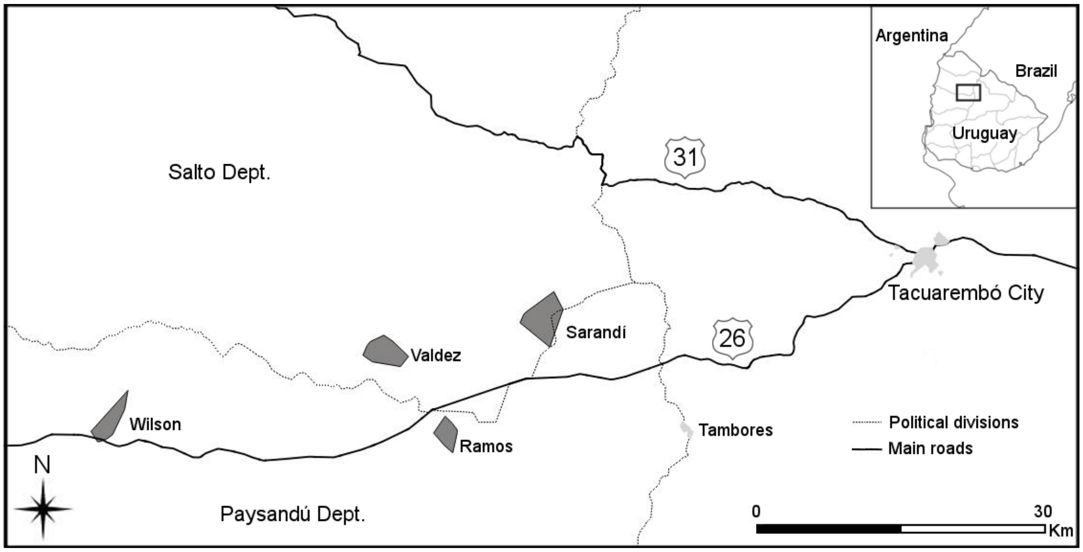
Migratory birds use a variety of geographic areas during their annual cycle, selecting stopover sites and stationary areas for foraging or reproduction, depending on local food resources and environmental conditions that meet an individual's energetic demands (Huston 1998, Lindström 2007). During patch selection, birds engage in flocking and other social behaviors that balance the benefits of access to food resources while minimizing the potential cost of predation risk (MacArthur and Pianka 1966, Myers 1980, Lima and Dill 1990, Lima and Bednekoff 1999). The spatial distribution and abundance of individuals within a site may vary spatially and temporally, and depends on seasonal changes in the structure and composition of suitable habitats (Pomeroy 2006, Leyrer et al. 2012, Masse et al. 2014, Jedlikowski et al. 2016). Further, resource availability, competition, and predation can also determine space use at smaller spatial scales such as the home range or microhabitat selection within areas of high use (Rosenzweig 1991, Aebischer et al. 1993, Lima 1993, Millspaugh et al. 2019).

Among social animals, changes in degree of sociality and group size are a common response to variation in predation risk (Quenette 1990, Lima and Bednekoff 1999). To achieve high feeding rates, migratory birds may form larger flocks as an antipredator behavior to increase the probability of predator detection and reduce the individual probability of being attacked (Myers 1980, Cresswell 1994, Lima 1995, Barbosa 1997, Whitfield 2003, Pomeroy 2006). The "many-eyes hypothesis" argues that as group size increases in socially foraging animals, there are progressively more individuals scanning the environment for predators (Lima 1995, Olson et al. 2015). Therefore, as group size increases, individual foragers can allocate more time to feeding (Lima and Dill 1990, Lima 1995). Predation risk can also vary over shorter time periods over the course of a day, and the "predation risk allocation hypothesis" predicts that optimal antipredator behavior in a given situation is driven by time and location (Myers 1980, Lima and Bednekoff 1999). Thus, if predation risk varies with time of day or with concealment due to vegetative cover or other habitat characteristics, individual animals may opt to be solitary or join a group, and use open areas or rely on protection from concealment in more complex habitats (Lima 1990, Lima and Bednekoff 1999, Kullberg and Lafrenz 2007).

We examined habitat selection and space use of Upland Sandpipers (*Bartramia longicauda*) during the nonbreeding season in temperate grasslands of northcentral Uruguay. Upland Sandpipers are a long distance migratory bird, and previous efforts have collated natural history and specimen records to map their broad-scale distribution at the nonbreeding grounds in South America (White 1988, Blanco and López-Lanús 2008, Vickery et al. 2010). Focal studies of individual birds during the nonbreeding and breeding seasons have started to provide insights into movements and space use at a local scale. The foraging behavior of Upland Sandpipers consists of an active search of the ground with visual prey detection and a run-and-peck behavior similar to plovers (Charadriidae; Houston et al. 2011). The diet of sandpipers during the nonbreeding season in Uruguay includes grasshoppers, ground beetles, and other small arthropods (Alfaro et al. 2015). During the breeding season, Upland Sandpipers prefer to forage in disturbed areas with short vegetation height where they feed on grasshoppers and other surface-dwelling arthropods (Dechant et al. 1999, Fritcher et al. 2004, Powell 2006, Ahlering and Merkord 2016). Foraging in grazed sites and burned areas with little cover probably allows sandpipers easier movement, more efficient prey detection, and access to higher densities of arthropod prey (Sandercock et al. 2015). On the other hand, Upland Sandpipers require habitats with greater vegetative structure for nesting, which offers concealment to incubating birds but may increase their vulnerability to ground-based predators (Metcalfe 1984, Colwell and Dodd 1995, Sandercock et al. 2015). Surveys of grassland bird communities at nonbreeding sites in South America found that Upland Sandpipers were associated with intermediate values of vegetation patchiness in grasslands managed with grazing (Azpiroz et al. 2012, Azpiroz and Blake 2016). However, individual variation in habitat use and selection of sandpipers at nonbreeding grounds remains poorly understood.

The Northern Campos of Uruguay is a complex ecoregion with habitats that are a mosaic of different vegetation height and density that are determined by soil quality and depth, livestock grazing, and agricultural activities (Lezama et al. 2006, 2011, Baeza et al. 2010, 2011). Understanding habitat requirements of migratory birds at the nonbreeding grounds is important because south temperate grasslands are currently exposed to many anthropogenic changes in land cover and land use (Vickery et al. 1999, Isacch and Cardoni 2011, Azpiroz and Blake 2016, Aldabe et al. 2019). Threats to native grasslands in South America include conversion to agriculture, afforestation, and intensification of livestock grazing (Ramankutty and Foley 1999, Tilman et al. 2001, Baldi and Paruelo 2008). Ecological conditions in anthropogenic landscapes can change faster than grasslands grazed by native herbivores, resulting in differences in the abundance and persistence of local plant and animal populations in modified grasslands (Fahrig and Merriam 1994, Galetto et al. 2007, Baldi and Paruelo 2008).

Fig. 1. Map of the study area in the Northern Campos, showing four ranches where Upland Sandpipers (*Bartramia longicauda*) were captured and monitored during four austral spring and summer seasons, 2008–2012. Grey polygons show the minimum convex polygon (geo-referred) including all sandpiper locations at each ranch (west to east, Wilson: 749.8 ha, Valdez: 942.2 ha, Ramos: 513.2 ha, and Sarandí: 1360.6 ha). Coordinates for locations of each ranch are reported in Table A1.1.



In our field project, we examined the habitat selection and space use of Upland Sandpipers on private lands managed for livestock production and considered the possible consequences of human activities on the spatial ecology of sandpipers. We tracked radio-marked birds to investigate how species occurrence and flock size were affected by vegetation height and cover, and how variation in the spatial and temporal distributions of birds was affected by a landscape with different grazing and agricultural activities. We hypothesized that vegetation height and cover would determine habitat selection of individual sandpipers on feeding or roosting locations, and social behavior as solitary birds to increasing flock size. Based on habitat selection and social behavior at breeding sites, we predicted that nonbreeding sandpipers would select grasslands with short vegetative structure to improve prey detection and form flocks while foraging to reduce potential predation risk.

METHODS

Study system

Our study area was located in northcentral Uruguay (31.50°-31.44°S and 56.51°-56.26°W), covering a total area of ~1800 km^2 in Salto and Paysandú Departments (Fig. 1). The area is part of the Northern Campos ecoregion of Uruguay, close to the Haedo Ridge and included in the Basaltic region, which is characterized by rolling topography with rocky and shallow soils (Altesor et al. 2005, Lezama et al. 2006, Azpiroz and Blake 2009, Baeza et al. 2010, Azpiroz et al. 2012). Livestock grazing is the main agricultural use throughout this region, including sheep, cattle, and horses, which together with the native pampas deer (*Ozotoceros bezoarticus*), create a mosaic of different grass structure. The vegetative community is mainly composed of native grasses including *Piptochaetium montevidense*, *Bothriochloa laguroides*, *Richardia humistrata*, *Baccharis coridifolia*, *Panicum hians*, *Portulaca papulosa*, and *Paspalum dilatatum* (Lezama et al. 2006, 2011, Baeza et al. 2010). The region also includes scattered stands of introduced *Eucalyptus* trees that were planted for shade and wood products, native forests along creeks and rivers, and a small but increasing area of agricultural fields used for cultivation of grains and other crops, including rice, barley, sorghum, wheat, sunflower, and soybeans (Baeza et al. 2010, Azpiroz et al. 2012).

Upland Sandpipers use native grasslands and occasionally croplands at both the breeding and nonbreeding grounds (Blanco and López-Lanús 2008, Houston et al. 2011, Azpiroz et al. 2012). In Uruguay, Upland Sandpipers can be found at inland sites throughout the country, but are most frequently observed in the Northern Campos (Blanco and López-Lanús 2008, Azpiroz and Blake 2009, Azpiroz et al. 2012). Upland Sandpipers occasionally occur in mixed species flocks, and other grassland shorebirds regularly observed in our study area during the austral summer included American Golden-Plovers (*Pluvialis dominica*) and Buff-breasted Sandpipers (*Tryngites subruficollis*; Azpiroz and Blake 2009, Azpiroz et al. 2012, Alfaro et al. 2015). Predators of Upland Sandpipers at breeding grounds in North America include a range of mesocarnivores and small raptors (Houston et al. 2011, Sandercock et al. 2015). Comparable species of diurnal predators observed at our study sites in Uruguay included crab-eating fox (*Cerdocyon thou*), pampas fox *Lycalopex gymnocercus*), pantanal cat (*Lynchailurus braccatus*), Swainson's Hawk (*Buteo swainsoni*), White-tailed Hawk (*Geranoaetus albicaudatus*), Savanna Hawk (*Buteogallus meridionalis*), Crested Caracara (*Caracara plancus*), Long-winged Harrier (*Circus buffoni*), Aplomado Falcon (*Falco femoralis*), and Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*).

Macro- and microhabitat analyses

Our field study was conducted during four austral spring and summer seasons for the 3.5-mo period between mid-November to late-February from 2008 to 2012. We worked at four different ranches where we captured, radio-marked, and monitored sandpipers during the nonbreeding season (west to east): Wilson, Valdez, Ramos, and Sarandí ranches (Fig. 1, Table A1.1). Our study sites were selected depending on the presence of nonbreeding sandpipers, logistics of access from secondary roads, and land-owner permission to work on private lands. All ranches were managed with grazing for livestock production and had similar communities of native grasses.

Birds were captured at roosting sites during the night using high-powered spotlights and a long-handled dip net. We individually marked sandpipers with a numbered metal band and a unique combination of colored leg bands. We also marked all birds with small VHF radio transmitters attached to the back with an elastic leg-loop harness (model PD-2, 3.8 g, Holohil Systems, Carp, ON), a method with effective radio retention and high seasonal survival on Upland Sandpipers (Mong and Sandercock 2007). We used portable radio receivers with a Yagi antenna (R2000, ATS, Isanti, MN) to relocate and approach radio-tagged birds on foot every one to seven days. We determined locations by visual sightings of radio-marked birds and recorded locations in UTM coordinates with a handheld GPS unit (Garmin GPS V, Lenexa, KS).

We analyzed locations of Upland Sandpipers at nonbreeding sites within the Northern Campos ecoregion with the goals of analyzing macrohabitat selection in relation to habitat availability, and also microhabitat use based on locations of marked birds. For our analysis of macrohabitat selection, background habitat availability was determined using a vegetation map of the Basaltic region including our study area (Baeza et al. 2011). The habitat map was based on a previous characterization of vegetative communities (Lezama et al. 2006, 2011), and a recent vegetation map (Baeza et al. 2010). Native grasslands composed 91% of the 28,000 km² area of the Northern Campos ecoregion and were categorized into two main vegetation communities: B1 (36%) and B2 grasslands (56%; Baeza et al. 2011). The B1 plant community included open grasslands with short vegetation cover on shallow soils: meso-xerophytic grasslands and the lithophytic steppes over rocky outcrops. The meso-xerophytic grasslands have a low herbaceous layer (5–10 cm) of grasses and forbs, and a height stratum (~30 cm) dominated by erect grasses and the shrub *Baccharis coridifolia.* The lithophytic steppes are mainly one low stratum (5–10 cm) dominated by a spike moss, *Selaginella sellowii* (Baeza et al. 2010). In contrast, the B2 plant community included dense meso-hydrophytic grasslands with high vegetation cover on deep soils. The meso-hydrophytic grasslands have one low stratum of prostrate grasses (< 5 cm) and a taller canopy of erect grasses (≥ 30 cm; Baeza et al. 2010; M. Alfaro, *personal observation*). Other habitats in the ecoregion included agricultural crops (5%), native forest (2%), planted forest (1%), and open water (0.1%; Baeza et al. 2011).

To analyze habitat selection by Upland Sandpipers in the Northern Campos, we plotted locations of radio-tagged birds on the vegetation map for the Basaltic region. We investigated macrohabitat selection based on locations of marked birds observed in different vegetation units in relation to the proportional availability of habitat strata at two spatial scales: (i) ranches, with each study site limited by the set of locations for all radio-marked birds at a given site, and (ii) home range, within the minimum convex polygon calculated for the locations of each individual radio-tagged bird. The proportion of habitats used and available were determined using tools of Program QGIS (ver. 3.4.4 Madeira, Open Source Geographical Information System, Quantum GIS Development Team 2015). To investigate microhabitat use and sociality at each location, we recorded group size as the number of birds seen with the radio-marked bird, along with the vegetation height and the percentage of vegetation cover of shorter and higher vegetation stratum. An adult Upland Sandpiper standing upright is ~30 cm tall (M. Alfaro, *personal observation*), so we considered grasses higher than 30 cm as suitable protective cover. Based on this rule of thumb, we categorized vegetation height at each bird location into two strata for grasses < 30 cm or > 30 cm. For each strata, we measured maximum vegetation height of the shorter and higher strata to the nearest centimeter. The percent cover of each strata was determined using a visual estimate within a radius of 20 m from the location of the GPS point where the bird or flock were seen.

Statistical analyses

We grouped vegetation communities into five discrete categories after Baeza et al. (2011): B1 (meso-xerophytic grasslands and lithophytic steppes with low vegetation cover), B2 (meso-hydrophytic grasslands with dense vegetation cover), AG (agricultural lands), F (forested patches of exotic trees for cattle refuge), and O (others, native forest). We estimated the area occupied by the different land covers within a minimum convex polygon (MCP) enclosing all radio-marked birds at each ranch, and separately for all locations from each individual bird. The relative level of selection for each vegetation community was evaluated contrasting the observed use vs. availability at each location for a sighting of a radio-marked bird with a *G*-test (Sokal and Rohlf 1995). Specifically, the *G*-test compared the observed numbers of individuals using each habitat with the expected counts if individuals are distributed among land cover types in proportion to their availability (Sokal and Rohlf 1995). Results are expressed as the log10 ratio of the used and available proportions of land cover use (Aebischer et al. 1993). The log-ratio is expected to be zero if birds use each habitat in the same proportion that it is available, a positive if habitat use is greater than availability, and negative if a habitat is avoided. We estimated individual home ranges based on MCP from birds with 15 or more visual resightings to ensure accurate home range size estimates (Seaman et al. 1999, Singer et al. 2015). Estimates of home range area based on MCP may include outliers due to forays and are often biased high compared to estimates from kernel methods, but kernel methods require more locations per individual than we were able to obtain in this study (Seaman et al. 1999, Singer et al. 2015). Program QGIS was used for all calculations, and estimates of MCP are presented as the mean standard deviation.

For our analysis of microhabitat use at the location of each sighting, we compared the frequency of occurrence of birds and flock size with the percentage cover of tall grass > 30 cm in height. We tested our short grass-flocking behavior prediction using generalized linear models (GLM) linked to Poisson distribution because our response variable was count data (Zuur et al. 2009). Group size was treated as the response variable, and linear, quadratic, or cubic effects of mean weighted vegetation height were the explanatory variables. The addition of quadratic and cubic terms allowed us to test curvilinear relationships (symmetric or not) expected when the response variable is count data (Zuur et al. 2009). Candidate models were selected based on minimum values of Akaike's Information criterion (AIC; Zuur et al. 2009). To better describe our results of group size distribution we also fit quantile regressions, a regression similar to a typical regression to the mean but inferring the trend in a specific percentile (Cade and Noon 2003). Quantile regressions can be used when the effects of the predictor variables such as vegetation height are not well represented by changes in the response variable such as group size because there were other unmeasured factors such as inter- or intraspecific interactions that were potentially limiting (Cade and Noon 2003, Cade et al. 2005). We explored quantile regressions between 95th to 99th percentiles because we were interested in the functional relationship for the highest values in the observed distribution for group size of sandpipers. To test for possible effects of sites and years on flock size, we used boxplots, explored differences in variance with ANOVA (including the interaction between sites and years), and compared groups using Tukey multiple comparisons of means. All models and statistical analysis were performed using base functions, or functions of the vegan and quantreg packages in an R environment (version 1.1.46, R Core Team 2019). We considered results to be statistically significant at $P < 0.05$, or $P < 0.01$ in cases where we conducted five or more univariate tests (i.e., $/n = 0.05/5 = 0.01$).

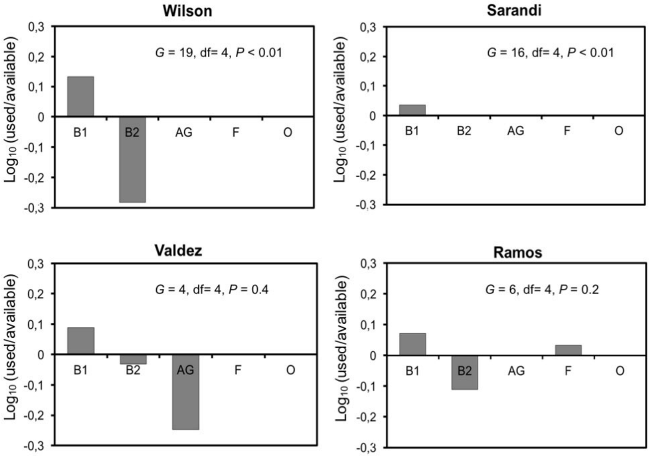
RESULTS

During the four austral seasons of spring-summer in 2008–2012, we radio-marked a total of 62 Upland Sandpipers at four capture sites in the Northern Campos of Uruguay. Of these 62 individuals, 15 birds were captured in the 2008–2009 season, 20 in 2009–2010, 9 in 2010–2011, and 18 in 2011–2012 (Table A1.2). We recorded a total of 506 sightings of the radio-tagged birds feeding or resting in the study area, including 105, 190, 79 and 132 sightings in our four different field seasons. Number of sightings per individual sandpiper varied between 1 to 18 records and each individual was monitored from capture day to end of February each season (data on capture date is in Table A1.2). Marked individuals were monitored for the duration of the nonbreeding season except in two cases in which the VHF radio failed (individual 30257), or the harness failed and the bird dropped the radio (individual 30243). The period of time each bird was monitored varied between 35 to 100 days (mean = 55.1 ± 16.8, $N = 62$).

Habitat selection at two spatial scales

We estimated the proportion of each vegetation community available at two spatial scales: at four different ranches and within individual home ranges (Tables A1.3 and A1.4). At the spatial scale of ranches, habitat selection by Upland Sandpipers indicated that they used B1 grasslands more often than expected by the proportional availability, with less use of the B2 (grasslands), AG (agricultural lands), and F (forested sites) strata than expected, and no use of other (O) vegetation unit (Fig. 2). Habitat use was significantly different from availability at two ranches (Sarandí: $G = 16$, df = 4, $P < 0.01$; Wilson: $G = 19$, df = 4, $P < 0.01$), whereas habitat use by sandpipers was not significantly different from the proportional availability of vegetative strata at the remaining two sites (Valdez: $G = 4$, df = 4, $P = 0.4$; Ramos: $G = 6$, df = 4, $P = 0.2$).

Fig. 2. Log-ratios (used/available) of vegetation cover types at four ranches in the Northern Campos, Uruguay. Positive values indicate preferred use; negative values indicate avoidance. The five different vegetation communities included: B1: meso-xerophytic grasslands and the lithophytic steppes, B2: meso-hydrophytic grasslands, AG: agricultural lands with cultivated crops, F: forested sites, and O: other habitats. Results of the *G*-test comparing vegetation used and available are reported in each panel. $N = 506$ observations.



Of 62 radio-marked sandpipers, we were able to estimate home range size for nine individuals with 15 or more sightings: one bird at Sarandí, six at Valdez, and two at Ramos (Table A1.4). The area of the minimum convex polygons (MCP) for individual Upland Sandpipers were relatively small during the nonbreeding season in Uruguay, and ranged in area between 38.6 ha to 149.8 ha (mean = 90.7 ± 39.6, $N = 9$). When comparing habitat availability in ranches versus used inside the nine individual's MCP, six individuals used more B1 grasslands than expected by availability (Table 1). Two individuals at Valdez ranch and one at Ramos showed no significant differences between use and proportional availability of habitat, but tended to use more B2 grasslands (Table 1).

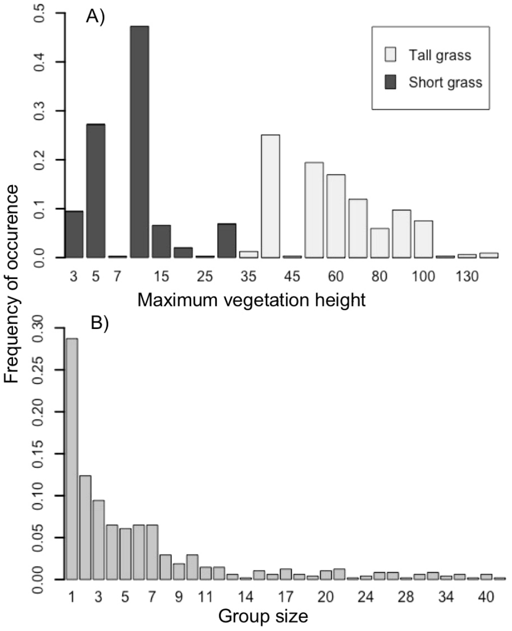
Spatial usage at individual sightings

We recorded measurements of vegetation height at the locations of foraging sites used by radio-marked Upland Sandpipers during 88 different days across our four field seasons. The shortest vegetation heights ranged between 3 to 30 cm (mean = 9.92 ± 6.6, $N = 349$) whereas sites with the greatest structure varied between 35 to 150 cm (mean = 62.46 ± 22.03, $N = 319$; Fig. 3A). The percentage of tall grass cover used by sandpipers at patches in a 20 m radius varied as follows: 2% of individuals used patches with less than 10% of high strata, 94% between 10 to 50%, and 4% between 60 to 100%. Our results indicate that most birds used foraging patches with relatively short vegetation cover. At Ramos ranch, we occasionally observed sandpipers roosting in the shade of a stand of eucalyptus trees. Use of shade was recorded twice during midday when ambient temperatures were around 40°C. At Valdez ranch, some birds were observed using artificial grasslands (sorghum and ray-grass). In our detections of radio-marked birds, we recorded that birds were alone in 27% of the cases, 62% were

Table 1. Results of the *G*-test of goodness of fit comparing habitat use vs. proportional availability of vegetative strata for nine Upland Sandpipers (*Bartramia longicauda*) at three ranches (Sarandí, Valdez, and Ramos, Table A1.3) in the Northern Campos of Uruguay (significant level $P < 0.05$). Home ranges of sandpipers were calculated with minimum convex polygons (MCP). The second to fourth columns show proportions of B1 (meso-xerophytic grasslands and the lithophytic steppes), B2 (meso-hydrophytic grasslands), and AG (agricultural lands) vegetation communities used at the scale of an individual home range. Two additional habitat strata, F (forested sites) and O (other habitats), did not occur within individual home ranges and were not included in the *G*-test.

	Percent use of habitat strata (%)			Test of habitat selection		
Ranch-individual	B1	B2	AG	*G*	df	P ≤
Sarandí-30244	100	0	0	16.8	2	0.01
Valdez-30249	26.7	73.3	0	0.89	2	0.64
Valdez-30267	38.9	61.1	0	35.4	2	0.01
Valdez-30268	37.5	62.5	0	6.3	2	0.04
Valdez-30269	46.7	53.3	0	12.7	2	0.01
Valdez-30271	37.5	62.5	0	10.4	2	0.01
Valdez-30285	44.5	55.5	0	27.1	2	0.01
Ramos-52212	100	0	0	29.7	2	0.01
Ramos-52213	46.7	53.3	0	1.5	2	0.47

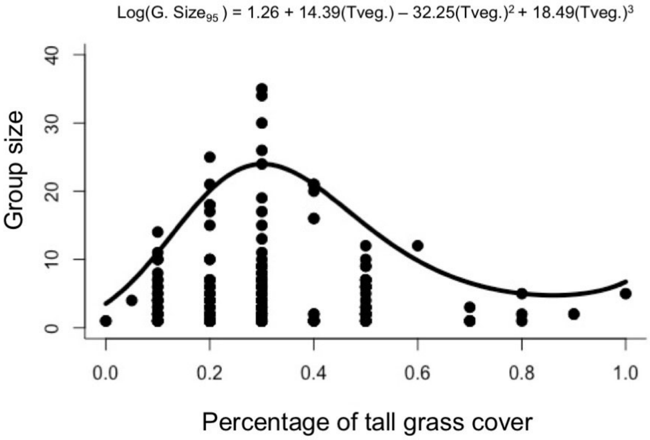
Fig. 3. (A) Frequency distribution of the tallest vegetation height (cm) at short (*N* = 349) and tall (*N* = 319) strata in patches used by Upland Sandpipers (*Bartramia longicauda*) during the nonbreeding season in managed grasslands of the Northern Campos of Uruguay. (B) Frequency distribution for group size of flocks of Upland Sandpipers at nonbreeding grounds in the Northern Campos, Uruguay (*N* = 477 records).



in small groups of 2 to 20 birds, and only 8% of records were of larger flocks of > 20 sandpipers (*N* = 477, Fig. 3B).

Our results suggest that birds frequently used patches of grasslands with a short grass sward (Fig. 3A). Using generalized linear models, we found no significant relationship between average group size and percentage of tall grass cover. However, most of the individuals were observed in small groups, and group size distribution was constrained to patches with low levels of tall grass cover. To describe this tendency, quantile regressions based on the 95th percentile (0.95 to 0.99 percentiles showed the same pattern) showed a single top model based on AIC model selection (Model D in Table 2). A third order quantile polynomic regression indicated that group size followed a significant and humped association with tall grass cover (Fig. 4), where larger group sizes were only observed at sites with low vegetation height. Lower order polynomic models were nonsignificant; they probably failed to capture the long tail observed in the distribution with occurrences of < 5 individuals at > 60% tall grass cover (Table 2).

Fig. 4. Quantile regression (0.95 quantile, black line) describing the relationship between the group size of Upland Sandpipers, *Bartramia longicauda*, (G. size) versus the percentage of tall grass cover (Tveg) in the Northern Campos of Uruguay for the third order polynomial model $\log(y) = b_0 + b_1x + b_2x^2 + b_3x^3$. P values of each parameter are reported in Table 2. *N* = 237 observations.



Flock size of nonbreeding sandpipers showed significant differences among the four ranches (Wilson, Sarandí, Valdez, Ramos) and our four field seasons (2008–2009 to 2011–2012; Table 3, Fig. 5). Paired comparisons of means showed significant differences between Sarandí and Valdez versus Ramos, and significant differences between first and second versus the third and fourth seasons (Table 4).

DISCUSSION

Our four-year telemetry study is the first investigation of the space use and habitat requirements of individual Upland Sandpipers during the nonbreeding season in South America, and our work resulted in four major findings. First, the Northern Campos ecoregion of Uruguay was an important area for Upland Sandpipers during the nonbreeding stage of their annual cycle. Second, radio-marked birds maintained relatively small home

Table 2. Results of the model selection for models examining the relationship between the group size of Upland Sandpiper, *Bartramia longicauda*, (y) and percentage of tall grass cover (x) in the Northern Campos ecoregion of Uruguay. Models were run using quantile regressions up to 95th percentile.

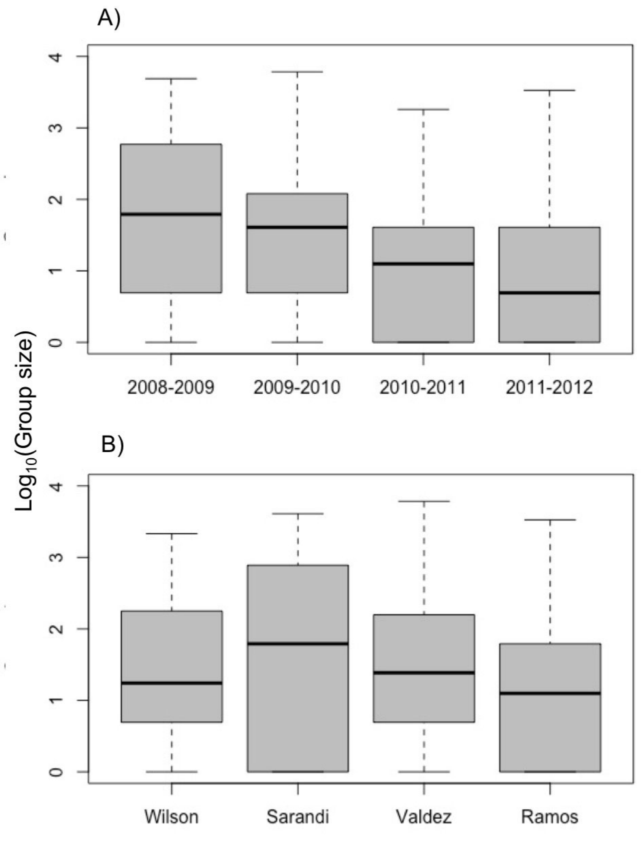
Model	b_0	b_1	b_2	b_3	df	AIC	ΔAIC	w_i
Cubic	1.26^{***}(0.4)	14.39^{***}(3.9)	32.25^{**}(9.9)	18.49^{**}(6.6)	233	811.20	0	0.999
Quadratic	2.34^{***}(0.3)	3.43^{*}(1.7)	-4.16^{*}(1.7)	-	234	830.65	19.45	0.001
Linear	2.78^{***}(0.3)	0.52 (1.2)	-	-	235	846.76	35.56	0.001
Null	2.94^{***}(0.1)	-	-	-	236	845.55	34.35	0.001

Alternative models included: Null) $\log(y) = b_0$, Linear) $\log(y) = b_0 + b_1x$, Quadratic) $\log(y) = b_0 + b_1x + b_2x^2$, and Cubic) $\log(y) = b_0 + b_1x + b_2x^2 + b_3x^3$. Slope coefficients ($b_0$ to b_3) with standar error in parenthesis and significant values, *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$; df, degrees of freedom; AIC, Akaike's information criterion; ΔAIC = AIC - min(AIC); w_i = rounded Akaike weights. *N* = 237 observations.

Table 3. Results of ANOVA analyses comparing Upland Sandpiper (*Bartramia longicauda*) group size (Log10(group size)) between ranches (Wilson, Sarandí, Valdez, Ramos), seasons (2008–2009, 2009–2010, 2010–2011, 2011–2012) and interaction between them in the Northern Campos of Uruguay. Df = degree of freedom, Sum sq. = square sum, Mean sq. = square mean, F value = Fisher-test value. Total number of observations (*N* = 477) included four ranches: Wilson (*N* = 32), Sarandí (*N* = 38), Valdez (*N* = 222), Ramos (*N* = 185), and four seasons: 2008–2009 (*N* = 91), 2009–2010 (*N* = 171), 2010–2011 (*N* = 70), and 2011–2012 (*N* = 145).

Test	df	Sum sq.	Mean sq.	F	P ≤
Group size vs. Site	3	17.1	5.69	5.66	0.01
Group size vs. Season	3	48.10	16.04	15.97	0.01
Group size vs. Site * Season	2	3.3	1.67	1.66	0.19

Fig. 5. (A) Boxplots showing variation in flock size of Upland Sandpipers (*Bartramia longicauda*) among four austral spring summer seasons (2008–2012) and (B) among four ranches in the Northern Campos of Uruguay. Solid black lines are the median (50%), boxes are the interquartile range (25–75%), and whiskers are the 95% range (2.5 to 97.5%).



ranges that averaged 90.7 ha in area. Third, birds showed preferential use of meso-xerophytic (B1) and meso-hydrophytic (B2) grassland habitats. Last, the social organization of nonbreeding birds was usually small flocks of 2–20 birds, but occasionally formed larger flocks of up to 40–50 birds in habitats of short vegetative height.

The ecological drivers of space use and sociality of Upland Sandpipers during the nonbreeding season included predation risk, food resources, climatic conditions, and the possible interactions among these factors. Animals are able to detect and respond to spatial and temporal variation in the risk of predation, which determines their antipredator decisions like flocking or using vegetation cover for protection, as predicted by the predation risk allocation hypothesis (Lima and Bednekoff 1999). We found a large difference in space use between Upland Sandpipers at nonbreeding and breeding sites. Our estimates of home range size based on minimum convex polygons for nonbreeding birds in Uruguay (90.7 ha, this study) were an order of magnitude smaller than our previous estimates of home range size based on kernel methods for Upland Sandpipers tracked during the breeding season in Kansas (~8.4 km²; Sandercock et al. 2015). Sandpipers were tagged and tracked with the same methods, but our comparison is conservative because estimates of home range size based on MCP and kernel methods tend to be biased high and low, respectively. Space requirements may be greater during the breeding season because Upland Sandpipers require multiple habitat types at this stage of the annual cycle: disturbed habitats with short vegetation for feeding versus undisturbed sites with tall vegetation for concealment of ground nests and incubating birds (Bowen and Kruse 1993, Klemek 2008, Garvey et al. 2013, Sandercock et al. 2015). Alternatively, a difference in home range area may indicate that space requirements are reduced at nonbreeding sites, possible because

Table 4. Results of Tukey multiple paired comparisons of mean group size of Upland Sandpipers (*Bartramia longicauda*) between pairs of sites (Wilson, Sarandí, Valdez, Ramos) and seasons (2008–2009, 2009–2010, 2010–2011, 2011–2012) in the Northern Campos of Uruguay. Diff. = difference

Pairs (x, y)	Mean x	Mean y	SD x	SD y	Diff.	99% Confidence interval		P ≤
						Lower Bound	Upper Bound	
Wilson, Sarandí	6.4	10.5	7.34	11.58	0.33	-0.29	0.94	0.53
Wilson, Valdez	6.4	7.3	7.34	8.62	0.51	0.02	1.00	0.04
Wilson, Ramos	6.4	4.4	7.34	4.88	0.30	-0.19	0.80	0.40
Sarandí, Valdez	10.5	7.3	11.58	8.62	0.19	-0.27	0.64	0.71
Sarandí, Ramos	10.5	4.4	11.58	4.88	-0.02	-0.48	0.43	0.99
Valdez, Ramos	7.3	4.4	8.62	4.88	-0.21	-0.47	0.04	0.15
2008–2009, 2009–2010	10.1	7.4	10.47	8.36	-0.21	-0.54	0.12	0.37
2008–2009, 2010–2011	10.1	3.8	10.47	3.96	-0.71	-1.12	-0.29	0.01
2008–2009, 2011–2012	10.1	4.0	10.47	4.92	-0.78	-1.13	-0.43	0.01
2009–2010, 2010–2011	7.4	3.8	8.36	3.96	-0.49	-0.86	-0.13	0.01
2009–2010, 2011–2012	7.4	4.0	8.36	4.92	-0.57	-0.86	-0.28	0.01
2010–2011, 2011–2012	3.8	4.0	3.96	4.92	-0.07	-0.45	0.30	0.95

arthropod food or habitat resources were more abundant. Our diet studies of Upland Sandpipers at the nonbreeding grounds indicate that birds feed mainly on aboveground adult insects like grasshoppers, beetles, and ants that can be easily detected in heterogeneous vegetation heights (Alfaro et al. 2015). American Golden-Plovers, Buff-breasted Sandpipers, and other grassland shorebirds that feed on insect larvae require habitats with homogeneous short vegetation (grass height < 10 cm) to detect prey (Isacch et al. 2005*a*, Isacch and Cardoni 2011, Aldabe et al. 2019). We examined habitat selection during daylight hours when raptors are potential predators but found no evidence of predation mortality of Upland Sandpipers at nonbreeding grounds (B.K. Sandercock, *unpublished data*). On the other hand, the largest groups of sandpipers were only found at sites with low levels (between 15–50% percent) of tall vegetation cover. Sparse stands of tall vegetation may provide refuge from raptors and other predators that use visual cues (Lima 1990, Kullberg and Lafrenz 2007), but sandpipers may also rely on their cryptic plumage instead of flocking for protection. Finally, it was a rare event but we occasionally observed groups of sandpipers roosting in the shade of eucalyptus trees or fence poles during hot temperatures. Use of shade has also been reported for Upland Sandpipers at breeding sites and was related to a selection of a cooler microclimate during the hottest periods of the day (Young and Thompson 2014). Shade roosting is unlikely to be an antipredator behavior because trees can provide perch sites for hunting raptors and may increase predation risk for birds in the adjacent grassland habitats.

We found evidence of interactions between habitat structure and the sociality of nonbreeding sandpipers. Sandpipers mainly used patches dominated by short vegetation cover, where birds were sometimes found in large groups (Fig. 4). We also observed variation in group size among seasons and sites. Flocking behavior and vigilance have been widely studied in animal social systems (MacArthur and Pianka 1966, Lima and Dill 1990, Lima 1995, Lima and Bednekoff 1999), but empirical determinants of these strategies at nonbreeding areas of migratory birds are scarce (Pomeroy 2006). Our observed variation in flock size could be related to interactions among foraging efficiency, predation risk, time and site allocation, and flocking behavior, which is consistent with both the predation risk allocation and many-eyes hypotheses (Lima 1995, Lima and Bednekoff 1999). Sandpipers may select habitats based on the spatial and temporal context of predation risk and food abundance (predation risk allocation hypothesis; Lima and Bednekoff 1999, Kullberg and Lafrenz 2007). Our results of flock size variations during the four seasons showed bigger group sizes during the first two seasons (2008–2010) compared with the last two (2010–2012). In a previous study about the diet of Upland Sandpipers at the same nonbreeding areas and during the same four austral summer seasons we found the same pattern of variation, different food composition during the first two seasons in relation with the last two (Alfaro et al. 2015). This combination of results supports the hypothesis of a relationship between food (composition and abundance) and predator's flock size. Alternatively, variation in flock size at patches dominated by short vegetation cover could also be related to intraspecific competition. At nonbreeding grounds in Argentina, Buff-breasted Sandpipers are solitary and defend feeding territories if predation risk is low, but will aggregate into small flocks if a predator approaches (Myers 1980). Similar behaviors could be used by Upland Sandpipers at feeding patches but better data on flock size and local predation risk are needed to understand their strategies of antipredator behavior. Trade-offs between habitat and sociality might also be influenced by local conditions such as elevation, soil depth, and vegetation composition, variables that are important determinants of habitat use by sandpipers during the breeding season (Dechant et al. 1999, Fritcher et al. 2004, Sandercock et al. 2015, Ahlering and Merkord 2016).

The distribution of Upland Sandpipers in Uruguay shows that they are associated with large tracts of native grasslands, a feature of the Northern Campos ecoregion but scarce in other biomes of southern South America (Baeza et al. 2011, Azpiroz et al. 2012, Azpiroz and Blake 2016). Management of native grasslands for livestock production is the dominant land use in the Northern Campos. Grazing can provide habitats of different vegetation height and cover in large areas, and can allow for coexistence of species with different habitat requirements (Fuhlendorf et al. 2006, Codesio et al. 2013, Ahlering and Merkord 2016, Azpiroz and Blake 2016). The spatial heterogeneity of vegetation structure generated by different practices of grazing can increase the species richness of grassland bird communities (Isacch et al. 2005*b*, Isacch and Cardoni 2011, Ahlering and Merkord 2016). The levels of vegetative cover preferred by Upland Sandpipers are available in grasslands managed with extensive systems of livestock production where animals graze in large paddocks year-round, that are commonly applied in Northern Uruguay (Baeza et al. 2010, MGAP 2015). Other migratory species of shorebirds including American Golden-Plovers and Buff-breasted Sandpipers, also use homogeneous short grass in areas of high levels of cattle grazing (Isacch and Cardoni 2011, Aldabe et al. 2019), or patches of lithophytic steppes in the Northern Campos (M. Alfaro, *personal observation*). However, the community of nonbreeding shorebirds appear to require less vegetative cover than many declining species of grassland birds that are endemic to South America. For example, the Pampas Meadowlark (*Sturnella defillippi*), Hudson's Canastero (*Asthenes hudsoni*), and Black-and-white Monjita (*Xolmis dominicanus*) require grasslands with dense cover of tall grass for nesting (Azpiroz et al. 2012, Azpiroz and Blake 2016). Thus, the diverse habitat requirements of migratory and resident birds indicates that it is important that grazing and other land uses maintain heterogeneity in native grasslands for conservation of avian biodiversity (Isacch and Cardoni 2011, Azpiroz and Blake 2016).

By examining the dynamics of how individual animals use habitats, we can begin to understand the conflicting demands that influence animal behavior and fitness (Rosenzweig 1991, Morris 2003, Gaillard et al. 2010). Similarly, our study attempted to advance on the mechanisms by connecting land use and its ongoing changes, with space use of migratory species. Migratory birds often have high site fidelity to breeding and nonbreeding sites that are used both within and among years (Smith and Houghton 1984, Huston 1998, Lindström 2007, Isacch and Martínez 2003). During the nonbreeding period in Uruguay, Upland Sandpipers molt and replace their flight feathers and plumage, an energetically costly activity that is important for successful completion of migration during their annual cycle, and a period of vulnerability if feather molt affects flight agility (Alfaro et al. 2018). Here, we reported that specific levels of grass height (mainly 20 to 40% tall grass cover) were important for Upland Sandpipers during the nonbreeding season, and that such vegetation structure was generated by different practices of livestock grazing in native grasslands.

However, most managed grasslands have not been developed to promote and provide the habitat for coexisting species with different habitat requirements. Instead, conversion of native grasslands to croplands has resulted in loss of habitat for many grassland birds (Vickery et al. 1999, Brennan and Kuvlesky 2005, Isacch and Cardoni 2011, Azpiroz et al. 2012, Codesido et al. 2013, Fedy et al. 2018). Loss of habitat could have severe consequences on the annual survival of Upland Sandpipers, and other migratory or resident species dependent on grassland ecosystems. The Northern Campos still maintains extended areas of native grasslands managed by different levels of livestock productivity. Nevertheless, no protected areas currently exist in the Northern Campos ecoregion and, during the four years we worked there, we saw a steady increase in crop production. If crop production continues to increase, less native grass would be available for cattle production creating patches of very low grass height not suitable for many grasslands birds. Native grasslands remain threatened, and the availability of those habitats is changing quickly with pressures on land use. Ongoing research about habitat selection of grassland birds are important tools for governmental decisions over managed grasslands in light of biodiversity conservation.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1461

Acknowledgments:

We are grateful to Natalia Zaldúa, Khara M. Strum, Emanuel Machin, Matías Zarucki, Juan Manuel Barreneche, Pablo Vaz, Gastón Varela, Lucía Rodríguez, Martín Llanes, Rafael Tosi, Carlos Calimares, and Mateo Garcia for assistance with field work. César Fagúndez helped with the characterization of the study area, and Santiago Baeza provided layers of the vegetation map of the Basaltic region. We thank Andrés Canavero for comments that greatly improved the manuscript. We are grateful to the private landowners who granted access to their property. Our field study received financial support with grants from the National Science Foundation as an International Supplement to the Konza Prairie LTER Program at Kansas State University (DEB-0218210), The Institute for Grasslands Studies at Kansas State University, Programa para el Desarrollo de las Ciencias Básicas (PEDECIBA, Universidad de la República), and Agencia Nacional de Investigación e Innovación (ANII, Uruguay). Our research was conducted under federal and state wildlife permits issued in the USA and national wildlife permits issued in Uruguay. Research protocols were approved by the Comisión Honoraria de Experimentación Animal at Universidad de la República del Uruguay, Montevideo, Uruguay (Exp. N° 241000-001186-12).

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Editor-in-Chief: Keith A.Hobson
Subject Editor: Erik Blomberg

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Appendix 1

Table A1.1. Location of the four ranches in the Northern Campos of Uruguay where Upland Sandpipers were captured and monitored during each season. *N* points = number of GPS points at each ranch area where radio-marked sandpipers were monitored.

Ranch	Coordinates	*N* points	Year(s)
Sarandí Ranch	31.4642ºS, 56.2329ºW	45	2008-2009
Valdez Ranch	31.4808ºS, 56.3430ºW	232	2008-2012
Wilson Ranch	31.5302ºS, 56.5316ºW	41	2008-2009
Ramos Ranch	31.5238ºS, 56.3049ºW	187	2009-2012

Table A1.2. Individual Upland Sandpipers captured (*N* = 62) at four ranches in the Northern Campos of Uruguay. Date = capture date. N records = number of GPS points where the bird was relocated by radio-telemetry. Period = period of time (in days) each bird was monitored since capture date to the end of February.

Band number	Date	Period	Ranch	*N* records
30238	12/18/2008	72	Wilson	6
30237	12/19/2008	71	Wilson	7
30239	1/04/2009	55	Wilson	14
30240	1/04/2009	55	Wilson	5
30241	1/04/2009	55	Wilson	4
30242	1/06/2009	53	Sarandi	5
30243	1/07/2009	52	Sarandi	6
30244	1/07/2009	52	Sarandi	15
30245	1/07/2009	52	Sarandi	13
30246	1/09/2009	50	Sarandi	4
30248	1/21/2009	38	Valdez	2
30249	1/21/2009	38	Valdez	15
30250	1/22/2009	37	Valdez	2
30256	1/23/2009	36	Valdez	6
30257	1/23/2009	36	Valdez	1
30267	11/19/2009	100	Valdez	18
30268	11/19/2009	100	Valdez	16
30284	11/22/2009	97	Valdez	6
30285	11/23/2009	98	Valdez	18
30269	12/09/2009	81	Valdez	15
30270	12/10/2009	80	Valdez	11
30271	12/10/2009	80	Valdez	16
30272	12/18/2009	72	Valdez	5
30273	12/18/2009	72	Valdez	7
30274	12/19/2009	71	Valdez	6
30275	1/06/2010	53	Ramos	13
30276	1/07/2010	52	Ramos	12
30277	1/08/2010	51	Ramos	6
30278	1/08/2010	51	Ramos	4
30279	1/08/2010	51	Ramos	2
30280	1/08/2010	51	Ramos	9

30281	1/09/2010	50	Ramos	8
30282	1/10/2010	49	Ramos	2
30283	1/10/2010	49	Ramos	7
30286	1/11/2010	48	Ramos	9
30287	12/30/2010	60	Valdez	9
30288	12/30/2010	60	Ramos	9
30289	1/04/2011	55	Valdez	14
30290	1/04/2011	55	Valdez	4
30291	1/05/2011	54	Ramos	14
30292	1/06/2011	53	Valdez	4
30293	1/06/2011	53	Valdez	12
30294	1/06/2011	53	Valdez	3
30295	1/13/2011	46	Ramos	10
30296	12/20/2011	70	Ramos	13
30297	12/22/2011	68	Ramos	12
30298	12/28/2011	62	Valdez	12
30299	12/28/2011	62	Valdez	6
30300	12/29/2011	61	Valdez	7
52201	1/18/2012	41	Ramos	6
52202	1/19/2012	40	Valdez	8
52203	1/19/2012	40	Valdez	12
52204	1/19/2012	40	Valdez	2
52205	1/20/2012	39	Ramos	6
52206	1/20/2012	39	Ramos	2
52207	1/20/2012	39	Ramos	11
52208	1/21/2012	38	Valdez	5
52209	1/21/2012	38	Valdez	2
52210	1/21/2012	38	Valdez	1
52211	1/22/2012	37	Ramos	11
52212	1/25/2012	35	Ramos	15
52213	1/25/2012	35	Ramos	15

Table A1.3. Proportion of vegetation available and the estimation of the minimum convex polygon (MCP) for the four ranches (Sarandi, Valdéz, Ramos and Wilson) in the Northern Campos, Uruguay. Minimum convex polygons enclosed all locations for the radio-marked sandpipers montitored at each ranch (in hectares). Habitats included B1 = meso-xerophytic grasslands and lithophytic steppes, B2 = meso-hydrophytic grasslands, AG = agricultural lands, F = forested sites, and Other = other habitats. *N* = is the number of pixels in the map (1 pixel = 30 x 30 m).

		Vegetation available (%)					
Ranch	MCP (ha)	B1	B2	AG	F	Other	*N*
Sarandí	1360.6	92.2	7.7	0	0	0.1	15,134
Valdez	942.2	29.2	67.6	2.3	0.3	0.6	10,473
Ramos	513.2	57.1	41.4	0.3	0.5	0.7	5,710
Wilson	749.8	57.5	42.1	0	0.3	0.1	8,339

Table A1.4. Proportion of vegetation available inside the minimum convex polygons (MCP, hectares) for nine individual Upland Sandpipers with more than 15 locations in the Northern Campos, Uruguay. Habitats included: B1 = meso-xerophytic grasslands and lithophytic steppes, B2 = meso-hydrophytic grasslands, AG = agricultural lands, F = forested sites, and Other = other habitats. *N* = is the number of pixels in the map (1 pixel = 30 x 30 m).

			Vegetation available (%)					
Ranch	Band No.	MCP (ha)	B1	B2	AG	F	Other	*N*
Sarandí	30244	149.8	91.9	8.1	0	0	0	1615
Valdez	30249	62.8	24.3	75.4	0.3	0	0	692
Valdez	30267	38.6	14.9	84.2	0.9	0	0	443
Valdez	30268	139.8	26.2	73.7	0.1	0	0	1558
Valdez	30269	109.5	29.7	70.3	0	0	0	1210
Valdez	30271	66.2	23.1	76.9	0	0	0	733
Valdez	30285	118.3	21.3	78.5	0.2	0	0	1320
Ramos	52212	56.7	86.2	13.8	0	0	0	622
Ramos	52213	74.8	40.7	59.3	0	0	0	850