

EFFECTS OF CATTLE GRAZING AND FIRE ON THE ABUNDANCE, HABITAT SELECTION, AND NESTING SUCCESS OF THE BAY-CAPPED WREN-SPINETAIL (*SPARTONOICA MALUROIDES*) IN COASTAL SALTMARSHES OF THE PAMPAS REGION

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Abstract. The Bay-capped Wren-Spintail (*Spartonoica maluroides*, Furnariidae) is the most specialized and threatened bird inhabiting *Spartina*-dominated saltmarshes in southeastern South America. These marshes are being modified at an increasing rate, primarily by cattle grazing and fire, which make this spintail highly vulnerable. To assess how land use affects the Bay-capped Wren-Spintail, we estimated its density under different intensities of fire and cattle grazing, studied selection of nesting habitat and nest success, and experimented with nest predation to determine predation rates and types of predators. We found similar population densities, nest microhabitats, and rates of nest predation in marshes with a low intensity of or no grazing. In contrast, the species was absent from marshes with a high intensity of grazing and fire. Nest height was the best predictor of daily survival rates. Nest-predation experiments demonstrated that nest height affects predation intensity and predator type. Our results suggest that low-intensity grazing and burning during winter are compatible with the presence and reproduction of the Bay-capped Wren-Spintail. Thus low-intensity cattle grazing is a viable alternative for the sustainable use of saltmarshes in southeastern South America.

Key words: *furnariid, grassland, nest predation, Spartina densiflora, South America, Argentina, Spartonoica maluroides.*

Efecto del Pastoreo por Ganado y Fuego sobre la Abundancia, Selección de Hábitat y Éxito Reproductivo de *Spartonoica maluroides* en Marismas Costeras de la Región Pampeana

Resumen. *Spartonoica maluroides* (Furnariidae) es el ave más especializada y amenazada que habita marismas costeras de esparto de *Spartina densiflora* del sudeste de América del Sur. Estos ambientes están siendo modificados a un ritmo acelerado principalmente por el pastoreo del ganado y la quema de espartillares, determinando la vulnerabilidad que presenta este furnárido. Para evaluar cómo el uso del suelo afecta las poblaciones de *S. maluroides*, se estudió la abundancia, el hábitat de nidificación y el éxito reproductivo en marismas bajo diferentes intensidades de pastoreo por ganado y quema. Además, se llevaron a cabo experimentos de depredación de nidos para determinar cómo la altura del nido afecta las tasas de depredación y el tipo de depredadores. *S. maluroides* presentó similar abundancia, éxito reproductivo y sitio de nidificación en marismas con bajo o nulo pastoreo. Por otro lado, la especie no fue registrada en marismas con alta presión de pastoreo y quemas. La altura del nido fue la variable que mejor explicó la tasa de supervivencia diaria. La tasa de depredación y el tipo de depredadores difirieron en relación a la altura del nido sobre el suelo. Nuestros resultados indican que el pastoreo con baja presión sería compatible con la presencia y reproducción de *S. maluroides*. De esta manera, el manejo ganadero con baja intensidad de uso es una alternativa viable para el uso sustentable de las marismas del sudeste de América del Sur.

INTRODUCTION

The Bay-capped Wren-Spintail (*Spartonoica maluroides*), a member of the predominantly South American family Furnariidae, is a small bird that inhabits saltmarshes along the coast as well as, locally, inland brackish marshes and humid grasslands in north-central Argentina, southeastern Brazil, and Uruguay (Canevari et al. 1991, Ridgely and Tudor 1994, Isacch and Martínez 2001, Isacch et al. 2004). Because of its

dependence on halophytic tall grasslands (Isacch and Martínez 2001, Isacch et al. 2004, Cardoni et al. 2007, 2011) the wren-spintail is vulnerable to habitat transformation and has been categorized as globally “near threatened” (Birdlife International 2010). The species is a partial migrant, most birds disappearing from breeding sites in central and southern Argentina and the winter population increasing substantially at the northern limit of the distribution (Isacch et al. 2004, Di Giacomo 2005, Cardoni et al. 2011, Isacch and Cardoni 2011).

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Saltmarshes in southeastern South America are inhabited by a relatively low number of bird species (Isacch et al. 2004, Greenberg and Maldonado 2006, Cardoni et al. 2007, 2011, Isacch and Cardoni 2011), but some of those species are highly dependent on this type of habitat (Greenberg and Maldonado 2006). The Bay-capped Wren-Spinetail, in particular, lives almost exclusively in saltmarshes dominated by the cordgrass *Spartina densiflora* (Remsen 2003, Isacch et al. 2004, Cardoni et al. 2007, Cardoni 2011). *Spartina densiflora* is widely distributed along the southeastern coast of South America, with larger extensions associated with brackish water along river mouths and in coastal lagoons from southern Brazil to northern Patagonia in Argentina (Bortolus 2006, Isacch et al. 2006). *S. densiflora* usually grows as a monospecific marsh (Isacch et al. 2006) whose vegetative structure resembles to tall grassland.

Like other tall grasslands of the Pampas region, coastal saltmarshes are being modified at an increasing rate (Costa et al. 2009), primarily by cattle grazing and burning (Isacch et al. 2004, Isacch and Cardoni 2011). Cattle grazing in this habitat has been increasing in the last few decades as a consequence of the development of new technologies that have resulted in an expansion of agriculture (Viglizzo et al. 2001) and a displacement of cattle grazing to marginal areas such as saltmarshes (Bilenca and Miñarro 2004). Livestock production in grassland generally associated with prescribed fire (Knapp et al. 1999). The use of prescribed fire to enhance vegetation for cattle results in loss and fragmentation of tall grasslands and has led to declines in populations of many grassland-dependent birds (Askins 1993, Vickery et al. 1994). Degradation of grasslands results from high intensity management of burning and grazing (Briggs et al. 2005, With et al. 2008), decreasing vegetation cover and homogenizing the landscape, thereby decreasing the biomass of foliar arthropods (Dennis et al. 2008), altering the abundance and richness of bird species (Gonnet 2001, Isacch and Martínez 2001, García et al. 2008), changing the suitability of the grassland for nesting and feeding birds (Vickery et al. 2001, Chase 2002, Gonnet 2001), and affecting breeding success (Sutter and Ritchison 2005) and nest predation (Zalba and Cozzani 2004).

The Bay-capped Wren-Spinetail is sensitive to a decrease of tall grass cover, by either natural (e.g., bioturbation by burrowing crabs; Cardoni et al. 2007) or anthropogenic (e.g., fire and cattle grazing; Isacch and Martínez 2001, Isacch et al. 2004, Isacch and Cardoni 2011) causes. In other cases, anthropogenic disturbance may enhance habitat for the Bay-capped Wren-Spinetail, as in the case of *Spartina alterniflora* marshes of northern Patagonia, which the wren-spinetail colonizes when discharged sewage increases vegetation cover and height (Cardoni et al. 2011).

Because coastal saltmarshes in Argentina are marginally productive for livestock, there is considerable variation in the intensity of their use by ranchers (Marino 2008). Thus there are saltmarshes grazed and burned at different intensities. Given this context, the goal of our study was to assess how grazing affects populations of the Bay-capped Wren-Spinetail. Specifically, we (1) estimated population densities

under different intensities of fire and cattle grazing, (2) studied selection of nesting habitat and nesting success, and (3) conducted nest-predation experiments to quantify predation rates and identify predators.

METHODS

STUDY SITE

Our study site was the Mar Chiquita coastal lagoon (37° 40' S, 57° 23' W), a UNESCO Biosphere Reserve in Argentina (Isacch 2008). The main habitats around the lagoon are mudflats and plains covered with halophytic plant communities dominated by *Spartina densiflora* (Isacch et al. 2006). Human activities in the region are mainly agriculture and livestock production (León et al. 1984). The reserve consists of government property (national, provincial, and municipal), where land use is restricted, and private property (~60% of the area of the reserve), consisting of ranches dedicated mainly to livestock production with no constraints on management (Isacch 2008).

BIRD AND VEGETATION SURVEYS

We carried out our study from October 2006 to January 2008 in *Spartina densiflora* marshes with different intensities of land use determined by the combined effect of burning and cattle grazing. Bird and vegetation surveys extended from December 2006 to November 2007. We defined three categories of land use: (1) high intensity, fields burned systematically year round and with higher livestock density (~1.3 cows ha⁻¹); (2) low intensity, fields burned only in winter and with lower livestock density (~0.5 cows ha⁻¹); (3) ungrazed, fields without grazing and fire in the previous 6 years. The livestock were present year round in the plots of both high- and low-intensity use. We surveyed for Bay-capped Wren-Spinetails in 24 randomly distributed fixed-width strip transects (Bibby et al. 1997) 100 m in length and 60 m in width. Transects were distributed equally in each land-use category (eight transects per category) and separated from each other by at least 200 m. We surveyed each transect four times per season (summer, autumn, winter, and spring) and the datum for each transect by season was the average number of birds over the four surveys. Transects were positioned in at least two areas per category of land use. We were cautious to distribute transects through areas of similar environmental conditions to avoid covariation between physical variables (such as salinity and flooding) and land uses. Birds were surveyed within 4 hr after sunrise and during the last 3 hr of daylight. We did not count birds when the wind speed was higher than 20 km hr⁻¹ or on rainy days (Conner and Dickson 1980). Vegetation surveys included two samples in quadrats of 1 by 1 m in each bird transect and were repeated in each of the four seasons. In each sample we recorded the percentage cover of tall grass and the mean height (cm) of the tall-grass stratum. We averaged the two vegetation samples per transect to obtain one measurement for each transect.

We used a two-way analysis of variance (ANOVA; Zar 1999) to evaluate the null hypothesis of no difference in vegetation variables (cover and height) by season (summer, autumn,

winter, and spring) and category of land use (ungrazed, low intensity and high intensity), applying an a posteriori Tukey test when necessary (Zar 1999). Because counts of birds per transect were very low (0 to 2 birds in most cases), the data are clearly discrete (most values are 0, 1, or 2) and not normally distributed (most values are closer to 0 and very few are higher than 2, resulting in an asymmetrical distribution). Then we pooled counts of birds by land-use category and compared the number of birds in areas of low-intensity use with those in ungrazed areas by season with a chi-squared test. We recorded frequently burned and heavily grazed marshes with no Bay-capped Wren-Spinetails.

NEST-SITE SELECTION AND BREEDING SUCCESS

We systematically searched for nests during two breeding seasons (October 2006–January 2007; October 2007–January 2008), in marshes of all three intensities of use. We marked the nests, recorded their coordinates by GPS, and visited them at intervals of 2–4 days to record number of eggs, dates of hatching and fledging, and instances of predation, following standard procedures to avoid attracting predators to nests (Martin and Geupel 1993). We inferred predation when nests, eggs, or nestlings were damaged or removed between visits. We considered a nest successful if one or more young fledged. With this information, we estimated the clutch size, hatching success, and fledging success (Bart and Robson 1982, Klett et al. 1986, Martin and Geupel 1993). For each nest, we recorded its height above the ground, height of vegetation over the nest, and cover and height of vegetation around the nest. We also recorded the area and perimeter of the patch of tall grass in which the nest was found and the distance from the nest to the patch's edge. Our study area consists of both continuous and patchy grasslands, the latter being a mosaic of patches of tall grass of various sizes surrounded by a matrix of short grass maintained by fire and grazing. Continuous grassland and patches were almost evenly distributed, so we assumed connectivity among patches in the study area was similar. In addition, to evaluate nest-site selection within a patch, we recorded vegetation height and cover in a 1 by 1-m quadrat placed at random in patches with nests.

We used a *t*-test to evaluate the null hypothesis of no difference of nest variables between marshes with and without cattle grazing (Zar 1999). We also ran a two-way ANOVA to evaluate the null hypothesis of no difference in nest-site selection by comparing the vegetation structure at the nest site with that at a random site within the same vegetation patch and between marshes with and without cattle grazing.

We used nest-survival models in the program Mark (White and Burnham 1999) to estimate daily survival rates and to test the effects of land-use intensity on these rates. We calculated Akaike's information criterion (AIC_c), the lowest AIC_c indicating the best, most parsimonious model (Burnham and Anderson 1998) as well as Akaike weights, which represent the relative likelihood of the specified model, given the data, and quantifies the difference in AIC_c values among competing models. The sum of Akaike weights among all models in an analysis equals one. We based statistical inference on these

AIC_c model-selection procedures (Burnham and Anderson 1998). We considered a model to have strong support if it was within 2 AIC_c of the model having the lowest AIC_c value and a variable to have strong support if the sum of Akaike weights for all models containing that variable was >0.9 .

NEST-PREDATION EXPERIMENT

For a better interpretation of the results of reproductive behavior, we conducted an experiment to determine rates of predation of artificial nests placed at different heights from the ground. We selected nest height above the ground because that variable explained the survival of the natural nests (see Results). Artificial nests are a useful, nondestructive tool for testing ecological and behavioral mechanisms that influence nesting birds' risk of predation (Major and Kendal 1996, Bayne and Hobson 1999). Potentially predatory rodents that inhabit *Spartina densiflora* marshes are *Akodon azarae* (Azara's Grass Mouse) and *Oxymycterus rufus* (Red Hociudo), whose average population densities are 89 ± 33 individual ha^{-1} and 30 ± 14 individual ha^{-1} , respectively (Baladrón 2010). Potential bird predators were *Milvago chimango* (Chimango Caracara), *Circus buffoni* (Long-winged Harrier), and *Embernagra platensis* (Great Pampa-Finch) (Cardoni 2011). We manufactured artificial nests from stems of *Spartina densiflora*, the same material Bay-capped Wren-Spinetails use (Narosky 1973, Fraga and Narosky 1985). We set 54 artificial nests in an 8-ha patch of *Spartina densiflora* (mean vegetation cover 81%, mean height 85 cm) at three heights above the ground: (1) 0 cm, on the ground; (2) 17 cm, the average height of Bay-capped Wren-Spinetail nests observed in the field; (3) 34 cm, twice the average observed height. Nests were placed in groups of three, one per category of nest height, separated by 1 m. Groups were 25 m apart. Each nest contained one plasticine egg of the same size (17.7×14 mm) and color as the Bay-capped Wren-Spinetail's eggs (Fraga and Narosky 1985) and was firmly attached to the nest by a thin wire. We considered a nest was to have been preyed upon if the plasticine egg was missing or any mark was left on the egg. Using the characteristics of the marks left on the plasticine eggs, we identified whether the predator was a bird or a mammal, comparing tooth marks on the plasticine eggs with rodent skulls in the collection at the Vertebrate Laboratory of the Universidad Nacional de Mar del Plata. We used a chi-squared test to evaluate the null hypothesis of no difference in the frequency of predation by nest height (Zar 1999).

RESULTS

VEGETATION AND BAY-CAPPED WREN-SPINETAIL ABUNDANCE

The vegetation consisted almost exclusively of *Spartina densiflora*; in only 2% of plots did we record *Sarcocornia perennis*. The cover of tall grass varied by season and category of land use (two-way ANOVA; season: $F_3 = 3.36$, $P < 0.05$; land use: $F_2 = 1292.75$, $P < 0.0001$) and there is an interaction between the two variables ($F_6 = 2.47$, $P < 0.05$; Table 1). Cover of tall grass was greater in summer than in winter but

TABLE 1. Vegetation cover and height of *Spartina densiflora* marshes by season under different regimes of cattle grazing and prescribed fire.

| | Vegetation cover (%) | | Vegetation height (cm) | |
|----------------|----------------------|------|------------------------|------|
| | Mean | SD | Mean | SD |
| Summer | | | | |
| Non-grazed | 96.8 | 2.8 | 93.8 | 5.7 |
| Low intensity | 81.4 | 6.6 | 84.6 | 8.7 |
| High intensity | 2 | 1.7 | 2.9 | 2 |
| Autumn | | | | |
| Non-grazed | 97.5 | 2.5 | 90.2 | 4.9 |
| Low intensity | 77.5 | 10.3 | 60.4 | 21.9 |
| High intensity | 1.1 | 1.3 | 1.6 | 2 |
| Winter | | | | |
| Non-grazed | 96.4 | 4.1 | 91.2 | 4.7 |
| Low intensity | 64.3 | 13.6 | 69.7 | 9 |
| High intensity | 1.1 | 1.2 | 1.6 | 2 |
| Spring | | | | |
| Non-grazed | 99.6 | 0.9 | 89.7 | 6.1 |
| Low intensity | 73.6 | 12.1 | 79.4 | 5.1 |
| High intensity | 5 | 4.7 | 4.6 | 4.3 |

not different from that in autumn and spring. It was greatest in ungrazed marshes and lowest in marshes grazed at high intensity. This pattern applied in autumn, winter, and spring, but in summer cover in ungrazed and low-intensity plots was similar (Table 2). The height of the tall grass stratum followed a pattern similar to that of cover, varying by season, land use, and an interaction of season and land use (two-way ANOVA; season: $F_3 = 4.74, P < 0.005$; land use $F_2 = 778.75, P < 0.0001$; season \times land use $F_6 = 3.36, P < 0.01$; Table 1). The grass was higher in summer and spring, highest in ungrazed marshes, and lowest in marshes grazed

at high intensity. It was highest in winter and spring in ungrazed plots (Table 2).

We did not record the Bay-capped Wren-Spinetail in marshes grazed and burned at high intensity, so we excluded this land-use category from the following analysis. The abundance of the Bay-capped Wren-Spinetail (individuals per transect) in areas grazed at low intensity and ungrazed areas did not differ (chi-squared test; summer: $\chi^2 = 9.2, df = 4, P = 0.06$; autumn: $\chi^2 = 4, df = 3, P = 0.26$; winter: $\chi^2 = 2, df = 2, P = 0.37$; spring: $\chi^2 = 1.87, df = 3, P = 0.61$; Fig 1). The abundance of the Bay-capped Wren-Spinetail tended to be higher during spring and summer and lower during winter (Fig. 1).

NEST-HABITAT SELECTION AND BREEDING SUCCESS

During the breeding seasons of 2006–07 and 2007–08, we found 52 nests of the Bay-capped Wren-Spinetail in *Spartina densiflora* marshes grazed at low intensity or not at all (Fig. 2). In the marshes burned and grazing frequently we found no nests, since tall grass cover was completely removed and the habitat’s physiognomy was that of a short grassland (grass always <15 cm), so we present results of marshes grazed at low intensity and ungrazed marshes only.

Of the 52 nests, 22 were in saltmarshes with no grazing and 30 were in marshes under low intensity grazing. Nests contained more eggs in 2007–08 (mean = 3.50, SD = 0.57) than in 2006–07 (mean = 3.07, SD = 0.64; $t = 2.15, df = 41, P < 0.05$). Other variables recorded were similar in the two years. Five nests failed in 2006–07 (25%, 2 in ungrazed marshes and 3 in marshes grazed at low intensity), and 19 nests failed in 2007–08 (59%, 10 in ungrazed marshes and 9 in marshes grazed at low intensity).

The cover and height of vegetation at Bay-capped Wren-Spinetail nests in ungrazed and lightly grazed marshes were similar. Vegetation cover at the nest differed from that at a

TABLE 2. A posteriori pairwise comparisons by the Tukey test for the interaction between land use and season after a two-way ANOVA test for vegetation cover (below diagonal) and height (above diagonal). Land-use categories correspond with three intensities of cattle grazing and prescribed fire (NG, not grazed; low, low-intensity use; high, high-intensity use). Seasons: S, summer; A, autumn; W, winter; Sp, spring. Where a difference is significant, “<” or “>” denotes lower or higher mean values between y and x axis, respectively; “ns,” not significant.

| | S-NG | S-Low | S-High | A-NG | A-Low | A-High | W-NG | W-Low | W-High | Sp-NG | Sp-Low | Sp-High |
|---------|------|-------|--------|------|-------|--------|------|-------|--------|-------|--------|---------|
| S-NG | | ns | > | ns | > | > | ns | > | > | ns | ns | > |
| S-Low | < | | > | ns | > | > | ns | ns | > | ns | ns | > |
| S-High | < | < | | < | < | ns | < | < | ns | < | < | ns |
| A-NG | Ns | > | > | | > | > | ns | > | > | ns | ns | |
| A-Low | < | ns | > | < | | > | < | ns | > | < | < | > |
| A-High | < | < | ns | < | < | | < | > | ns | < | < | ns |
| W-NG | Ns | > | > | ns | > | > | | > | > | ns | ns | > |
| W-Low | < | > | > | < | < | > | < | | > | < | ns | > |
| W-High | < | < | ns | < | < | ns | < | < | | < | < | ns |
| Sp-NG | Ns | > | > | ns | > | > | ns | > | > | | ns | > |
| Sp-Low | < | ns | > | < | ns | > | < | ns | > | < | | > |
| Sp-High | < | < | ns | < | < | ns | < | < | ns | < | < | |

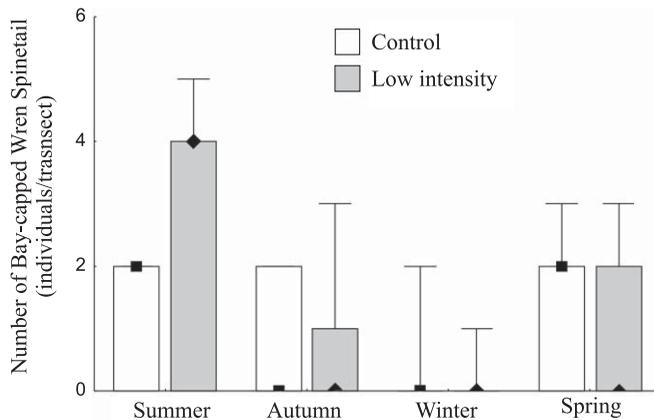


FIGURE 1. Number of Bay-capped Wren-Spinetails counted in saltmarshes with light and no grazing by season. Boxes represent the 25% and 75% quantiles, whiskers represent minima and maxima, and the median is the point within the box.

random site within the same patch (two-way ANOVA; site: $F_{1,68} = 0.01$, $P = 0.95$; grazing: $F_{1,68} = 25.84$, $P < 0.0001$; site \times grazing: $F_{1,68} = 15.76$, $P < 0.001$, Fig. 3A). Vegetation height at the nest site was similar in ungrazed and lightly grazed marshes, but at random sites within the patch vegetation was

higher in the former (two-way ANOVA; site: $F_{1,52} = 4.54$, $P < 0.05$; grazing: $F_{1,52} = 5.10$, $P < 0.05$; site \times grazing: $F_{1,52} = 5.15$, $P < 0.05$, Fig. 3B). Patches were larger in ungrazed marshes (mean = 5.1 ha, SD = 1.8) than in lightly grazed marshes (mean 1 ha, SD = 0.9; $t_{41} = 9.7$, $P < 0.0001$). The average length of a patch's perimeter was also greater in ungrazed marshes (mean = 1.6 km, SD = 0.6) than in lightly grazed marshes (mean = 2 km, SD = 0.01; $t_{41} = 6.23$, $P < 0.0001$).

Daily survival rates of Bay-capped Wren-Spinetail nests were 0.967 and 0.987 in 2006–07 and 2007–08, respectively; the overall rate was 0.974. The most parsimonious fixed-effects model of nest survival included the variables year and nest height. This model was 0.64 units better than the second model, which included only the year. A third model that included only the nest height was 0.77 units worse than the first model (Table 3). The best model had a positive slope ($\beta = 0.43$, SE = 0.28), indicating a gradual increase in survival with nest height. In ungrazed and lightly grazed marshes, nest height in the two years was similar (ungrazed: $t_{19} = 1.20$, $P = 0.24$; lightly grazed: $t_{21} = 0.27$, $P = 0.79$). The placement of nests lightly grazed marshes (mean = 19.30, SD = 8.25) averaged higher than that in ungrazed marshes (mean = 14.81, SD = 5.09; $t_{42} = 2.15$, $P = 0.037$).

NEST-PREDATION EXPERIMENTS

The nest-predation experiments were successful in demonstrating an interaction between nest height and predation.

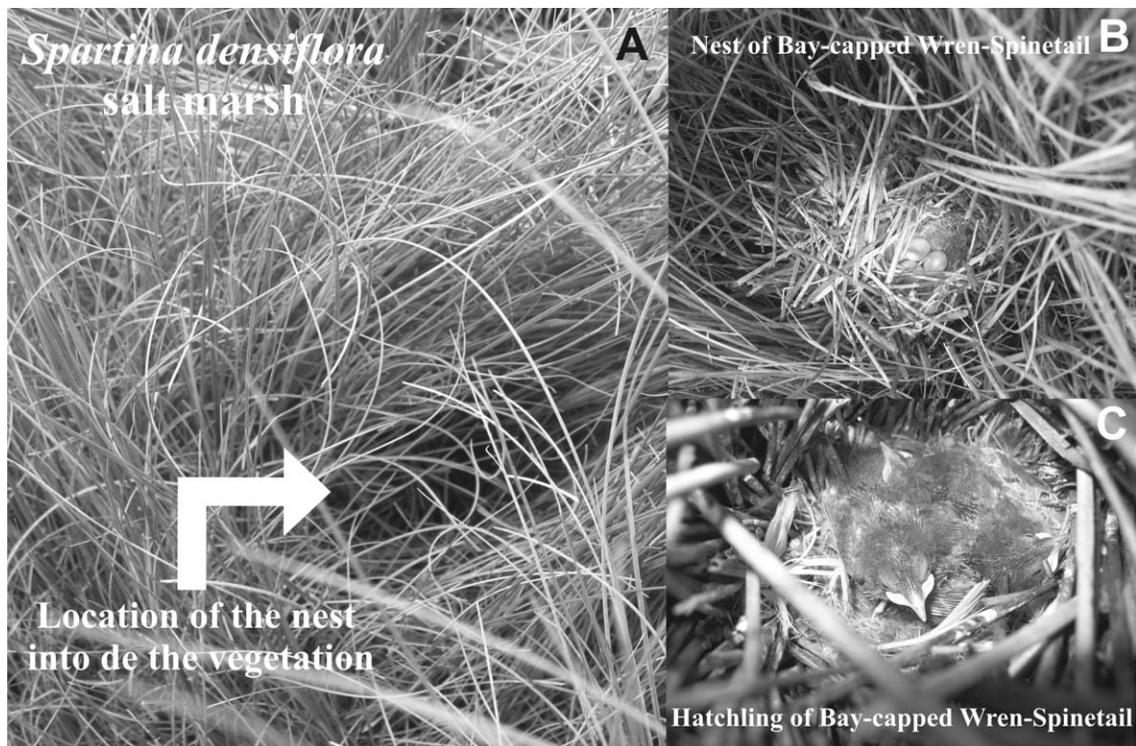


FIGURE 2. Location of a Bay-capped Wren-Spinetail nests inside the vegetation of a *Spartina densiflora* marsh. (A) A nest with three eggs; (B) a nest with hatchlings (C).

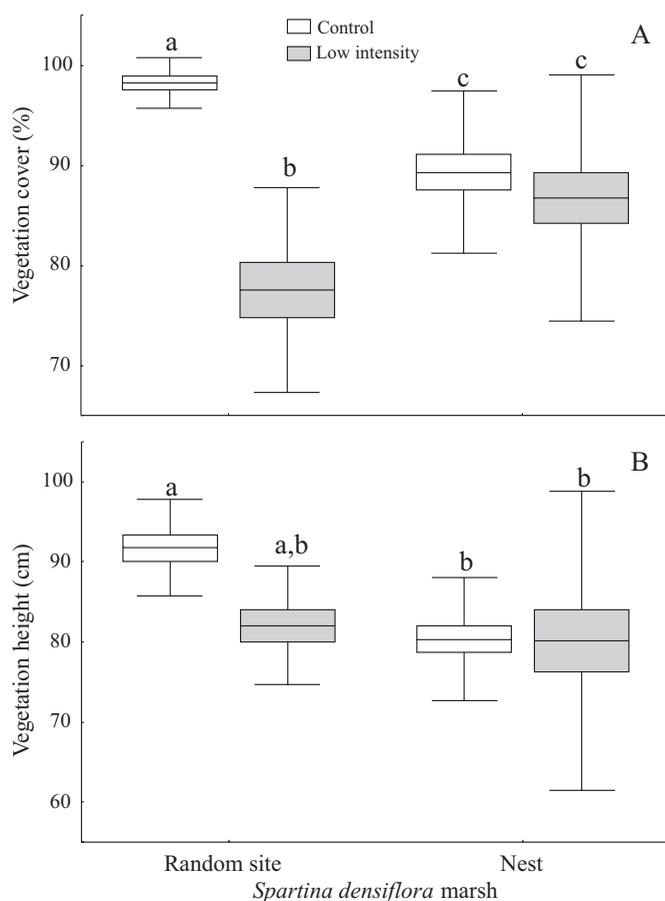


FIGURE 3. Vegetation cover (A) and height (B) of grass in grazed (gray boxes) and ungrazed (white boxes) marshes of *Spartina densiflora* at nests of the Bay-capped Wren-Spinetail and at random points away from the nest. Boxes represent the standard error, whiskers the standard deviation, and the lines inside the boxes the average. Different letters above the plot represent significant differences (a posteriori Tukey test, $P < 0.05$).

Predation was greater on nests at the ground level (18/18) and at the highest level (18/18) than on those at the middle level (4/18; $\chi^2 = 8.6$, $df = 2$, $P = 0.013$). Furthermore, there was a difference in the frequency of the various predators: plasticine eggs in nests at the ground and middle levels had only rodent marks, whereas nests at the highest level had both rodent (60%) and bird marks (40%) ($\chi^2 = 12.52$, $df = 4$, $P = 0.014$).

DISCUSSION

The Bay-capped Wren-Spinetail showed a strong dependence on saltmarshes in which *Spartina densiflora* grows dense (>50% of the ground area) and tall (>70 cm). The differences in cover of tall grass between grazing regimes of low and high intensity can be better explained by frequency of fire than by rate of grazing. The Bay-capped Wren-Spinetail was absent from marshes where the pressure of grazing (~ 1.3 cows ha^{-1})

TABLE 3. Results of selection of models of survival of Bay-capped Wren-Spinetail nests. Models are sorted in increasing order according to ΔAIC_c . K , number of model parameters; Dev, the model's deviance; ΔAIC_c , the difference between the AIC_c value for the specified model and the model with the lowest AIC_c ; w_i , the model's weight. Survival of nests was modeled with the incorporation of covariates and compared with the null model of constant survival, $S(.)$. The following variables were included in the analysis: VC, vegetation cover; VH, vegetation height; NH, nest height above the ground; HON, vegetation height over the nest; AREA, patch area; PERI, patch perimeter; DNE, distance from the nest to the vegetation patch's edge; YEAR, breeding season; GRAZED, grazed by cattle or not.

| | K | Dev | ΔAIC_c | w_i |
|-------------------------|-----|---------|----------------|-------|
| $S(YEAR + NH)$ | 3 | 887 699 | 0 ^a | 0.17 |
| $S(YEAR)$ | 2 | 914 248 | 0.64 | 0.12 |
| $S(NH)$ | 2 | 915 577 | 0.77 | 0.11 |
| $S(HON)$ | 2 | 921 777 | 13.90 | 0.08 |
| $S(.)$ | 1 | 942 271 | 14.27 | 0.08 |
| $S(DNE)$ | 2 | 926 320 | 18.44 | 0.06 |
| $S(NH + VH)$ | 3 | 906 746 | 19.05 | 0.06 |
| $S(YEAR + GRAZED + NH)$ | 4 | 887 698 | 20.24 | 0.06 |
| $S(YEAR + GRAZED)$ | 3 | 910 606 | 22.91 | 0.05 |
| $S(VH)$ | 2 | 933 046 | 25.16 | 0.05 |
| $S(AREA)$ | 2 | 937 516 | 29.63 | 0.04 |
| $S(PERI)$ | 2 | 938 677 | 30.80 | 0.03 |
| $S(GRAZED)$ | 2 | 940 082 | 32.20 | 0.03 |
| $S(VC)$ | 2 | 940 405 | 32.52 | 0.03 |

^aMinimum value of $AIC_c = 948 062$.

and frequency of fire were high. Grazing with low density of livestock (~ 0.5 cows ha^{-1}) and infrequent fire did not affect the nesting success of the Bay-capped Wren-Spinetail. Under the latter regime, grazing generated a mosaic of patches of tall and short grass in which the ground cover and height of patches of tall grass was less than in ungrazed marshes. This difference in vegetation affected where birds placed their nests: nests were located higher in lightly grazed marshes than in ungrazed marshes. Nest height was the variable that best explained nest failure, which was caused mostly by predation. Lower nests were highly vulnerable to predation by rodents, whereas higher nests were depredated by both birds and rodents.

The response of the Bay-capped Wren-Spinetail to vegetation changes generated by anthropogenic disturbance (e.g., fire, cattle grazing, sewage discharge) has been reported in several studies on grasslands and saltmarshes in the Pampas (Isacch and Martínez 2001, Isacch et al. 2004, Cardoni et al. 2011, Isacch and Cardoni 2011). In all cases the birds responded to a single habitat variable such as the percentage cover of tall grass (i.e., high cover of grasses >70 cm tall). This species is a partial migrant, most birds vacating central and southern Argentina in the nonbreeding season (Isacch and Martínez 2001, Isacch et al. 2004, Isacch and Cardoni 2011, Cardoni 2011) and increasing in numbers in the northern

part of its range (Remsen 2003, Di Giacomo 2005). Different responses of species to habitat loss and fragmentation are generally related to interspecific variation in ability to persist in local patches and to colonize patches by moving across a fragmented landscape (Vos et al. 2001). Because of the dependence of Bay-capped Wren-Spinetail on tall grassland and its partial migration, conservation of the species calls for the preservation of tall grasslands, not only in breeding areas but also along its routes of migration.

Microhabitat structure and plant-species composition are the main factors in nest-site selection in birds (Misenhelter and Rotenberry 2000, Gjerdrum et al. 2005). Therefore, disturbances that affect these habitat components are expected to have consequences on birds' reproductive performance. In both lightly grazed and ungrazed *Spartina* marshes, nesting Bay-capped Wren-Spinetails selected sites with similar values of cover of tall grass and height of grass. This result suggests a strong selectivity for nest sites with specific microhabitat characteristics even when the surrounding vegetation has different habitat characteristics. Although we found that Bay-capped Wren-Spinetails selected similar values of vegetation features in ungrazed and grazed saltmarshes, the quality of the nest site could be dissimilar in marshes under different grazing regimes. The quality of nest sites not only depends on the vegetation features, it also can be affected by microclimate, food availability, and nest predation (Stauffer and Best 1982). Therefore, the quality of Bay-capped Wren-Spinetail nest sites could be different in ungrazed and grazed marshes. For example, livestock density may affect the numbers and biomass of foliar arthropods, affecting insectivorous birds of conservation concern (Dennis et al. 2008). The Bay-capped Wren-Spinetail is an insective that gleans invertebrates from the foliage (e.g., Remsen 2003, Dias et al. 2009; Cardoni, pers. obs.). Nest survival in marshes with and without cattle grazing did not differ, but we do not know if the performance of fledglings may be affected by any of these factors.

Birds apparently respond to grazing and fire mostly because of their effect on vegetation (Bock and Webb 1984). Changes in the cover and height of vegetation affect the rate of nest predation (Kantrud and Kologiski 1982, Saab et al. 1995, Willson et al. 2001), which is the main cause of birds' reproductive failure (Ricklefs 1969). Saltmarshes dominated by *Spartina* are lower (~0.8 m) than tall grasslands or other marshes (~1.5 m; Post et al. 1983, Isacch et al. 2004, Reinert 2006). Consequently the range of heights in which the nest may be placed is relatively narrow, entailing a compromise between the effect of flooding (affecting nests placed lower) and the effect of predation (affecting nests placed higher). The height above ground was the variable that affected success of Bay-capped Wren-Spinetail nests (see Table 2); the probability of predation of lower nests is higher. The experiment with artificial nests showed lower predation rates at middle heights (17 cm, mean height of real nests of the Bay-capped Wren-Spinetail). Predators on higher nests included both birds and rodents, but only rodents depredated nests on the ground and

at intermediate heights. The relationship between type of predator and predation intensity at different heights could explain nest survival being highest at intermediate heights. Rodents are terrestrial predators, and the intensity of predation by them decreases as nest height increases. By contrast, the intensity of predation by birds, which reach the nest from the air, decreases with the nest's height from the canopy of the grassland to the ground (Kleindorfer et al. 2005). In coastal saltmarshes, flooding is an additional cause of nest failure, the chance of failure being greater for lower nests (DiQuinzio et al. 2002, Gjerdrum et al. 2005). Therefore, for saltmarsh birds, nest height is an important variable influencing nest failure by both predation and flooding.

Understanding how salt-marsh birds respond to current management is essential for their conservation within the context of these human-dominated landscapes. In the Pampas, the Bay-capped Wren-Spinetail is the bird most closely associated with coastal saltmarshes, the most abundant species associated with *Spartina densiflora* habitats (Isacch et al. 2004, Cardoni et al. 2007, Cardoni 2011, Isacch and Cardoni 2011). In this region, coastal saltmarshes include extensive areas of *S. densiflora* (i.e., Samborombón Bay and Mar Chiquita; Isacch et al. 2006). These habitats have been declared "important bird areas" (Di Giacomo 2005) and "valuable grassland areas" (Bilenca and Miñarro 2004). Grazing by domestic livestock on these habitats has been increasing in recent years as cattle raising has been displaced by the expansion of croplands (Paruelo et al. 2005). Saltmarshes are one of the last refuges for birds of tall grasslands in the Pampas. Our results indicate that light grazing and burning during winter may be compatible with the presence and reproduction of the most specialized and threatened bird inhabiting *S. densiflora* marshes (Cardoni 2011). Thus livestock production with a modest effect on the habitat may be a viable alternative for the sustainable use of coastal saltmarshes of southeastern South America.

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LITERATURE CITED

- ASKINS, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology* 11:1–34.
- BALADRÓN, A. 2010. Impacto de la depredación de aves rapaces sobre pequeños mamíferos en el Sudeste bonaerense. Ph.D. thesis, Universidad Nacional de Mar del Plata, Buenos Aires, Argentina.
- BART, J., AND D. S. ROBSON. 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63:1078–1090.
- BAYNE, E. M., AND K. A. HOBSON. 1999. Do clay eggs attract predators to artificial nests? *Journal of Field Ornithology* 70:1–7.

- BIBBY, C. J., N. D. BURGESS, AND D. HILL. 1997. Bird census techniques. Academic Press, London.
- BILENCA, D., AND F. MIÑARRO. 2004. Identificación de áreas valiosas de pastizales en las pampas y campos Argentinos, Uruguay y sur de Brasil (AVPs). Fundación Vida Silvestre, Buenos Aires, Argentina.
- BIRDLIFE INTERNATIONAL [ONLINE]. 2010. Species factsheet: *Spartonoica maluroides*. <<http://www.birdlife.org>> (16 June 2010).
- BOCK, C. E., AND B. WEBB. 1984. Birds as grazing indicator species in southeastern Arizona. *Journal of Wildlife Management* 48:1045–1049.
- BORTOLUS, A. 2006. The austral cordgrass *Spartina densiflora* Brong.: its taxonomy, biogeography and natural history. *Journal of Biogeography* 33:158–168.
- BRIGGS, J. M., A. K. KNAPP, J. M. BLAIR, J. L. HEISLER, G. A. HOCH, M. S. LETT, AND J. K. MCCARRON. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243–254.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- CANEVARI, M., P. CANEVARI, G. R. CARRIZO, G. HARRIS, J. RODRÍGUEZ MATA, AND R. J. STRANECK. 1991. Nueva guía de las aves argentinas, vol. 2. Fundación Acindar, Buenos Aires, Argentina.
- CARDONI, D. A. 2011. Adaptaciones evolutivas y respuestas a la actividad antrópica de aves de marismas del atlántico sudoccidental: un análisis a diferentes escalas temporales. Ph.D. thesis, Universidad Nacional de Mar del Plata, Buenos Aires, Argentina.
- CARDONI, D. A., J. P. ISACCH, AND O. O. IRIBARNE. 2007. Indirect effects of the burrowing crab (*Chasmagnathus granulatus*) in the habitat use of saltmarsh birds. *Estuaries and Coast* 30:382–389.
- CARDONI, D. A., J. P. ISACCH, M. E. FANJUL, M. ESCAPA, AND O. O. IRIBARNE. 2011. Relationship between anthropogenic sewage discharge, marsh structure and bird assemblages in a SW Atlantic saltmarsh. *Marine Environmental Research* 71:122–130.
- CHASE, M. K. 2002. Nest site selection and nest success in a Song Sparrow population: the significance of spatial variation. *Condor* 104:103–116.
- CONNOR, R. N., AND J. G. DICKSON. 1980. Strip transect sampling and analysis for avian habitat studies. *Wildlife Society Bulletin* 8:4–10.
- COSTA, C. S. B., O. O. IRIBARNE, AND J. M. FARINA. 2009. Human impacts and threats to the conservation of South American salt marshes, p. 337–359. In B. R. Silliman, E. D. Grosholz, and M. D. Bertness [EDS.], *Human impacts on salt marshes: a global perspective*. University of California Press, Los Angeles.
- DENNIS, P., J. SKARTVEIT, D. I. MCCracken, R. J. PAKEMAN, K. BEATON, A. KUNAVER, AND D. M. EVANS. 2008. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology* 45:279–287.
- DI GIACOMO, A. S. 2005. Áreas importantes para la conservación de las aves en la Argentina. Sitios prioritarios para la conservación de la biodiversidad. *Temas de Naturaleza y Conservación* 5. Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- DIAS, R. A., M. S. S. GONÇALVES, AND V. A. G. BASTAZINI. 2009. First nesting record of the Bay-capped Wren-Spintail *Spartonoica maluroides* (Aves, Furnariidae) in Brazil, with nest and nesting descriptions and notes on breeding behavior. *Iheringia Serie Zoologia* 99:449–455.
- DIQUINZIO, D. A., P. W. C. PATON, AND W. R. EDDLEMAN. 2002. Nesting ecology of Saltmarsh Sharp-tailed Sparrows in a tidally restricted salt marsh. *Wetlands* 22:179–185.
- FRAGA, R., AND S. NAROSKY. 1985. Nidificación de aves Argentinas (Formicariidae a Cinclidae). Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- GARCÍA, C., D. RENISON, A. M. CINGOLANI, AND E. FERNÁNDEZ-JURICIC. 2008. Avifaunal changes as a consequence of large-scale livestock exclusion in the mountains of central Argentina. *Journal of Applied Ecology* 45:351–360.
- GJERDRUM, C., C. S. ELPHICK, AND M. RUBEGA. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: the importance of nest habitat, timing, and study site differences. *Condor* 107:849–862.
- GONNET, J. M. 2001. Influence of cattle grazing on population density and species richness of granivorous birds (Emberizidae) in the arid plain of the Monte, Argentina. *Journal of Arid Environments* 48:569–579.
- GREENBERG, R., AND J. E. MALDONADO. 2006. Diversity and endemism in tidal marsh vertebrates. *Studies in Avian Biology* 32:32–53.
- ISACCH, J. P. 2008. Implementing the biosphere reserve concept: the case of Parque Atlántico Mar Chiquito biosphere reserve from Argentina. *Biodiversity and Conservation* 17:1799–1804.
- ISACCH, J. P., AND D. A. CARDONI. 2011. Different grazing strategies are necessary to conserve endangered grassland birds in short and tall salty grasslands of the flooding Pampas. *Condor* 113:724–734.
- ISACCH, J. P., AND M. M. MARTÍNEZ. 2001. Estacionalidad y relaciones con la estructura del hábitat de la comunidad de aves de pastizales de paja colorada (*Paspalum quadrifarium*) manejados con fuego en la Provincia de Buenos Aires, Argentina. *Ornitología Neotropical* 12:345–354.
- ISACCH, J. P., C. S. B. COSTA, L. RODRÍGUEZ-GALLEGO, D. CONDE, M. ESCAPA, D. A. GAGLIARDINI, AND O. O. IRIBARNE. 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *Journal of Biogeography* 33:888–900.
- ISACCH, J. P., S. HOLZ, L. RICCI, AND M. M. MARTÍNEZ. 2004. Post-fire vegetation change and bird use of a salt marsh in coastal Argentina. *Wetlands* 24:235–243.
- KANTRUD, H. A., AND R. L. KOLOGISKI. 1982. Effects of soils and grazing on breeding birds of uncultivated upland grasslands of the northern Great Plains. *Wildlife Research Report* 15. U.S. Fish and Wildlife Service, Washington, DC.
- KLEINDORFER, S., B. FESS, AND H. HOI. 2005. Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Animal Behavior* 69:307–313.
- KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. *Resource Publication* 158. U.S. Fish and Wildlife Service, Washington, DC.
- KNAPP, A. K., J. M. BLAIR, J. M. BRIGGS, S. L. COLLINS, D. C. HARTNETT, L. C. JOHNSON, AND E. G. TOWNE. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49:39–50.
- LEÓN, R. J. C., G. M. RUSCH, AND M. OESTERHELD. 1984. Pastizales pampeanos—impacto agropecuario. *Phytocoenología* 12: 201–218.
- MAJOR, R., AND C. KENDAL. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138:298–307.
- MARINO, G. D. [ED.]. 2008. Buenas prácticas ganaderas para conservar la vida silvestre de las pampas. Una guía para optimizar la producción y conservar la biodiversidad de los pastizales de la Bahía Samborombón y la cuenca del Río Salado. Aves Argentinas, Buenos Aires, Argentina.

- MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- MISENHELTER, M. D., AND J. T. ROTENBERRY. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81:2892–2901.
- NAROSKY, S. 1973. Observations on the nesting of *Spartonoica maluroides*. *Ibis* 115:142–143.
- PARUELO, J. M., J. P. GUERSCHMAN, AND S. R. VERÓN. 2005. Expansión agrícola y cambios en el uso del suelo. *Ciencia Hoy* 15:14–23.
- POST, W., J. S. GREENLAW, T. L. MERRIAM, AND L. A. WOOD. 1983. Comparative ecology of northern and southern populations of the Seaside Sparrow, p. 123–136. *In* T. L. Quay, J. B. Funderburg, Jr., D. S. Lee, E. F. Potter, and C. S. Robbins [EDS.], *The Seaside Sparrow, its biology and management*. North Carolina Biological Survey, Raleigh, NC.
- REINERT, S. E. 2006. Avian nesting response to tidal-marsh flooding: literature review and a case for adaptation in the Red-winged Blackbird. *Studies in Avian Biology* 32:77–95.
- REMSEN, J. 2003. Family Furnariidae (Ovenbirds), p. 162–357. *In* J. del Hoyo, A. Elliott, and D. Christie [EDS.], *Handbook of the birds of the world, vol. 8: broadbills to tapaculos*. Lynx Edicions, Barcelona, Spain.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1–48.
- RIDGELY, R. S., AND G. TUDOR. 1994. *The birds of South America: the suboscine passerines*. University of Texas Press, Austin, TX.
- SAAB, V. A., C. E. BOCK, T. D. RICH, AND D. S. DOBKIN. 1995. Livestock grazing effects in western North America, p. 311–353. *In* T. E. Martin, and D. M. Finch [EDS.], *Ecology and management of neotropical migratory birds: a synthesis and review of critical issues*. Oxford University Press, New York.
- STAUFFER, D. F., AND L. B. BEST. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. *Wilson Bulletin* 94:329–337.
- SUTTER, B., AND G. RITCHISON. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. *Journal of Field Ornithology* 76:345–351.
- VICKERY, J. A., J. R. TALLOWIN, R. E. FEBER, E. J. ASTERAKI, P. W. ATKINSON, R. J. FULLER, AND V. K. BROWN. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38:647–664.
- VICKERY, P. D., M. L. HUNTER, AND S. M. MELVIN. 1994. Effects of habitat area on the distribution of grassland birds in Maine. *Conservation Biology* 8:1087–1097.
- VIGLIZZO, E. F., F. LECTORA, A. J. PORDOMINGO, J. N. BERNARDOS, Z. E. ROBERTO, AND H. DEL VALLE. 2001. Ecological lessons and applications from one century of low external-input farming in the Pampas of Argentina. *Agriculture, Ecosystems and Environment* 83:65–81.
- VOS, C. C., J. VERBOOM, P. F. M. OPDAM, AND C. J. F. TER BRAAK. 2001. Toward ecologically scaled landscape indices. *American Naturalist* 158:24–41.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138.
- WILLSON, M. F., J. L. MORRISON, K. E. SIEVING, T. L. DE SANTO, L. SANTISTEBAN, AND I. DIAZ. 2001. Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conservation Biology* 15:447–456.
- WITH, K. A., A. W. KING, AND W. E. JENSEN. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 118:3152–3167.
- ZALBA, S. M., AND N. C. COZZANI. 2004. The impact of feral horses on grassland bird communities in Argentina. *Animal Conservation* 7:35–44.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.