

## RESEARCH ARTICLE

# Low reproductive success of the endangered Iberá Seedeater in its only known breeding site, the Iberá Wetlands, Argentina

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## ABSTRACT

Subtropical grasslands are highly susceptible to habitat conversion and number among South America's most threatened ecosystems. The grasslands of northeastern Argentina have been identified as a priority conservation area for threatened capuchino seedeaters because they constitute the main breeding area of these migratory birds. The Iberá Seedeater (*Sporophila iberensis*) is a newly described species in the Iberá Wetlands in Argentina whose biology is still poorly understood. The endangered species inhabits grasslands but has only been reported to breed in the Iberá Wetlands ecoregion of northeastern Argentina. To explore the species' association with grassland vegetation, we studied the breeding biology (clutch size, hatching success, and fledgling production) of the Iberá Seedeater and the main parameters that influence nest survival and nest-site selection. We conducted nest searches and banded adults and nestlings in Iberá National Park during the breeding seasons of 2016–2018. The breeding season of the Iberá Seedeater was highly synchronous and the cumulative probability of nest survival was 0.16. The daily nest survival rate decreased as the breeding season advanced, survival was lower for nests supported by *Rhynchospora corymbosa* than *Paspalum durifolium*, the two main nest substrates, and the main causes of nest failure were nest predation and strong winds. Additionally, the population exhibited male-biased site fidelity and a low female return rate. In contrast to other capuchinos, whose breeding biology is associated with upland grasslands, the Iberá Seedeater nested exclusively in flooded lowland grasslands on marsh plants. Thus, effective lowland grassland management is key to maintain the vegetation structure required for reproduction in the Iberá Seedeater.

**Keywords:** breeding biology, daily survival rate, flooded lowland grasslands, grassland management, nest substrate, site fidelity

## LAY SUMMARY

- Capuchino seedeaters are austral migrants strongly associated with subtropical grasslands, which are among the ecosystems that suffer the highest rates of habitat conversion.
- The Iberá Seedeater is a recently described, endangered species that has a poorly understood biology, restricted breeding range, and faces unknown threats.
- We located and monitored nests, banded adults and nestlings, and took vegetation measurements to assess nest-site selection between 2016 and 2018 in Iberá National Park.
- Breeding site fidelity was male-biased, and nest survival was relatively low, decreased as time of breeding advanced, and differed among nest substrates.
- Breeding occurred exclusively in flooded lowland grasslands, suggesting that the species could be sensitive to changes in vegetation structure and water levels.

## Bajo éxito reproductivo de la especie amenazada *Sporophila iberensis* en su único sitio reproductivo conocido, los Esteros del Iberá, Argentina

### RESUMEN

Los pastizales subtropicales se encuentran entre los ecosistemas más amenazados de Sudamérica por su elevada tasa de pérdida de ambiente. Los pastizales del noreste argentino han sido identificados como área prioritaria para la conservación de los capuchinos debido a ser la zona reproductiva principal de estos passeriformes migratorios. *Sporophila iberensis* es una especie recientemente descrita en los Esteros del Iberá en Argentina cuya biología es aún muy poco conocida. Esta especie amenazada habita pastizales y el único sitio reproductivo reportado son los humedales del noreste argentino. Para conocer el grado de asociación entre la biología reproductiva de *S. iberensis* y los pastizales evaluamos

los principales parámetros reproductivos (tamaño de puesta, éxito de eclosión y productividad de volantones), los factores que influyen en la supervivencia de los nidos, la selección del sitio de nido y la fidelidad al sitio de reproducción. Entre los años 2016 y 2018 realizamos búsquedas de nidos y anillamos adultos y pichones en el Parque Nacional Iberá. El periodo reproductivo de *S. iberensis* es altamente sincrónico y la probabilidad acumulada de supervivencia de los nidos fue de 0.16. La tasa de supervivencia diaria disminuyó con el avance de la temporada reproductiva y fue menor para los nidos construidos sobre *Rhynchospora corymbosa* que sobre *Paspalum durifolium*, los dos sustratos principales de los nidos, siendo principalmente afectada por la depredación y por los vientos fuertes. La población muestra una fidelidad al sitio reproductivo sesgada en los machos y una baja tasa de retorno de las hembras. En contraste con otros capuchinos, cuya biología reproductiva está asociada a pastizales de lomadas arenosas, encontramos que *S. iberensis* nidifica exclusivamente en pastizales inundados. Por lo tanto, un manejo eficiente de los pastizales inundables resulta clave para la conservación de esta especie amenazada.

**Palabras clave:** biología reproductiva, especies sustrato, fidelidad de sitio, manejo de pastizales, pastizales inundables, tasa de supervivencia diaria

## INTRODUCTION

The genus *Sporophila* comprises ~43 species of small (8–10 g), sexually dimorphic, Neotropical finches (Mason and Burns 2013). Capuchino seedeaters are a group of 10–12 highly sympatric species that exhibit low levels of genetic and ecological divergence, yet are phenotypically differentiated (Lijtmaer et al. 2004, Campagna et al. 2012, 2018). Most capuchinos are austral migrants that winter in central Brazil, breed in southern subtropical grasslands, and are notable in that they feed on small grass seeds and are thus strongly associated with natural grasslands (Da Silva 1999).

Subtropical grasslands are among the ecosystems that suffer the highest rates of habitat conversion (Watson et al. 2016). Accordingly, 7 capuchino species are globally threatened or near-threatened as a result of habitat loss and the illegal pet trade (Hilty and Bonan 2019). The restricted breeding range of capuchinos and their susceptibility to changes in land use make them useful indicator species for the identification of important conservation sites, such as Endemic Bird Areas (Stattersfield et al. 1998) and Important Bird Areas (Di Giacomo 2005b, Devenish et al. 2009). The grasslands of northeastern Argentina have been identified as one of the priority conservation areas of *Sporophila* seedeaters, given the high diversity of species of the genus present in this region (Da Silva 1999). Nonetheless, these grasslands are under great anthropogenic pressure due to a massive increase in afforestation and an increase in grazing pressure and the associated annual fires used to improve forage quality (Di Giacomo et al. 2010, Viglizzo et al. 2011, Azpiroz et al. 2012).

The Iberá Seedeater (*Sporophila iberensis*) is a recently described capuchino species that have been categorized as Endangered by the IUCN (Di Giacomo and Kopuchian 2016, BirdLife International 2020). This classification is based on its small population size and extremely limited breeding range (BirdLife International 2020). Records of the Iberá Seedeater are limited to northeastern Argentina and southeastern Paraguay, with two recent sightings in southern Brazil (Di Giacomo and Kopuchian 2016, Galluppi-Selich et al. 2018).

However, the only known breeding site of the species is the Iberá Wetlands, a vast network of swamps, shallow lakes, and grasslands located in northeastern Argentina (Turbek et al. 2019; Figure 1). Given the species' recent discovery, the biology of the Iberá Seedeater is still poorly understood and its breeding requirements, migratory status, and threats remain unknown.

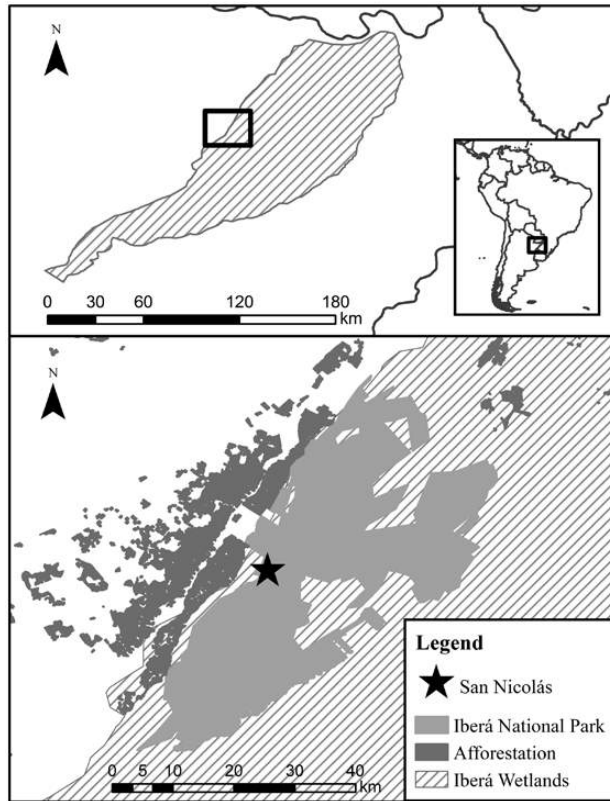
The reproductive period is a key determinant of the growth or decline of avian populations (Gill 1995). Thus, an understanding of breeding biology is necessary to identify possible threats. Many choices are made during the reproductive period that have a direct impact on an individual's fitness (Gill 1995). In selecting nest sites, for example, birds attempt to maximize the probability of nest survival by providing a safe site concealed from potential predators (Martin and Roper 1988, Misenhelter and Rotenberry 2000). Previous studies have found that some nest substrates have negative effects on fitness components (Schmidt and Whelan 1999, Scheiman et al. 2003, Lloyd and Martin 2005, Rodewald et al. 2010), potentially due to differences in the physiognomy of substrate species that facilitate predation (Schmidt and Whelan 1999). Also, the rate of breeding site fidelity and natal philopatry in migratory birds are key ecological and genetic determinants of population trajectories (Newton 2008).

The main goal of this study was to examine the breeding biology of the Iberá Seedeater and the species' dependence on grassland vegetation. We analyzed the species' main breeding parameters and assessed whether the use of different nest substrates affects nesting success. We also evaluated nest-site selection in the species and the breeding site fidelity of banded individuals. Increased understanding of the breeding biology of the Iberá Seedeater is necessary to provide conservation recommendations based on scientific evidence.

## METHODS

### Study Area

This study was conducted in Portal San Nicolás (28.1282°S, 57.4346°W) in Iberá National Park, located in the ecoregion



**FIGURE 1.** Location of the study site, San Nicolás (Iberá National Park), in the Iberá Wetlands region located in the province of Corrientes, northeastern Argentina. Afforestation adjacent to Iberá National Park is shown.

of the Iberá Wetlands (Figure 1). The ecoregion is located in the center of the province of Corrientes, Argentina, and has an extent of 13,000 km<sup>2</sup> (Figure 1). The Iberá Wetlands is composed of a mosaic of different habitats, such as marshes, lagoons, streams, rivers, savannas, grasslands, and thorny and humid forests (Burkart et al. 1999). The landscape of the study site consists of an open savanna with a gradual slope that results in seasonally flooded grasslands, dominated by *Paspalum durifolium*, in the lowlands and drained grasslands, dominated by *Andropogon lateralis*, in the uplands, where *Elionurus muticus* is also locally abundant (Carnevali 1994). San Nicolás was dedicated to livestock production until its acquisition by the Conservation Land Trust in 2002 when it was designated as a private protected area. Livestock was entirely removed in 2009 and the property was donated to the National Parks Administration in 2017 to create Iberá National Park. Beyond the park's boundaries, grasslands are used for grazing and are experiencing afforestation.

### Nest Searches and Monitoring

We conducted extensive nest searches of the Iberá Seedeater during the breeding season (October to

December) from 2016 to 2018 in both flooded lowland and upland grasslands. We identified territories by following territorial males that possessed the characteristic plumage patterning and song of the Iberá Seedeater (Di Giacomo and Kopuchian 2016). Given that only females construct the nest, nest searches focused primarily on female behavioral cues (Martin and Geupel 1993).

We georeferenced each nest with a GPS device and marked the nest with a small piece (i.e. ≤5 cm) of flagging tape placed at a minimum distance of 1 m from the nest (Winter et al. 2003). The flagging tape aided in nest identification in tall grasslands during subsequent visits and reduced the amount of time spent near the nest area. We visited nests every 2–4 days until the chicks fledged or the nest failed. The number of eggs and nestlings was recorded on each visit. We considered a nest abandoned if the eggs were cold to the touch for two consecutive visits and we no longer observed the female attending the nest and depredated if all of the eggs or nestlings disappeared between two consecutive visits (Di Giacomo et al. 2011b). In contrast, we considered a nest successful if the fledglings were observed directly in the field or through the use of parental behavioral cues, such as alarm calling following fledging. For six nests, we also set Reconyx HyperFire HC500 camera traps, during both incubation and brooding, at a minimum distance of 1 m from the nest to detect potential predators (Reconyx, Holmen, Wisconsin, USA). Camera traps were programmed to take 3 pictures per trigger, with a picture interval of 1 s, and no quiet period.

### Adult and Nestling Banding and Resighting

In the breeding seasons of 2016 and 2018, we banded adults and nestlings. We attracted males to a mist net using playback and captured females near the nest once the nestlings were born. Chicks were banded 6–8 days after hatching. We banded all individuals with a numbered metal band and a unique combination of three colored bands for subsequent identification in the field. We searched for banded individuals in our study site throughout the breeding seasons of 2017–2019. However, we did not conduct nest searches in 2019. For each resighted bird, we recorded the location with a Garmin GPS device, the band combination and sex of the individual, and the associated nest ID when applicable (Garmin International, Olathe, Kansas, USA). The resighting distance was measured as the distance between the last and first nests of subsequent breeding seasons, or resighting location if an individual was not associated with a nest, using Garmin BaseCamp, version 4.6.3 (Di Giacomo et al. 2011b).

### Vegetation Structure Measurements

Once a nest was no longer active, we took a series of vegetation measurements to assess nest-site selection. Nest-site

variables included (1) the nest substrate species, (2) the nest substrate height, (3) the nest height (i.e. distance from the ground to the top of the nest), and (4) the degree of nest concealment. All measurements were taken in centimeters (cm). In 2017 and 2018, we determined nest concealment by photographing 7 cm wide disks (i.e. the maximum outer diameter of the nests) with a grid of 1 cm<sup>2</sup> squares placed both above the nest (i.e. overhead concealment) and in the nest (i.e. lateral concealment). Photographs were taken at a distance of 1 m from the nest in both orientations. We counted the number of exposed squares (i.e. squares not covered by vegetation) and calculated nest concealment as 1 minus the proportion of exposed squares, such that well-concealed nests received a higher score than more visible ones (Davis 2005).

In 2018, we assessed vegetation structure at (1) the nest site and (2) a randomly selected site, located at a minimum distance of 5 m and a maximum of 30 m from the nest and determined from a set of random orientations and distances from the nest substrate, avoiding unused habitat by the species (i.e. dominated by *Cyperus* spp.). We used two vertical rods attached by a 5 m string to take vegetation measurements. We placed one rod either on the nest substrate (for nesting sites) or an unused central point (for randomly selected sites) and placed the other rod on each cardinal point (Nalwanga et al. 2004). We recorded the central plant species and grass height at each 1-m interval and noted the percentage cover of grass, forb, and water in each of the four cardinal directions (Nalwanga et al. 2004).

We were unable to take measurements of nest substrate and height when nests were still active when we left the field, nest substrate identification was uncertain (i.e. the nest fell from the substrate), or nest height was altered (either by predators or storms that blew them off the nest substrate).

## Data Analysis

**Breeding parameters.** We defined clutch size as the maximum number of eggs laid in the nest and included nests in the analysis only when the number of eggs remained constant for at least two consecutive days (i.e. when the female completed laying). We assessed hatching success only for nests that were found during incubation, survived until the nestling phase, and hatching was considered complete (i.e. when the number of chicks remained constant on two consecutive visits). We used nonparametric tests given that the data were not normally distributed.

**Nest survival.** We generated daily survival rates (DSR) with the nest survival model in program MARK (White and Burnham 1999). Nests that were found

during construction and were either abandoned or fell off the substrate species before egg-laying began, as well as nests for which the final fate was undetermined, were not included in the analysis. We calculated nest survival as  $DSR^t$ , where  $t$  was 23 days corresponding to the length of the nest cycle, which comprised 1 day for egg-laying, 12 days for incubation, and 10 days for the nestling period (Turbek et al. 2019).

We used program MARK to examine several factors that could have affected nest survival. We built candidate models with different combinations of 7 nest variables: (1) year, (2) a linear trend for the time of breeding (days elapsed since the start of the breeding season, determined to be October 14), (3) a quadratic trend for the time of breeding, (4) nest substrate (i.e. plant species), (5) nest substrate height, (6) nest height, and (7) nest age (days elapsed since the laying of the first egg on day 0). We included year and a linear trend for the time of breeding to account for interannual and within-year changes in weather patterns and predator communities (Dinsmore and Dinsmore 2007). We also included a quadratic trend for the time of breeding to consider a mid-season dip or peak in survival (Repenning and Fontana 2016). Nest substrate, substrate height, and nest height were incorporated into the models because phenotypic features of the substrate and height of the nest could either facilitate or limit predation (Schmidt and Whelan 1999, Rodewald et al. 2010). Finally, we considered nest age to account for the expected increase in predation risk following hatching (Skutch 1949). We imputed missing values using the mean value of each variable and constructed models by combining the variables that had more support than the null-hypothesis model of constant survival,  $S(.)$  in MARK notation (Burnham and Anderson 2002). We checked for nest fate independence in successive nesting attempts with a chi-square goodness-of-fit test (Di Giacomo et al. 2011b).

**Nest concealment.** Nest concealment was modeled separately, rather than included in the general nest survival analysis, to avoid reducing the power of the test (Cooch & White 2017) as only a subset of the nests had data on nest concealment ( $n = 27$ ). We evaluated the effect of nest concealment on nest survival in program MARK using the nests that had concealment data and including the variables that performed better than the null model in the general analysis. Also, we performed parametric and nonparametric tests to evaluate the relationship between nest substrate and nest concealment.

**Vegetation structure.** We used the following procedure to assess differences between the vegetation structure of nests and randomly selected sites. To evaluate the effect of grass height on nest-site selection, we implemented a generalized linear mixed model (GLMM) with a binomial

logit-link function. For the GLMM model, we included the ID of each nest site or randomly selected site as a random effect to account for the fact that grass height measurements were clustered within sites. Also, we used a generalized linear model (GLM) with a binomial error and a logit link function to examine the effect of grass, water, and forb cover on nest-site selection. In both models, the response variable was the presence/absence of the nest. To analyze whether the Iberá Seedeaters selected a particular plant species as its nest substrate or used nest substrates according to plant availability, we performed a chi-square goodness-of-fit test where we considered the nest substrate species that were used and the central plant species from the randomly selected sites (Aguilar et al. 2008).

**Model selection.** Before initiating model building and selection, we checked for correlations between variables. We excluded one of the correlated variables from the model if Pearson's correlation coefficient was  $>0.7$ . Because grass and water cover were correlated, we removed water cover from the vegetation structure model ( $r = 0.73$ ,  $P < 0.05$ ).

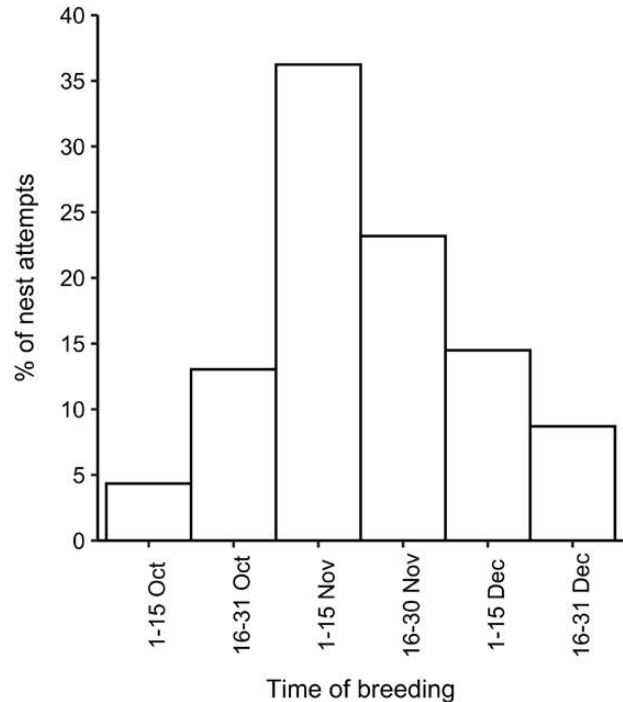
We built possible candidate models and used the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ) to select the best fit models from the suite of candidate models (Burnham and Anderson 2002). We considered models with an  $\Delta AIC_c$  under 2 to be equally supported, as models with a greater value are gradually less supported by the data (Burnham and Anderson 2002). We calculated Akaike weights ( $w_i$ ) to measure the relative support of the models considered.

Unless otherwise specified, we performed all analyses with R 3.6.2 (R Core Team 2019) and used the packages *lme4* and *MuMIn* for linear-mixed models (Bates et al. 2015, Barton 2019). We used Shapiro-Wilks tests to assess normality, set significance levels to  $P < 0.05$ , and express results as mean  $\pm$  SE.

## RESULTS

### Breeding Parameters

We first observed individuals of the Iberá Seedeater at the study site during the last week of September, which coincides with the beginning of the wet season. The earliest nesting attempt was recorded on October 14, 2017, while the latest nest initiation date was November 2, 2016. We found and monitored a total of 69 nests during the breeding seasons of 2016–2018. Nest initiation peaked in early November, at which point 36% of the nests were initiated, and ended towards the beginning of January (Figure 2). Females engaged in nest construction and egg incubation, while both males and females provisioned nestlings. Iberá Seedeaters built their nests in flooded lowland grasslands on  $93 \pm 2$  cm substrates ( $n = 49$ ) at an average



**FIGURE 2.** Percentage of nest attempts by female Iberá Seedeaters during the breeding seasons of 2016–2018 in Iberá National Park, Corrientes, Argentina ( $n = 69$  nests).

height of  $44 \pm 2$  cm ( $n = 42$ ). We identified six plant species used as nest substrate: *Paspalum durifolium* ( $n = 36$ ), *Rhynchospora corymbosa* ( $n = 12$ ), *Andropogon* spp. ( $n = 3$ ), *Chromolaena laevigata* ( $n = 2$ ), *Ludwigia* spp. ( $n = 2$ ), and *Schizachyrium* spp. ( $n = 1$ ). For further analyses that considered nest substrate, we grouped *Andropogon* spp., *Chromolaena laevigata*, *Ludwigia* spp., and *Schizachyrium* spp. as “other”. Clutch size was  $2.0 \pm 0.1$  (range: 1–3 eggs,  $n = 40$ ), hatching was asynchronous (i.e. eggs hatched on consecutive days), and hatching success was  $0.95 \pm 0.03$  ( $n = 22$ ). We observed brood reduction in only one nest. Successful nests fledged  $1.9 \pm 0.2$  chicks (range: 1–3,  $n = 15$ ). However, only 22% of nests successfully fledged nestlings. Nest predation was the main cause of nest failure; 61% of nests were lost to predation, 14% were abandoned, and 25% were found on the ground after storms characterized by strong winds. Nests were blown off mainly before egg-laying began, with 9 fallen nests found during nest-building, 1 during egg-laying, and 1 during the incubation period. Four of the 6 nests that were equipped with camera traps were successful, one was abandoned three days after the camera was placed, and the final nest, which contained nestlings, was predated by a Crab-eating Fox (*Cerdocyon thous*) on November 20, 2016. The camera traps were active for a total of 38 days.

**TABLE 1.** Support for models predicting daily survival rates of Iberá Seedeater nests throughout three breeding seasons from 2016 to 2018 in Iberá National Park, Corrientes, Argentina ( $n = 48$ ).  $T$  = linear term for the time of breeding;  $TT$  = quadratic term for the time of breeding;  $AIC_c$  = Akaike's information criteria corrected for small samples;  $\Delta AIC_c$  =  $AIC_c$  relative to the best-fit model;  $k$  = number of parameters;  $w_i$  = model weight.

Model	$\Delta AIC_c$	$k$	$w_i$
$T$ + Nest substrate	0.00 <sup>a</sup>	4	0.50
Year + Nest height	2.21	4	0.17
$T$ + Year	3.19	4	0.10
Year	3.76	3	0.08
Nest substrate	4.31	3	0.06
$T$ + Nest height	5.32	3	0.03
Nest substrate + Nest height	5.79	4	0.03
$T$	7.40	2	0.01
Nest height	8.00	2	0.01
Null	8.93	1	0.01
$TT$	9.05	3	0.01
Nest Age	10.76	2	0.002
Nest substrate height	10.81	2	0.002

<sup>a</sup> $AIC_c = 182.79$ .

Field observations indicate that the species is socially monogamous. Within each breeding season, we observed one banded male and/or one banded female per breeding territory, and the social bond was always maintained during reneating attempts ( $n = 2$ ). We considered reneating to occur when two or more nests were assigned to the same breeding pair (either the male or female was banded) within a breeding season. Reneating always occurred after a failed attempt. Seven of 42 pairs conducted more than one nesting attempt, but none of these reneating attempts were successful. The average number of nests attempted by a breeding pair in a breeding season was  $1.19 \pm 0.07$  (range: 1–3,  $n = 42$ ). An average of  $12 \pm 3$  days (range: 5–27,  $n = 8$ ) elapsed between nesting attempts, and the distance between successive nests by the same breeding pair was  $60.8 \pm 15.4$  m (range: 5.6–130.9,  $n = 8$ ).

We banded a total of 43 males, 20 females, and 31 nestlings in 2016 and 2018. We resighted 47% of banded males in the subsequent year after banding, while the proportion of resighted females and nestlings was only 10% and 9%, respectively. The percentage of resighted males decreased the second and third year after banding, with resighting rates of 28% and 6%, respectively. We did not resight any banded females or nestlings two or three years after banding. Adult resightings generally occurred close to the territory where they were banded (<200 m distance, range: 12–2440 m,  $n = 30$ ), except for two males that we resighted at a distance greater than 500 m. The banded nestlings we resighted were observed at a distance of 2.4 and 4.4 km from their nest of origin.

### Nest Survival

We excluded 21 nests from the original data set that did not meet the basic information required for inclusion in

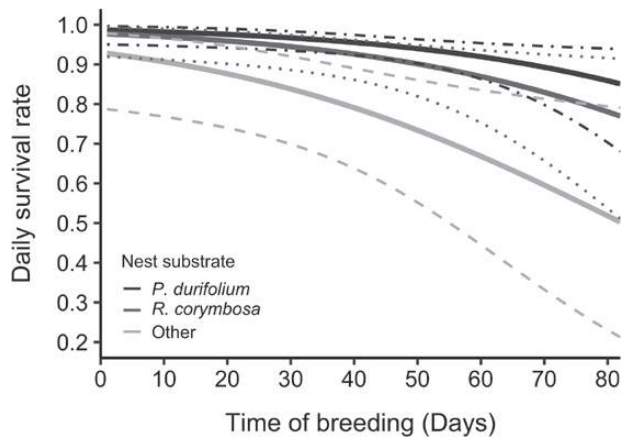
**TABLE 2.** Parameter estimates ( $\beta$ ), standard error (SE), and 95% confidence interval limits (CI) of the explanatory variables of the best-supported model that determined the survival rate of Iberá Seedeater nests during the breeding seasons of 2016–2018 in Iberá National Park, Corrientes, Argentina ( $n = 48$ ).  $T$  = linear term for the time of breeding.

Explanatory variable	$\beta$	SE	95% CI	
			Lower	Upper
$T$	-0.03	0.01	-0.06	-0.01
<i>P. durifolium</i>	1.73	0.49	0.78	2.69
<i>R. corymbosa</i>	1.20	0.53	0.16	2.23
Other	2.59	0.65	1.32	3.85

the nest survival analysis. Nine nests were blown off the substrate during nest building by storms, two were abandoned during nest construction, and the fate of 10 nests was unknown, as the nests were still active when fieldwork was concluded. As nest survival was independent of nesting attempt order ( $\chi^2 = 3.0$ ,  $P = 0.16$ ), we included reneating attempts in the nest survival analysis. The average DSR was  $0.92 \pm 0.01$ , and the estimated cumulative probability of nest survival during the nesting cycle was 0.16 ( $n = 48$ ). Models that included nest substrate, linear time of breeding, nest height, and year performed better than the null model, which assumed constant survival (Table 1). On the other hand, models that incorporated a quadratic term for the time of breeding, substrate height, and nest age performed worse than the null model (Table 1). The most parsimonious model, and the only model with a  $\Delta AIC_c$  under 2, included the variables time of breeding and nest substrate (Table 1). The selected model had an Akaike weight of 0.50, and DSR was higher for nests supported by *P. durifolium* ( $0.95 \pm 0.01$ ) than those constructed on *R. corymbosa* ( $0.92 \pm 0.03$ ) or other species ( $0.81 \pm 0.06$ , Table 2, Figure 3). Accordingly, the cumulative probability of nest survival was higher for nests constructed on *P. durifolium* (0.28) than those built on *R. corymbosa* (0.15) or other substrate species (0.01). DSR decreased as the breeding season advanced, implying that survival probabilities were highest at the beginning of the season (Table 2, Figure 3).

### Nest Concealment

The quadratic term for the time of breeding, substrate height, and nest age were not included in the analysis which included the nest concealment variables, as they performed worse than the null model in the general analysis (Table 1). The variables nest substrate, time of breeding, lateral concealment, and year performed better than the null model in the second analysis, while the variables overhead concealment and nest height performed worse (Table 3,  $n = 27$ ). Two model had a  $\Delta AIC_c$  under 2; the model with the highest Akaike weight ( $w_i = 0.55$ ) was the same model as the one selected by



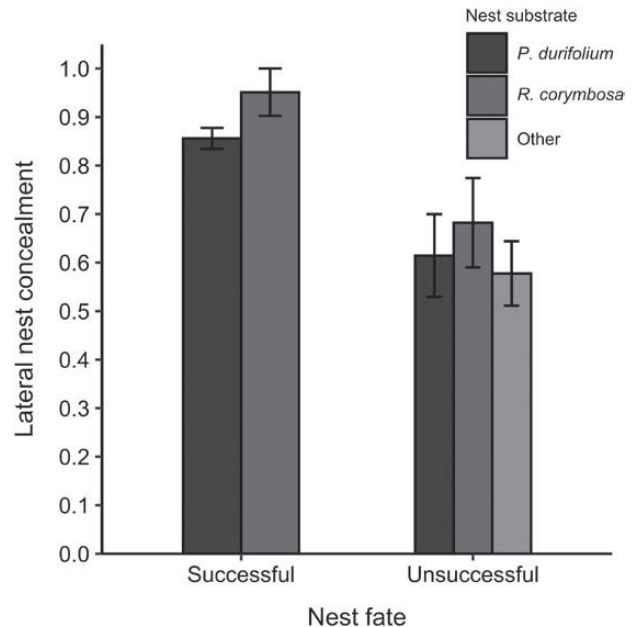
**FIGURE 3.** Graphical representation of the variation in the daily survival rate of Iberá Seedeater nests through the breeding season on three different nest substrates: *Paspalum durifolium* (black), and *Rhynchospora corymbosa* (dark grey) and other nest substrates (light grey), during the breeding seasons of 2016–2018 in Iberá National Park, Corrientes, Argentina ( $n = 48$  nests). Standard errors (SE) are represented with dot-dash, dotted, and dashed lines for *P. durifolium*, *R. corymbosa*, and other nest substrates, respectively.

**TABLE 3.** Support for models predicting daily survival rates of Iberá Seedeater nests throughout two breeding seasons from 2017 to 2018 in Iberá National Park, Corrientes, Argentina ( $n = 27$ ).  $T$  = linear term for time of breeding;  $AIC_c$  = Akaike's information criteria corrected for small samples;  $\Delta AIC_c$  =  $AIC_c$  relative to the best-fit model;  $k$  = number of parameters;  $w_i$  = model weight.

Model	$\Delta AIC_c$	$k$	$w_i$
$T$ + Nest substrate	0.00 <sup>a</sup>	4	0.55
$T$ + Lateral Concealment	1.47	2	0.26
Year + Lateral Concealment	3.69	2	0.09
$T$	5.36	2	0.04
$T$ + Year	5.61	3	0.03
Nest Substrate + Lateral concealment	7.79	4	0.01
Year	7.97	3	0.01
Lateral concealment	8.97	2	0.01
Nest substrate	9.37	3	0.01
Null	11.53	1	0.002
Nest height	12.42	2	0.001
Overhead concealment	13.32	2	0.001

<sup>a</sup> $AIC_c = 101.6$ .

the general analysis and included the variables time of breeding and nest substrate. Lateral nest concealment and time of breeding were also selected as important predictors of nest fate (Table 3). DSR decreased as lateral concealment decreased ( $\beta = 1.69$ ; 95% CI:  $-0.55, 3.94$ ) and as the breeding season advanced ( $\beta = -0.05$ ; 95% CI:  $-0.09, -0.01$ ). Predated nests had an average lateral concealment value of  $0.62 \pm 0.05$  ( $n = 20$ ), while successful nests averaged  $0.89 \pm 0.02$  ( $n = 7$ ). Overhead nest concealment averaged  $0.67 \pm 0.05$  for predated



**FIGURE 4.** Relationship between lateral nest concealment, nest substrate, and nest fate for 27 Iberá Seedeater nests found during the 2017 and 2018 breeding seasons in Iberá National Park, Corrientes, Argentina. Error bars are standard errors (SE).

nests ( $n = 20$ ) and  $0.70 \pm 0.03$  for successful nests ( $n = 7$ ). Neither lateral ( $F = 1.42, P = 0.26$ ) nor overhead concealment ( $H = 2.03, P = 0.36$ ) differed among nest substrate species (Figure 4). Lateral concealment averaged  $0.71 \pm 0.06$  ( $n = 13$ ),  $0.76 \pm 0.08$  ( $n = 7$ ), and  $0.58 \pm 0.07$  ( $n = 7$ ) on nests supported by *P. durifolium*, *R. corymbosa*, and other nest substrates, respectively (Figure 4). Overhead concealment averaged  $0.72 \pm 0.07$  ( $n = 13$ ),  $0.53 \pm 0.12$  ( $n = 7$ ), and  $0.72 \pm 0.05$  ( $n = 7$ ) on nests supported by *P. durifolium*, *R. corymbosa*, and other nest substrates, respectively.

### Vegetation Structure

The null model was selected both in the GLMM that examined the effect of grass height and the GLM that analyzed the effect of grass cover (with correlated water cover) and forb cover on nest-site selection, indicating that nest sites and randomly selected sites were similar in their vegetation structure (Burnham et al. 2011; Tables 4 and 5). Grass averaged  $52.6 \pm 1.0$  cm in height and covered the largest area, with  $78 \pm 2\%$  cover, while water and forb cover averaged  $8 \pm 2\%$  and  $15 \pm 2\%$  ( $n = 66$ ), respectively in nest sites and randomly selected sites.

Also, the availability of *R. corymbosa* (18%), *P. durifolium* (76%), and other plant species (6%) did not differ from their frequency of use as nest substrates (21%, 58%, and 21% respectively,  $\chi^2 = 3.7, df = 2, P = 0.16$ ), suggesting that female Iberá Seedeaters do not exhibit a preference for either plant species.

**TABLE 4.** Support for the generalized linear mixed model (GLMM) predicting grass height of Iberá Seedeater nesting sites and randomly selected sites throughout the 2018 breeding season in Iberá National Park, Corrientes, Argentina ( $n = 66$ ).  $AIC_c$  = Akaike's information criteria corrected for small samples;  $\Delta AIC_c$  =  $AIC_c$  relative to the best-fit model;  $k$  = number of parameters;  $w_i$  = model weight.

Model	$\Delta AIC_c$	$k$	$w_i$
Null	0.0 <sup>a</sup>	2	0.73
Grass height	2.0	3	0.27

<sup>a</sup> $AIC_c = 114.1$ .

## DISCUSSION

This study provides the first complete account of the breeding behavior of the Iberá Seedeater in the Iberá Wetlands, the only reported breeding site of the newly discovered and endangered species. Unlike other capuchinos, which nest in upland grasslands, we found that the Iberá Seedeater is strongly tied to flooded lowland grassland vegetation for reproduction. However, similar to other capuchinos, this species has a socially monogamous mating system, and females provide most of the parental care, building the nest, incubating the eggs, and feeding the chicks with the male's assistance (Facchinetti et al. 2008, Vizentin-Bugoni et al. 2013, Repenning and Fontana 2016). The breeding season of the Iberá Seedeater was highly synchronous, with around 60% of nesting attempts taking place in a single month (November). This concentrated pattern of nest initiation is expected for migratory species, like capuchinos, which generally possess shorter breeding periods than resident species (Franz and Fontana 2013, Repenning and Fontana 2016). We found that overall nest survival was low and breeding success decreased as the time of breeding advanced and differed among nest substrates. Also, female return rates to the breeding site in consecutive years were extremely low for a migrant passerine.

The cumulative probability of nest survival during the nesting cycle was 0.16. While other *Sporophila* species have higher nest survival rates of around 0.24–0.29 (Rovedder 2011, Franz 2012, Rosoni et al. 2019), another endangered seedeater, *S. beltoni*, reportedly has a similarly low nest survival probability (0.20, Repenning and Fontana 2016). As is the case for many Neotropical passerines, the main cause of nest failure for the Iberá Seedeater was nest predation (Martin 1993). A previous study reported a higher abundance of mesopredators (i.e. Pampas Fox [*Lycalopex gymnocercus*] and Crab-eating Fox) in our study region relative to other grassland areas (Di Bitetti et al. 2009). The mesopredator release hypothesis, which states that the local extinction of apex predators triggers an increase in mesopredator abundance (Davis et al. 2018), is

**TABLE 5.** Support for generalized linear models (GLMs) predicting vegetation cover of Iberá Seedeater nesting sites and randomly selected sites throughout the 2018 breeding season in Iberá National Park, Corrientes, Argentina ( $n = 66$ ).  $AIC_c$  = Akaike's information criteria corrected for small samples;  $\Delta AIC_c$  =  $AIC_c$  relative to the best-fit model;  $k$  = number of parameters;  $w_i$  = model weight.

Model	$\Delta AIC_c$	$k$	$w_i$
Forb cover	0.0 <sup>a</sup>	2	0.49
Grass + Forb cover	1.57	3	0.22
Null	1.76	1	0.20
Grass cover	3.34	2	0.09

<sup>a</sup> $AIC_c = 91.8$ .

a possible explanation for the higher mesopredator abundance observed in the study region, as apex predators were eradicated from the northern region of Corrientes over 50 years ago (Giraud and Povedano 2003). High mesopredator abundance has been associated with increased nest mortality, negative population trends, and decreased species diversity in birds (Crooks and Soulé 1999, Schmidt 2003). Given that mesopredators are confirmed nest predators of the Iberá Seedeater, the predation rate in our study site could be greater than expected due to the high mesopredator abundance in the region. We recommend the use of camera traps for nest predator identification to gain a better understanding of the main cause of nest failure. We identified strong winds as the second most important cause of nest failure. While the nests of the sympatric Tawny-bellied Seedeater (*S. hypoxantha*), which are often constructed on shrubs, are described as seemingly fragile, yet resistant to strong gusts of winds (Di Giacomo 2005a, Franz 2012), Iberá Seedeater nests were supported primarily on grass tussocks. This difference in nest substrate could make Iberá Seedeater nests more susceptible to being blown over by strong winds. Extreme climatic events are predicted to increase in frequency as temperatures rise in subtropical Argentina, posing an even greater threat to the Iberá Seedeater (Barros et al. 2015). The combination of an abundant mesopredator population and greater vulnerability to storms could explain the Iberá Seedeater's relatively low nest success.

The daily survival rate decreased as the breeding season advanced. A similar negative temporal pattern for daily survival rate has been observed in some grassland passerines (Grant et al. 2005, Di Giacomo et al. 2011b, Franz 2012, Fromberger et al. 2020). These trends are usually explained by an increase in predator abundance or activity as the season advances or by changes in the vegetation structure that facilitate predation through decreased nest concealment (Grant et al. 2005, Di Giacomo et al. 2011b, Little et al. 2015). Also, individuals of migratory species that arrive on the breeding grounds early in the season often



acquire better territories and mates (Smith and Moore 2005). Thus, the observed decrease in nest success could also be explained by the poorer quality of late-arriving individuals. We were unable to test these hypotheses, as we did not assess predator abundance, seasonal variation in vegetation cover, or adult body condition in this study.

Nest substrate influenced nest success, and nests built on the most frequently used nest substrate, *P. durifolium*, had a higher probability of fledging than those built on *R. corymbosa*. Nonetheless, Iberá Seedeater females used nest substrates according to their availability. The use of different nest substrates has been found to influence nest survival in other passerines (Schmidt and Whelan 1999, Rodewald et al. 2010). Variation in nest survival is usually explained by vegetation characteristics of different substrate species that decrease nest protection or concealment and thus facilitate nest predation (Schmidt and Whelan 1999, Rodewald et al. 2010). We found that nests with greater lateral concealment had a higher probability of success, as is the case in another seedeater species (Repenning and Fontana 2016). However, the observed positive relationship between lateral nest concealment and nest survival could be an effect of the temporal variation in plant phenology (Gibson et al. 2016). We did not identify any relationship between nest concealment and substrate species. Given that well-concealed nests were more successful, the relationship between nest concealment and nest substrate should be further studied to gain a better understanding of the underlying mechanisms driving nest predation in the Iberá Seedeater.

While the Iberá Seedeater did not select a specific vegetation structure for its nest sites, nests were found exclusively in flooded lowland grasslands. The most frequently used nest substrates (i.e. *P. durifolium* and *R. corymbosa*) grow in open, flooded areas and form similar landscape assemblages (Thomas 1992, Zuloaga and Morrone 2005). No nests were found on the adjacent upland grasslands, which are dominated by tall grasses, such as *A. lateralis* and *E. muticus*. The Iberá Seedeater's strong dependency on flooded lowland grasslands was especially apparent in the 2017 breeding season, which ended abruptly when the grasslands dried up, i.e. we found the last active nest on the 30th of November (INTA 2020). These results demonstrate the strong reliance of the Iberá Seedeater on flooded lowland grassland vegetation.

Our resighting records of the Iberá Seedeater indicated sex-biased breeding site fidelity. Adult passerine migrants that display breeding site fidelity have reported return rates of around 30–60% (Newton 2008), implying that the resighting rates we observed for males (47%) are within the expected range, while female return rates (10%) are extremely low. Also, we resighted banded males, but not females, two years after banding. The low female return rate could be a consequence of either sex-biased site fidelity, sex-biased mortality, or the

fact that males are conspicuous and vocalize while females are dull-colored (Greenwood and Harvey 1982, Liker and Székely 2005, Newton 2008). Male-biased site fidelity is often explained by sex differences in territory acquisition and defense, while parental care theory predicts higher mortality for the sex that provides greater parental care (i.e. females) (Liker and Székely 2005, Newton 2008). The sex-biased return rate could indicate that the energetic cost of breeding and migration has a higher toll for females and thus causes female-biased mortality. The yearling return rate (9%), which is usually lower than adult return rates and ranges from 0.9 to 12% (Newton 2008), was within the range reported for other migrant passerine species. The resighted yearlings only dispersed 2.4–4.4 km from their natal nest after migration. These observations highlight the need to conserve the Iberá Wetlands, the only reported breeding site of the Iberá Seedeater, and further study on the apparent female-biased mortality to understand the species' underlying population dynamics.

### Conservation Implications

Our results show that the breeding biology of the endangered Iberá Seedeater is strongly tied to flooded lowland grasslands and suggest that the species could be sensitive to changes in breeding habitat, particularly vegetation structure and water levels. These changes could either result from natural causes (e.g., increases in the frequency of storms or droughts), or anthropogenic sources (e.g., afforestation, grazing, associated grassland drainage, and fire). Annual burning, a common grassland management practice used in northeastern Argentina's protected and grazing areas, has been found to negatively impact the breeding success of grassland birds (Di Giacomo 2011a, Azpiroz et al. 2012, Cardoni et al. 2012). Yet, threatened grassland birds have been reported to use burned patches for breeding purposes three years after a fire has taken place (Petry and Krüger 2010, Di Giacomo et al. 2011a). Although the fire was not a factor addressed in this study, we recommend that future analyses consider its effect on the breeding biology of the Iberá Seedeater.

We found low reproductive success in the Iberá Seedeater and identified predation as the main cause of nest failure. The reintroduction of the locally extinct jaguar to Iberá National Park by the Iberá Rewilding Program could cause mesopredator abundance to decrease (Zamboni et al. 2017). The continued study of this breeding population of Iberá Seedeaters is necessary to understand the impact of apex predator reintroduction on the breeding biology of threatened grassland passerines.

Finally, the low female return rate should be studied in further detail given its potential implications for population dynamics. Female-biased mortality could contribute to population declines in the only reported breeding site

of this species (Grüebler et al. 2008), while female-biased dispersal may increase the vulnerability of small or isolated populations to extinction (Dale 2001). A greater understanding of the species' biology throughout the annual cycle is necessary to identify the cause of the low female return rate. For instance, seedeaters are reported to winter in central Brazil and eastern Bolivia (Ridgely and Tudor 1989), where habitat conversion and the burning of grasslands occur at high rates (Klink and Machado 2005). Nonetheless, the wintering sites and migration routes of the Iberá Seedeater remain unknown and are key to identifying the threats the endangered species faces outside the breeding period.

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**Data availability:** Analyses reported in this article can be reproduced using the data provided by Browne et al. (2021).

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