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SEEDEATERS AND SEEDS AT A TECOMA SAVANNA IN THE SOUTHERN PANTANAL, BRAZIL

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Abstract · Seedeaters (*Sporophila* spp.) comprise a rich Neotropical bird group of seed consumers common in open habitats. In this study, we documented the feeding habits of seedeaters and seed production at a Tecoma savanna (dominated by *Tabebuia aurea*) in southern Pantanal, Brazil. We also analyzed the relationship between seed offer (abundance, richness, and diversity) and the number of seedeaters foraging across seasons. Six species (*Sporophila angolensis*, *S. caerulescens, S. collaris S. hypoxantha, S.leucoptera,* and *S. lineola*) occurred in the savanna, mainly in the height of the wet season, when seed production increased abruptly, attracting seedeaters. Seedeaters used 14 of 16 grass species that produced seeds. Indeed, the number of foraging seedeaters paralleled the abundance and diversity of seeds, and the number of species consumed. During much of the dry season, when seeds were not produced, the few remaining seedeaters mostly consumed arthropods and flowers. The diet of seedeaters ranged from mostly seeds (*S. angolensis*) to a moderate proportion of flowers and arthropods (*S. leucoptera*). The offer of a rich set of seeds attractive to seedeaters indicates that the Tecoma savanna is a seasonally important habitat for these birds. Of concern, large areas of native grasses in the Pantanal have recently been transformed into exotic pastures, and extensive fires have become common. Thus, conservation of this singular area is important for seedeaters, which move over wide areas searching for an abundant and diverse seed supply.

Resumo · *Sporophila* spp. e sementes em uma savana de ipês no Pantanal sul, Brazil

Aves granívoras do gênero *Sporophila* constituem um dos grupos neotropicais de Passeriformes mais ricos em espécies, sendo particularmente comuns em áreas abertas. Neste estudo, documentamos a produção de sementes e os hábitos alimentares de uma guilda de *Sporophila* em uma savana de ipês (dominada por *Tabebuia aurea*) no sul do Pantanal, Brasil. Também analisamos as relações entre a oferta de sementes de gramíneas (abundância, número de espécies e diversidade) e o número dessas aves forrageando ao longo das estações. Seis espécies (*Sporophila angolensis*, *S. caerulescens*, *S. collaris*, *S. hypoxantha*, *S. leucoptera* e *S. lineola*) ocorreram na savana, principalmente no auge da estação chuvosa, quando a produção de sementes aumentou abruptamente atraindo essas aves. Por outro lado, flores e insetos, foram comuns na dieta dos poucos indivíduos de espécies que permaneceram na savana em parte da estação seca. As *Sporophila* spp. consumiram 14 das 16 espécies de sementes produzidas. De fato, o número dessas aves forrageando na savana foi paralelo ao número, abundância e diversidade de espécies de sementes disponíveis. Além disso, suas dietas divergiam quanto às espécies de sementes e demais itens consumidos, apresentando um gradiente em que algumas espécies incluíam certos tipos de sementes, enquanto outras, além das sementes, consumiam flores e insetos. A disponibilidade de um rico conjunto de sementes atrativas às *Sporophila* spp. indica a savana de ipês como um habitat importante para essas aves. Elas têm declinado em grande parte de sua área de distribuição devido à perda de habitat e ao comércio ilegal de animais de estimação. É preocupante o fato de que, recentemente, no Pantanal, amplas áreas de gramíneas nativas foram convertidas em pastagens exóticas, ao mesmo tempo em que extensas queimadas tornaram-se muito frequentes. Assim, a conservação desta área singular é importante para manutenção das populações de *Sporophila* spp., que se deslocam por amplas áreas em busca de oferta abundante e diversificada de sementes.

Keywords: *Diet · Granivory · Phenology · Sporophila*

INTRODUCTION

In open habitats, seeds are important food resources due to traits such as massive production, nutritional quality, and diversified offer (Marone et al. 2000). However, seed production is variable in time and space, limiting its use by mobile animals or those

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adapted to consume alternative resources during seed decline (Schluter 1982a, 1982b). Vertebrates such as granivorous birds often search for seeds at diverse spatial scales, responding to local production patterns (Schluter 1982a, Jahn et al. 2020). Indeed, the local abundance of granivorous birds often mirrors seed production in a given area (Marone 1992). Although granivorous birds have strong beaks and gizzards that help to process the seeds (Grant & Grant 2006), they often forage on flowers, fruits, and arthropods to supplement their diet, mainly during breeding periods or when seeds decline (Price 1987, Poulin et al. 1994).

Seedeaters of the genus *Sporophila* comprise a prominent Neotropical bird group common in open grassy areas; they are relatively small bodied (ranging from 6 to 16 g) with stubby, conical bills adapted for feeding on seeds (Ridgely & Tudor 1994, Sick 1997). Seedeaters are often temporally abundant in a given area in response to seed production (Areta et al. 2013, Rosoni et al. 2019). However, few studies document seedeaters moving locally or regionally tracking seeds (Areta 2012, Areta et al. 2013). For example, some seedeater species breed in southern Brazil during summer while spending the winter in central Brazil, where and when the food supply is adequate (Cintra & Yamashita 1990, Da Silva 1999). Seedeaters' mobility and diet plasticity may influence how they respond to changes in seed production under anthropogenic pressures (Machado & Silveira 2010). However, the accelerated habitat loss and degradation of Brazilian open areas have suppressed grass species, which seeds are key resources for seedeaters (Da Silva 1999, Pozer & Nogueira 2004).

In Brazil, seedeaters are common in grassy areas of several biomes, including the Pantanal (Ridgely & Tudor 1994, Sick 1997). The Pantanal is a large seasonal floodplain comprised of a vegetation mosaic of dense gallery forests, patches of dry forests, savannas, and open fields (Silva et al. 1998). In the southern Pantanal, savanna-like habitats are prominent, and one such habitat is known as the Tecoma savanna (dominated by *Tabebuia aurea*; Silva et al. 1998). Locally, in the spring and summer, up to six seedeaters species may co-occur in this habitat type (*Sporophila angolensis*, *S. caerulescens*, *S. collaris*, *S. hypoxantha*, *S. leucoptera*, and *S. lineola*; J. Ragusa-Netto pers. observ.). The Tecoma savanna is seasonally flooded and includes a diversity of grass species (Soares & Oliveira 2009) that seedeaters may exploit according to their availability, as expected for granivorous birds with reduced or no dependence on a particular food source (Walker 2007).

We studied the seed production and the feeding habits of six species of *Sporophila* seedeaters at a Tecoma savanna in the Pantanal. We also analyzed the relationship between seed offer (seed abundance and diversity, and the number of grass species seeding) and the number of seedeaters foraging across seasons.

METHODS

Study site. This study was carried out in the South Pantanal flood plain in a Tecoma savanna cut by the Miranda River (19°35'S, 57°2'W, altitude ± 100 m, Municipality of Corumbá, State of Mato Grosso do Sul). The vegetation in the area is a mosaic conformed by dense gallery forest in the Miranda River, patches of deciduous forest interspersed with open grassy areas, and palm savannas (dominated by *Copernicia alba*) and Tecoma savannas dominated by *T. aurea*; Soares & Oliveira 2009). The largest area of the Tecoma savanna in the South Pantanal covers 63,779 ha (Silva et al. 1998). *Tabebuia aurea* trees are 4–8 m height, although some individuals may reach 12 m. They occur on small mounds (± 0.5–1.0 m) interspersed with open grassy areas. Individuals of *Byrsonima orbignyana* are often intermixed with *T. aurea*, although in smaller numbers (Soares & Oliveira 2009). Annual rainfall is around 1000 mm, mostly from November to March (70–80%, wet season [source: meteorological service of Corumbá International Airport, Brazil]). In this area of Pantanal, flood pulses typically occur from January to March. During floods, standing water in the Tecoma savanna is up to 1.0 m.

Seed production. To assess seed offer in the Tecoma savanna, we established three 2 km long trails, 1 km apart. Every trail had 20 plots (2 x 2 m, 100 m apart) designed to sample monthly seed production (from December 2000 to November 2001). We took as a proxy of seed production the total number of seed spikes belonging to all individuals of each species within a plot. Every month, one of us (Ieda M. N. Ilha, hereafter IMNI) counted all seed spikes present at each plot and grouped them per species to estimate the contribution of every species to seed production. Then, our monthly index of seed production resulted from the sum of all seed spikes present in the 60 plots sampled.

Seedeaters food resource use. We appraised seedeaters' feeding habits through direct observations of them foraging. Monthly, IMNI employed 20 h walking the trails described to sample seed production. We randomized the initiation point of the sampling walks and the direction to be followed. IMNI carried out these observations in the morning at times when seedeaters were often feeding, from sunrise to 10:00 h and in the afternoon from 15:00 h to sundown (GTM - 04:00). Whenever at least one feeding seedeater was spotted, IMNI recorded: a) plant species (whether native or exotic), b) food resource (flower or seeds), and c) species and the number of seedeaters feeding. When a seedeater captured a small animal (taking the bill length as reference, often ≤ 1cm), IMNI recorded the taxon as arthropod. Assuming that seedeaters were equally likely to be seen feeding on any food source, IMNI avoided resampling feeding birds during an observation period by walking trails in only one direction. Seedeaters were not individually marked, therefore, to avoid pseudoreplication, IMNI used only the initial observation of a feeding bird, recording the first ingestion of a specific food item eaten by each seedeater (i.e., sequential observations were discarded; Hejl et al. 1990). To improve assessments of the extent of food source use, we provide the percentage of individuals of each Sporophila species feeding on each food item from the total of feeding records of the species (Table 1).

Analyses. To analyze the relationship between the monthly total number of seedeaters feeding and a) seed abundance, b) the number of species producing seeds, and c) seed diversity, we used the Pearson correlation in which data were log-transformed to improve linearity. Therefore, we took the monthly indexes of seed production, the number of grass species seeding (only those eaten by seedeaters), and the number of seedeaters observed feeding on seeds every month as explanatory variables. We adopted that approach because our interest was to show how seedeaters used the Tecoma savanna as a feeding area instead of showing species-specific relationships. Moreover, we did that because no seedeater species intensely used seeds from any grass species (see results below). The three explanatory variables were collinear, so we took the residuals of each regression to assess the presence of confounding effects on the correlations with the number of seedeaters. Then, we correlated each factor with residuals of the number of seedeaters. In addition, we performed a Power test on the correlation analyses to assess the potential of Type I error, and we assumed that a Power greater than 0.8 ($\alpha = 0.05$) conformed to correlation robustness. We correlated the accumulated monthly rainfall with the monthly index of seed offer, as rainfall pulses may positively affect the magnitude of seed production (Pol et al. 2010). We used the Simpson index (D), the reciprocal of Simpson's original formula (Simpson 1949), to describe the food diversity offered to seedeaters. The Simpson index (and its derivatives) is sensitive to changes in the common species, whereas the more widely used Shannon index is more sensitive to changes in rare ones (Peet 1974). We used the Simpson index to minimize the influence of rarely produced foods and stress-out changes in the common ones since granivorous birds often use abundant food resources (Schluter 1982a, 1982b). We conducted a correspondence analysis (CA) to explore the variation in the use of items (arthropods, flowers, and seeds of grass species) by every seedeater species (Table 1). Like other ordination methods, CA attempts to place similar samples in similar positions in the ordination plot. The measure of distance between samples is proportional to the Chi-squared statistic. Samples considered for this ordination procedure consisted of the number of individuals of each seedeater species observed feeding on every item/species (Table 1). Here, a species of seedeater took a position in the graph due to its diet dominance (feeding item/species) relative to the diet of other species.

RESULTS

Seed production. A total of 16 grass species were recorded seeding in the phenology plots (Figure 1). Seed production started in October, the transition from the dry to the wet season, peaking in January-February. From March to May, seed production began to decrease leading to the absence of seeds from June to September (Figure 1). Rainfall totaled 1015.9 mm during the study year, with ca. 90% occurring from October to March. Seed production paralleled rainfall along the year (r = 0.88, P = 0.0001, Figure 2A). Four species were important for seed production, making up almost 80% of spike abundance (*Setaria geniculata,* 37.1%; *Andropogon hypogynus,* 22%; *Panicum laxum,* 10.5%; and *Paspalum hidrophylum*, 9.4%; N = 12076 seed spikes). Much of the monthly seed offer resulted from the production of these four species. On the other hand, species such as *Pennisetum nervosum* contributed slightly to seed totals (0.5%; Figure 1). In December, *S. geniculata* spikes dominated the phenology sample comprising 58% of the total produced (N = 2977). *Setaria geniculata* and *A. hypogynus*, when grouped, dominated seed production in January (67%, N = 4196 spikes) and February (55%, N = 3242; Figure 1). In March, when seed abundance declined, *S. geniculata* and *P. laxum* comprised 61% of seed production (N = 645). Finally, *Cynodon dactylon* and *Eleusine indica*, unused by seedeaters, produced minor proportions of spikes (2.2% and 0.6%, respectively), being.

Use of food resources by seedeaters. Seedeaters foraged mostly for seeds (82.3%, N = 232 instances of birds recorded feeding), which comprised from 73.5% (*S. leucoptera*, N = 98) to 95.4% (*S. angolensis*, N = 22) of their food items, while flowers and arthropods accounted for minor proportions (7.8%, 9.9%, respectively; Table 1). Only *S. leucoptera* ate these items in higher proportions (12.2 and 14.3%, N = 98; Table 1). Seedeaters consumed seeds from 14 grass species but foraged more often on five (*A. hypogynus*, *S. geniculata, P. laxum*, *Axonopus paraguayensis,* and *P. nervosum*, Table 1). Both *S. collaris* and *S. leucoptera* were extreme in consuming 13 species, whereas *S. angolensis* fed on only four, among which *A. hypogynus* was the most important food item (Table 1). The other three seedeaters' species consumed five to seven species, of which *Hymenachne amplexicaulis* and *Digitaria cuyabanensis* were taken in higher proportions (Table 1).

Table 1. Plant species and items eaten by seedeaters (*Sporophila angolensis,* N = 21 birds observed feeding; *S. caerulescens,* N = 17; *S. collaris,* N = 49; *S. hypoxantha,* N = 19; *S. leucoptera,* N = 90; *S. lineola,* N = 27), recorded monthly from Nov. 2000 – Dec. 2001) at a Tecoma savanna.

Seedeater species	Taxa	Item	Months	% of birds feeding
S. angolensis	*Andropogon hypogynus*	seed	Feb, Mar	14.3
	Axonopus paraguaiensis	seed	Feb, Mar	38.1
	Eragrestris rufescens	seed	Feb	43.1
	Setaria geniculata	seed	Feb, Mar	2.2
	Arthropods	animal	Apr	4.8
S. caerulescens	*Andropogon bicornis*	seed	Jan, Feb	11.8
	Andropogon hypogynus	seed	Jan, Feb	11.8
	Digitaria cuyabanensis	seed	Jan, Feb, Mar, Oct	17.6
	Eragrestris rufescens	seed	Oct	10.8
	Paspalum hydrophilum	seed	Jan	11.8
	Setaria geniculata	seed	Jan, Feb, Oct	11.8
	Panicum laxum	seed	Jan, Oct	12.8
	Heliotropium filiforme	flower	Oct	5.9
	Melochia parvifolia	flower	Oct	5.9
	Sebastiana hispida	flower	Nov	5.9
	Arthropods	animal	Sept	17.6
S. collaris	*Andropogon bicornis*	seed	Dec	2.04
	Andropogon hypogynus	seed	Jan, Feb, Dec	16.3
	Axonopus paraguaiensis	seed	Dec	4.1
	Digitaria insularis	seed	Jan, Feb, Dec	4.1
	Eragrestris rufescens	seed	Jan, Nov, Dec	8.2
	Erichloa punctata	seed	Jan, Dec	4.1
	Hymenachne amplexicaulis	seed	Jan, Dec	4.1
	Panicum maximum	seed	Jan, Feb, Mar	10.2
	Paspalum hydrophilum	seed	Dec	2.04
	Pennisetum nervosum	seed	Jan, Feb, Mar	8.2
	Setaria geniculata	seed	Jan, Feb, Mar	10.2
	Sorghum arundinaceum	seed	Jan, Feb, Mar	6.1
	Panicum laxum	seed	Jan, Nov, Dec	10.2
	Hyptis lappacea	flower	Nov	4.1
	Parthenim hysterophorus	flower	Nov	2.1
	Arthropods	animal	Dec, Jul	10.2
S. hypoxantha	*Andropogon bicornis*	seed	Dec, Jan	5.3
	Erichloa punctata	seed	Nov, Dec, Jan	15.9
	Hymenachne amplexicaulis	seed	Nov, Dec, Jan	36.8
	Paspalum hydrophilum	seed	Dec, Jan	10.5
	Setaria geniculata	seed	Nov, Dec, Jan	21.1
	Arthropods	animal	Feb	21.1
S. lineola	*Andropogon bicornis*	seed	Jan, Feb, Oct	11.1
	Axonopus paraguaiensis	seed	Jan	11.1
	Digitaria insularis	seed	Jan, Feb, Oct	14.8
	Setaria geniculata	seed	Jan, Feb	14.8
	Panicum laxum	seed	Jan, Feb, Oct	14.8
	Paspalum hydrophilum	seed	Jan, Feb, Mar, Oct	11.1
	Arthropods	animal	Sept	11.1
S. leucoptera	*Andropogon bicornis*	seed	Jan, Feb	2.2
	Andropogon hypogynus	seed	Jan, Feb, Dec	16.7
	Axonopus paraguaiensis	seed	Jan, Dec	6.7
	Digitaria insularis	seed	Jan, Dec	3.3
	Eragrestris rufescens	seed	Dec	2.2
	Erichloa punctata	seed	Dec	2.2
	Hymenachne amplexicaulis	seed	Jan	2.2
	Panicum maximum	seed	Jan, Feb, Mar, Nov	3.3
	Paspalum hydrophilum	seed	Dec	1.1
	Pennisetum nervosum	seed	Jan, Feb, Nov, Dec	7.8
	Setaria geniculata	seed	Jan, Dec	6.7
	Sorghum arundinaceum	seed	Jan, Feb, Mar	4.4
	Panicum laxum	seed	Jan, Nov, Dec	5.6
	Heliotropium filiforme	flower	Oct, Nov	1.1
	Hyptis lappacea	flower	Oct, Nov	5.6
	Parthenim hysterophorus	flower	Oct, Nov	3.3
	Scoparia montevidensis	flower	Oct, Nov	2.2
	Sebastiana hispida	flower	Sept, Oct, Nov	1.1
	Arthropods	animal	May, Jun	15.6

Seedeaters foraged on flowers of only six herbaceous species in the transition from the dry to the wet season (October and November). *Sporophila caerulescens* and *S. lineola* used only one species, while *S. angolensis* and *S. hypoxantha* consumed no flowers. On the other hand, *S. collaris* consumed flowers of three species, whereas *S. leucoptera* foraged on

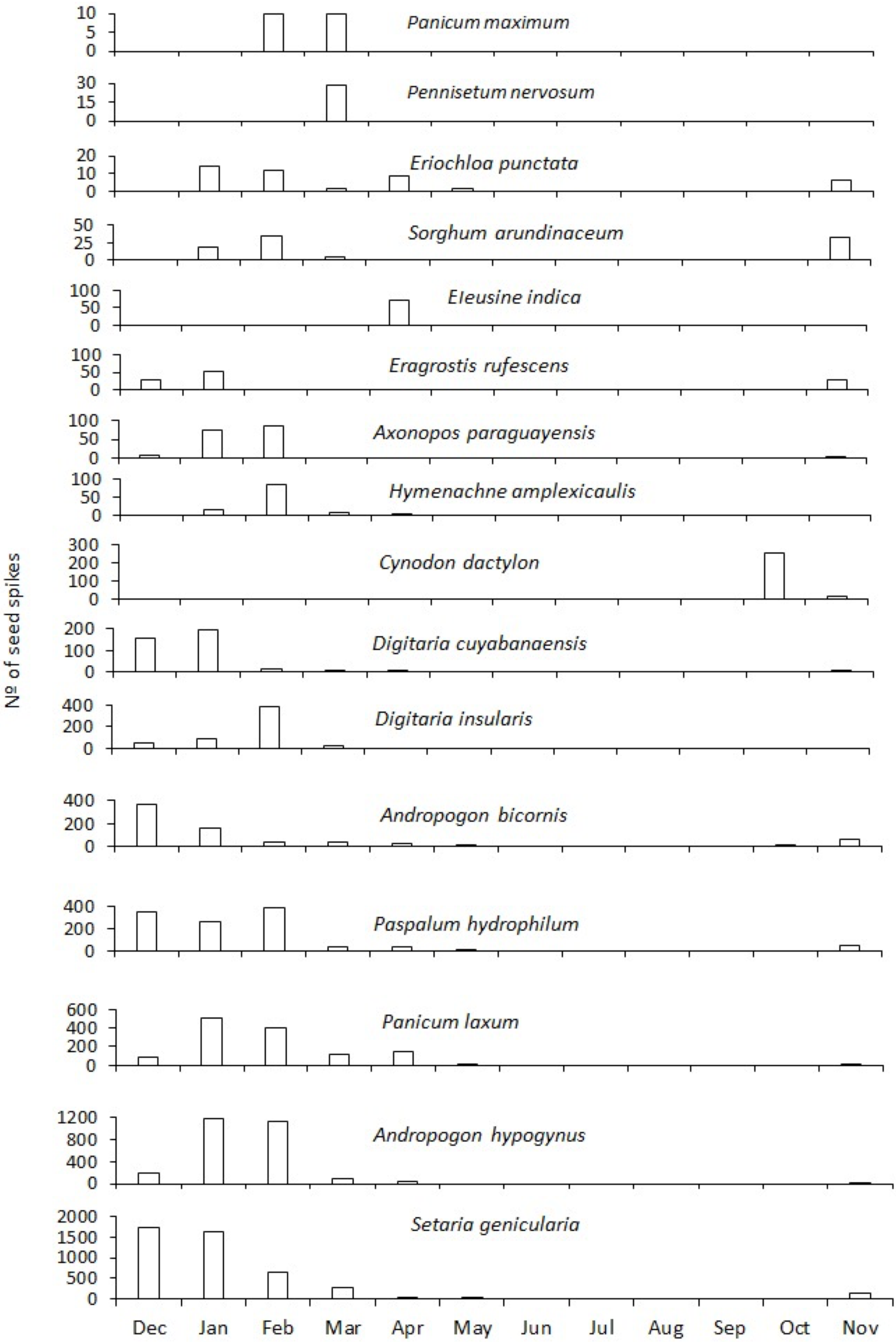

Figure 1. Total monthly (Dec 2000 – Nov 2001) number of seed spikes produced by 16 grass species in 60 plots of the Tecoma savanna (southern Pantanal, State of Mato Grosso do Sul, Brazil; 2000 and 2001).

five, among which *Hyptis lappacea* was an important food item (Table 1). Seedeaters mostly foraged on arthropods during the dry season. In the wet season, when seeds were plentiful, they composed 37.5% of the seedeaters' feeding items (N = 30 birds eating). Although all seedeater species ate arthropods, *S. leucoptera* fed on this item more often (47.0% of arthropods eaten by all seedeaters). This species mostly foraged on arthropods during the dry season, as only 7.1% of their consumption (N = 14) occurred in the wet season (Table 1).

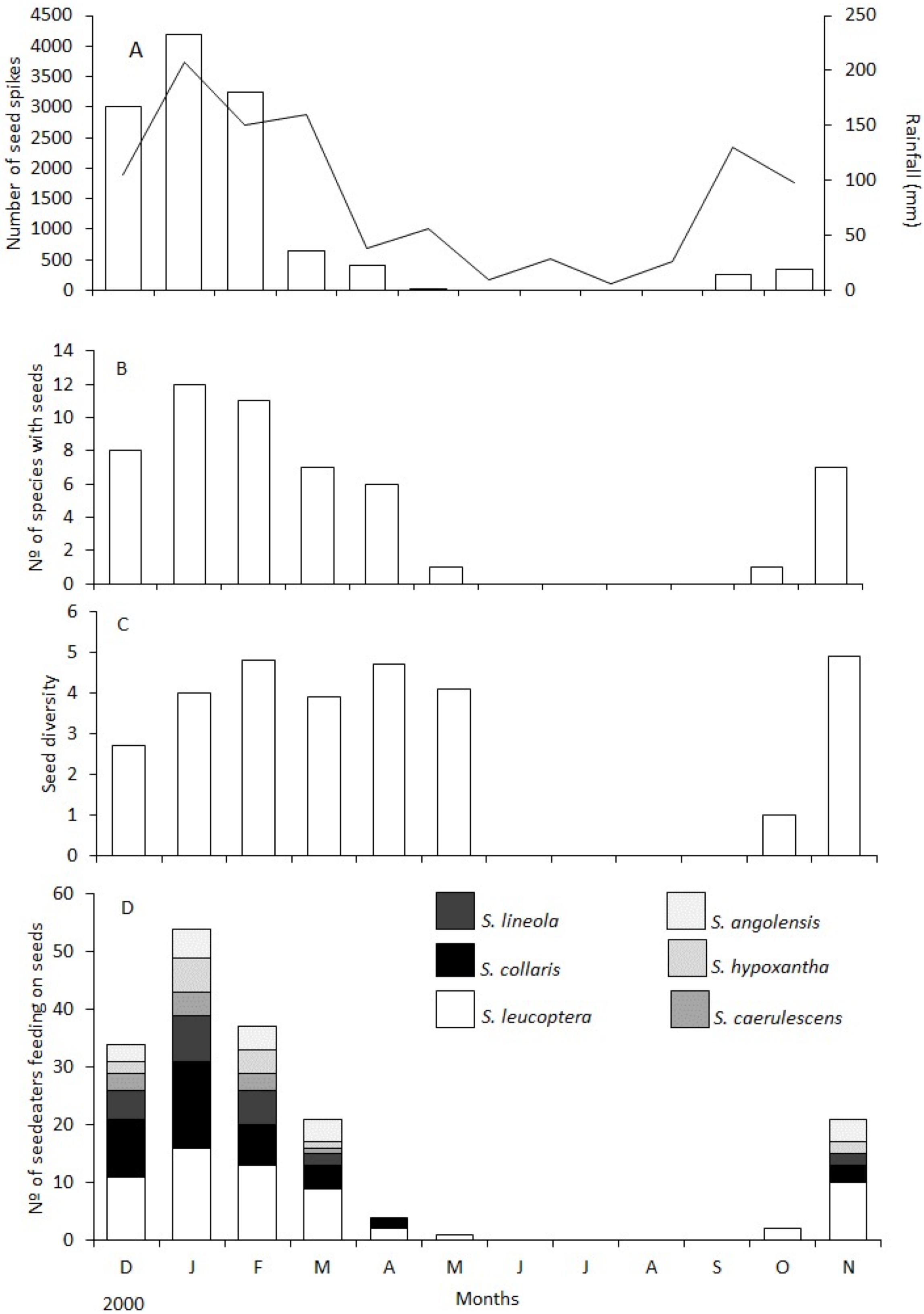

Figure 2. From top to bottom: A) Total seed production (seed spikes monthly recorded [see methods], and monthly rainfall (mm; line)), B) Monthly number of species with seeds, C) Monthly seed diversity, and D) Monthly number of *Sporophila* seedeaters feeding on seeds (N = 174 [the number of individuals feeding on arthropods and flower are not represented]) in the Tecoma savanna (southern Pantanal, State of Mato Grosso do Sul, Brazil; Dec 2000 – Nov 2001).

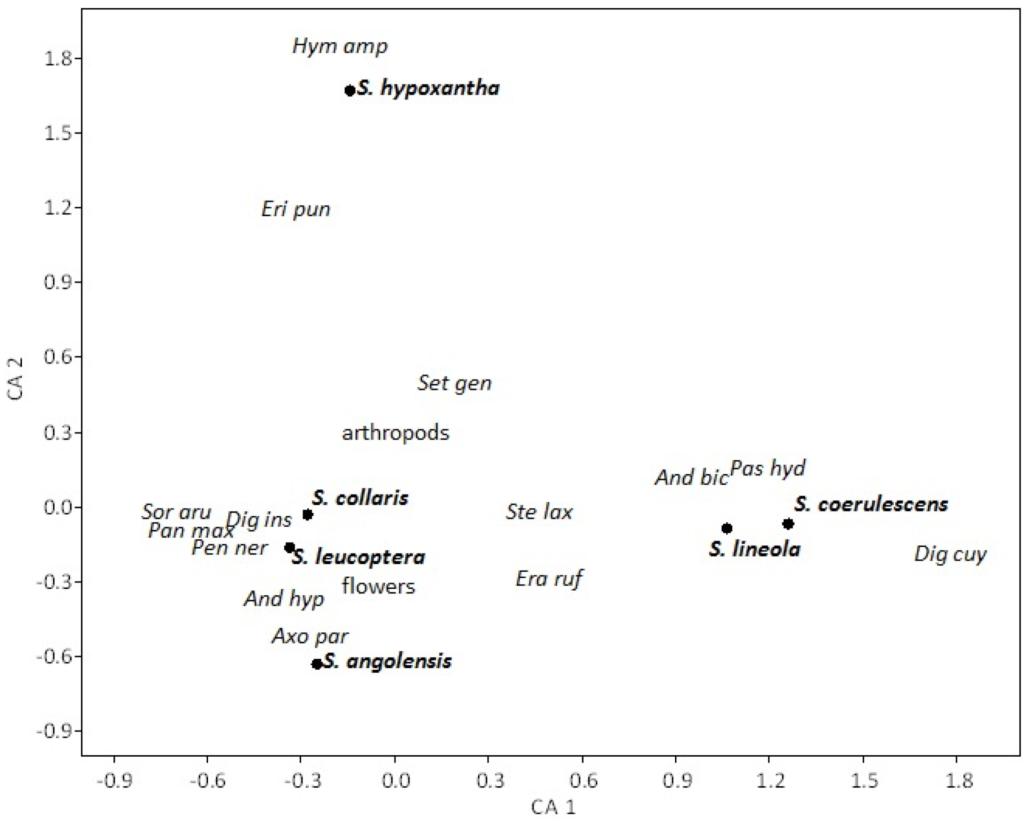

Figure 3. Association between each seedeater species (black circle) and food item eaten on CA (Correspondence Analysis; axis 1 = 37.8% of the variance, and axis 2 = 34.1%). The first three letters represent generic and species names of grass species with seeds (see Table 1).

Seedeater species exhibited different associations with species/items eaten. Axis 1 of correspondence analysis (CA 1 = 37.8% of the variance associated with bird species and respective food items/species) described the progressive decrease of seeds consumption from *S. caerulescens* to species that foraged on seeds, arthropods, and flowers (mainly *S. leucoptera*, and *S. collaris*; Figure 3, Table 1). On the other hand, axis 2 (CA 2 = 34.1%) separated the peculiar feeding habits of *S. hypoxantha* from that of *S. angolensis*. In between these extremes were species, including arthropods, flowers, and seeds (Figure 3, Table 1).

Seedeater occurrence in the Tecoma savanna varied pronouncedly throughout the year. They were abundant during the rainy months, mainly in January-February, and scarce across the dry season. Indeed, the number of seedeaters feeding on seeds paralleled seed production ($r = 0.97$, $P < 0.0001$; Power = 0.999; Figure 2A, D). Besides the abundance, the number of grass species bearing seeds varied, peaking in January (12 species) and dropping to zero from June to September. The number of seedeaters feeding on seeds paralleled the variations in the number of grass species exploited by seedeaters ($r = 0.96$, $P < 0.0001$; Power = 0.997; Figure 2 B, D). Finally, seed diversity fluctuations were abrupt and correlated to the number of seedeaters feeding in the Tecoma savanna ($r = 0.86$, $P < 0.0004$; Power = 0.986; Figure 2 C, D). To reinforce the significance of correlations, the residuals of the monthly number of seedeaters feeding had no relation with seed abundance ($r = 0.0008$, $P = 1$), the number of fruiting grass species ($r = - 0.009$, $P = 1$), and seed diversity ($r = 0.0003$, $P = 1$).

DISCUSSION

Seed production. In the southern Pantanal, most rainfall occurs from January to March, triggering intense fruiting in herbaceous species (Tannus et al. 2006). However, in this area, the predominance of sandy soils augments dry conditions, restraining the length of the fruiting period (Pozer & Nogueira 2004). Indeed, grasses from highly seasonal areas need significant more water input to trigger seed production depending on intense rainfall periods (Schwinning & Sala 2004). This was the case for the grasses, which produced seeds massively only during the wettest period of the year, as documented elsewhere (Pol et al. 2010). Indeed, in the southern Pantanal, the most eaten species are widespread across a gradient of soil humidity (Pozer & Nogueira 2004). Not surprisingly, such species (*A. hypogynus*, *S. geniculata, P. laxum*, *A. paraguayensis,* and *P. nervosum*) comprised much of seed production, making the bulk of seedeaters' foods.

Seedeaters' feeding habits. In the Tecoma savanna, seedeaters consumed various items, often comprised less than 10% of any species' diet. Each species consumed seeds of at least three species besides flowers and/or arthropods. They often overlapped in the intake of seeds from several grass species, for example, in a moderate use of the abundant *S. geniculata* and *A. hypogynus* seeds. The most common foragers, *S. collaris* and *S. leucoptera*, ate seeds of 14 species in reduced proportions, far from specialized seed use (Areta & Cockle 2012). Moreover, *A. hypogynus* seeds were the main food item for both *S. collaris* and *S. leucoptera*, although forming less than 17% of their exploited items. Then, in principle, the Tecoma savanna emerges as a feeding area where seedeaters foraged on a diverse seeds. The use of many seed species by seedeaters may be a strategy to increase nutritional reward because varied seeds may fulfill their requirements in terms of minerals and essential amino acids (Díaz 1996, Cueto et al. 2006). Further studies on the content of consumed seeds should clarify their contribution to the nutritional spectrum of seedeaters in this peculiar area in southern Pantanal.

Seedeaters were abundant in the wettest months when seed supply was abundant, and these birds foraged intensely on seeds of several grass species. Conversely, they were rare in the driest months when seed supply was reduced, and they often fed on flowers and arthropods. This variation in abundance resulted from the high mobility of *Sporophila* seedeaters tracking seasonal seed patches (Da Silva 1999, Areta et al. 2013). Therefore, the parallelism between seed offer and the number of seedeaters feeding suggests these birds moved to the Tecoma savanna due to the abundant seed supply instead of tracking particular seeds (Areta et al. 2013). Besides feeding, seedeaters might also be breeding in the Tecoma savanna. Indeed, seedeaters' movements toward feeding areas during spring and summer coincide with their breeding period, mainly for seedeaters species with the southern breeding distribution (Franz & Fontana 2013, Repenning & Fontana 2016, Rosoni et al. 2019).

In seasonal cerrado areas, blossoms are common during the dry and transition to the wet season (Tannus et al. 2006). The herbaceous plants' flowering during the dry season emerged as an alternative resource for seedeaters. During the dry season, seeds became increasingly scarce, and the few persistent seedeaters fed on alternative items to overcome this period (Table 1). In this respect, studies have documented the importance of flowers for granivorous birds during the dry season (Smith et al. 1978, Tebbich et al. 2004). Despite their low nutritional content, consumption of flowers might be advantageous due to their abundance (Symes et al. 2008), when seedeaters more often ate arthropods. Thus, lacking seeds, the remaining seedeaters, at least partly, switched their feeding habits until seeds became plentiful in the Tecoma savanna, similar to that documented in the Atlantic Forest (Areta et al. 2013).

To conclude, besides seed abundance and diversity, the number of seed species consumed influenced the seedeaters' use of the Tecoma savanna. This highlights the importance of a rich collection of scattered food patches for the abundance of seedeaters. Thus, the conservation of this bird group in the Pantanal depends on preserving key habitats having food resources, at least as documented here. The substitution of the native for exotic pastures (Seidl et al. 2001) impoverishes feeding areas that provide the adequate food supply seedeaters require (Da Silva 1999, Machado & Silveira 2010). In areas where native grasses were extensively substituted for exotic ones, seed diversity decreased, and seedeaters declined (Da Silva 1999, Filloy & Bellocq 2006). Another serious concern emerges from the recent occurrence of more frequent and extensive fires. Indeed, the intense degradation of feeding areas, among other reasons, may cause a severe decline in seedeater populations in the Neotropics (Filloy & Bellocq 2006). Management plans for seedeaters should aim at preserving wide areas, including abundant and diverse seed patches in sites where seedeaters also breed during the wet season (Areta et al. 2013, Franz & Fontana 2013, Repenning & Fontana 2016, Rosoni et al. 2019). Further studies may document the use of the Tecoma savanna as a stopover for the species studied here, which also breed to the south of our study area (Franz & Fontana 2013).

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REFERENCES

Areta, JI (2012) Winter songs reveal geographic origin of three migratory seedeaters (*Sporophila* spp) in southern Neotropical grasslands. *Wilson Journal of Ornithology.* 124: 688–697. https://doi.org/10.167 6/1559-4491-124.4.688

Areta, JI & KL Cockle (2012) A theoretical framework for understanding the ecology and conservation of bamboo-specialist birds. *Journal of Ornithology*, *153*(1), 163–170. https://doi.org/10.1007/s10336-012-0 861-z

Areta, JI, A Bodrati, G Thom, AE Rupp, M Velazquez, I Holzmann , E Carrano & CE Zimmerman (2013) Natural history, distribution, and conservation of two nomadic *Sporophila* seedeaters specializing on bamboo in the Atlantic Forest. *Condor* 115: 237–252. https://doi.org/10.1525/cond. 2013.120064

Cintra, R & C Yamashita (1990) Habitats, abundância e ocorrência das espécies de aves do Pantanal de Poconé, Mato Grosso, Brasil. *Papéis Avulsos de Zoologia* 37: 1–21.

Cueto, VR, L Marone & JL de Casenave (2006) Seed preferences in sparrow species of the Monte desert, Argentina: implications for seed-granivore interactions. *The Auk* 123: 358–367. https://doi.org/10.1093/auk/123.2.358

Da Silva, JMC (1999) Seasonal movements and conservation of seedeaters of the genus *Sporophila* in South America. *Studies in Avian Biology* 19: 272–280.

Díaz, M (1996) Food choice by seed-eating birds in relation to seed chemistry. *Comparative Biochemistry and Physiology Part A: Physiology* 113: 239–246. https://doi.org/ 10.1016/0300-9629(95)020 93-4

Filloy J & MI Bellocq (2006) Spatial patterns of *Sporophila* (seedeater) abundance in the southern neotropics: contrasting agricultural development and geographical position. *Biodiversity and Conser-vation* 15: 3329–3340. https://doi.org/10.1007/s10531-005-1341-z

Franz, I & CS Fontana (2013) Breeding biology of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) in southern Brazilian upland grasslands. *The Wilson Journal of Ornithology* 125: 280–292. https://doi.org/10.1676/12-059.1

Grant, PR & BR Grant (2006) Evolution of character displacement in Darwin's finches. *Science* 313: 224–226. https://doi.org/ 10.1126/science.1128374

Hejl, SJ, J Verner & W Bell (1990) Sequential versus initial observations in studies of avian foraging. *Studies in Avian Biology* 13: 166–173.

Jahn, AE, VR Cueto, CS Fontana, AC Guaraldo, DJ Levey, PP Marra & TB Ryder (2020) Bird migration within the Neotropics. *The Auk* 137: 1–23. https://doi.org/10.1093/auk/ukaa033

Machado, É & LF Silveira (2010) Geographical and seasonal distributions of the seedeaters *Sporophila bouvreuil* and *Sporophila pileata* (Aves: Emberizidae). *Papéis Avulsos de Zoologia* 50: 517–533. https://doi.org/10.1590/ S0031-10492010003200001

Marone, L (1992) Seasonal and year-to-year fluctuations of bird populations and guilds in the Monte desert, Argentina. Journal of Field Ornithology 63: 294–308. https://doi.org/ 10.1093/auk/123.2.358.

Marone, L, JL De Casenave & VR Cueto (2000) Granivory in southern South American deserts: conceptual issues and current eviden-ce. *BioScience* 50: 123–132. https://doi.org/ 10.1641/0006-3568(20 00)050%5B0123:GISSAD%5D2.3.CO;2

Peet, RK (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics* 5: 285–307. https:// doi.org/10.1146/annurev.es.05.110174.001441

Pol, RG, GI Pirk & L Marone (2010) Grass seed production in the central Monte desert during successive wet and dry years. *Plant Ecology* 208: 65–75. https://doi.org/10.1007/ s11258-009-9688-y

Poulin, B, G Lefebvre & R McNeil (1994) Diets of land birds from northeastern Venezuela. *The Condor* 96: 354–367. https:// doi.org/10.2307/1369320

Pozer, CG & F Nogueira (2004) Flooded native pastures of the northern region of the Pantanal of Mato Grosso: biomass and primary productivity variations. *Brazilian Journal of Biology* 64: 859–866. https://doi.org/10.1590/ S1519-69842004000500016

Price, T (1987) Diet variation in a population of Darwin's fin-ches. *Ecology* 68: 1015–1028. https://doi.org/ 10.2307/1938373

Repenning, M & CS Fontana (2016) Breeding biology of the Tropeiro Seedeater (*Sporophila beltoni*). *Auk* 133: 484–496. https://doi.org/10. 1642/AUK-15-226.1

Ridgely, RS & G Tudor (1994) *The birds of South America*. *Volume II*. *The suboscine passerines*. University of Texas Press, Austin, TX, USA.

Rosoni, JRR, MM Krügel, CS Fontana & ER Behr (2019) Território reprodutivo do coleiro-do-brejo (*Sporophila collaris*) no sul do brasil: seleção e descrição de áreas de nidificação e alimenta-ção . *Ornitología Neotropical* 30: 33–43. https://doi.org/ 10.58843/orn neo.v30i0.377

Schluter, D (1982a) Distributions of Galapagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology* 63: 1504–1517. https://doi.org/ 10.2307/1938876

Schluter, D (1982b) Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. *Ecology* 63: 1106–1120. https://doi.org/ 10.2307/1937248

Schwinning S & O Sala (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141: 211–220. https://doi.org/10.1007/s00442-004-1520-8

Seidl, AF, JDSV de Silva & AS Moraes (2001) Cattle ranching and deforestation in the Brazilian Pantanal. *Ecological Economics* 36: 413–425. https://doi.org/10.1016/ S0921-8009(00)00238-X

Sick, H (1997) *Ornitologia brasileira*. Editora Nova Fronteira, Rio de Janeiro, Brasil.

Silva, JDSV, J Silva & MDM Abdon (1998) Delimitação do Pantanal brasileiro e suas sub-regiões. Pesquisa agropecuária brasileira, 33: 1703–1711.

Simpson, EH (1949) Measurement of diversity. *Nature* 163: 688. https://doi.org/10.1038/163688a0

Smith, JN, PR Grant, BR Grant, IJ Abbott & LK Abbott (1978) Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* 59: 1137–1150. https://doi.org/ 10.2307/1938228

Soares, JJ & AKMD Oliveira (2009) O Paratudal do pantanal de

Miranda, Corumbá-MS, Brasil. *Revista árvore* 33: 339–347. https://doi.org/10.1590/S0100-67622009000200015

Symes, CT, SW Nicolson & AE McKechnie (2008) Response of avian nectarivores to the flowering of Aloe marlothii: a nectar oasis during dry South African winters. *Journal of Ornithology* 149: 13–22. https://doi.org/10.1007/s10336-007-0206-5

Tannus, JLS, MA Assis & LPC Morellato (2006) Reproductive phenology in dry and wet grassland in an area of Cerrado at southeastern Brazil, Itirapina-SP. *Biota Neotropica* 6: 1–15. https://doi.org/10.1590/S1676-06032006000300008

Tebbich, S, M Taborsky, B Fessl, M Dvorak & H Winkler (2004) Feeding behavior of four arboreal Darwin's finches: adaptations to spatial and seasonal variability. *The Condor* 106: 95–105. https://doi.org/10.10 93/condor/106.1.95

Walker, JS (2007) Dietary specialization and fruit availability among frugivorous birds on Sulawesi. Ibis 149: 345–356. https://doi.org/10. 1111/j.1474-919X.2006.00637.x.