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Breeding biology of the Sayaca Tanager (*Thraupis sayaca*) in southeast Brazil

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ABSTRACT

Thraupis is a genus of the American endemic Thraupidae (subfamily Thraupinae), comprising seven species that inhabit tropical forests to urban centres. The Sayaca Tanager (*Thraupis sayaca*) is a disturbance-tolerant species of high representativeness in plant-frugivore networks, but information on its breeding biology is scarce and often restricted to non-systematic surveys. We studied the breeding biology of the *T. sayaca*, following 39 active nests in a periurban area of southeast Brazil during two breeding seasons (2017/2018, 2018/2019). The breeding season ranged from early September to middle December, and the nests were placed in native and exotic plants and human buildings (nest height above ground: 3.35 ± 1.73 m, mean ± SD). Only females incubated and brooded, but both adults built the nests, fed the nestlings, and removed their faecal sacs. Clutch size was 2.86 ± 0.38 eggs and nest attentiveness was 71.2%. The incubation and nestling periods were, respectively, 13.4 and 17.4 days. Males and females did not differ on nestling provisioning and nest sanitation rates. Nestling provisioning (13.35 ± 6.25 trips/hour) increased with nestling age, while mean brooding time was 37.2% and decreased with nestling age. Apparent nest success was 38.7%, and nest survival according to the Mayfield method was 27.2%. Five nests (20.8%) were parasitised by the Shiny cowbird (*Molothrus bonariensis*), and we recorded five events of nest-site reuse. We concluded that the most remarkable breeding traits of *T. sayaca* in comparison with close-related tanagers are the use of anthropogenic nest sites, the higher clutch size and number of feeding trips, and the longer nestling period.

Introduction

The knowledge on the natural history of species is crucial to understand evolutive and biogeographical patterns of biodiversity (Ricklefs 1980; Conway and Martin 2000). Reproduction is a particularly important moment of life cycle due to the high energetic investment and its direct link with individual fitness. In birds, for instance, breeding traits such as clutch size, the duration of nest phases, and the investment on parental care are mutually connected and related to breeding success in complex ways (Tieleman et al.

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2004; Martin et al. 2017). The Neotropical avifauna has a highly representative portion of the world bird diversity in species richness and endemism (Stotz et al. 1996). The increasing efforts applied to explore the breeding biology of Neotropical birds have revealed the variety and complexity of their breeding traits (Auer et al. 2007; Marini et al. 2012; Marques-Santos et al. 2015), and their potential contributions as modelling species to the study of behavioural ecology (Dias et al. 2009; Marques-Santos et al. 2018). Nevertheless, basic aspects of the natural history of most Neotropical bird species are still poorly known.

Thraupidae (Passeriformes) is a speciose family of songbirds comprising *ca* 408 species in 105 genera endemic to Americas (Hilty and Bonan 2019). The breeding biology of several Thraupidae species has been recently described with special attention to finches (e.g. Gressler and Marini 2011; Chiarani and Fontana 2015) and seedeaters (e.g. Franz and Fontana 2013; Vizentin-Bugoni et al. 2013; Repenning and Fontana 2016; Ferreira and Lopes 2017; Rosoni et al. 2019). Although these efforts have considerably improved the knowledge of natural history of Thraupidae, the breeding biology of other representative groups of this diverse passerine family remains understudied.

The genus *Thraupis* and five close-related genera (*Ixothraupis, Chalcothraupis, Poecilostreptus, Stilpnia* and *Tangara*) compose a speciose monophyletic clade within subfamily Thraupinae with 65 species (Burns et al. 2016; Hilty and Bonan 2019). The Sayaca Tanager (*Thraupis sayaca*), one among seven *Thraupis* species, is widely distributed in South America, occurring in most of the Brazilian territory except in Amazonian Forest, Bolivia, Paraguay, Uruguay and northern Argentina (Sick 2001; Remsen et al. 2019). This species inhabits a variety of habitats, including riparian forests, savannas, plantations, and anthropic fields with isolated trees (Sick 2001; Pizo and dos Santos 2011). *Thraupis sayaca* is classified as a disturbance-tolerant species, being common in urban areas and one of the first to settle in restoration sites during early vegetation development (Athiê and Dias 2010; Batisteli et al. 2018). Due to this wide habitat distribution and tolerance, *T. sayaca* is amongst the main dispersers of a number of zoochoric plants, being especially relevant for plant-frugivore networks in disturbed landscapes (Pizo 2004; Pizo and dos Santos 2011).

To date, systematic studies focused on the breeding biology of *Thraupis* spp. or close-related genera cited above are still rare in the scientific literature (e.g. Gómez et al. 2000; Eisermann et al. 2011; Sheldon et al. 2014). The most complete available data on *T. sayaca* breeding provides the characterisation of nests, eggs, and nest placement, clutch size, the length of reproductive season, incubation and nestling periods, instances of nest-site reuse, and the sexual division of parental tasks (Di Giácomo 2005). Hayes (2014) reported breeding phenology and clutch size for 17 nests in Paraguay. Further information is scattered and from few (two to six) nests each study (Borges and Marini 2010; Marini et al. 2012; Marques-Santos et al. 2015; de la Peña and Salvador 2016). Furthermore, quantitative data on *T. sayaca* incubation rhythm and nestling care is lacking in the scientific literature.

Here, we describe the breeding biology of *T. sayaca* from a systematic nest searching and monitoring study in southeast Brazil. We report nesting phenology, nest site, nest and eggs characteristics, the duration of incubation and nestling periods, estimates of nest survival, nest site and nest reuse, brood parasitism by the Shiny cowbird (*Molothrus bonariensis*), and the first detailed information on parental behaviour (the time parents spent incubating eggs and brooding nestlings, and the rates of nestling provisioning and

nest sanitation). We also tested if males differ from females in the number of feeding trips to the nest, and the frequency of nest sanitation, and whether the feeding rate, the time spent brooding the young, and the proportion of faecal sacs ingested by parents vary with nestling age.

Materials and methods

Study area

This study took place at the campus of the Universidade Federal de São Carlos (21º59′02″S, 42º52′58″W), São Carlos municipality, southeast Brazil. The climate is classified as subtropical with two well-marked seasons, with mean monthly temperatures varying from 16.2ºC to 22.4ºC, and annual rainfall of 1435 mm, concentrated from September to Abril (Alvares et al. 2013). The study site is in the southern region of the Cerrado (Brazilian savanna) domain, but the original vegetation is highly converted in agriculture, mainly pastures and sugar cane plantations. The campus is a periurban area, and its urbanised portion where the study was conducted has well-spaced buildings surrounded by gardens with native and exotic shrubs and trees (Lessi et al. 2017).

Fieldwork

We captured adult birds with mist nets and marked them with unique combinations of coloured leg bands. We searched nests from August to February 2017/2018 and 2018/2019 by inspecting all the likely nesting sites (shrubs, trees and buildings) and following behavioural cues of adults. Nests were monitored using a mirror attached to a pole every 2–3 days to determine nest fate. We also checked the nests daily near expected dates of hatching and fledging to register the duration of incubation and nestling periods. We made 1-h duration sessions of focal observation using binoculars 8 × 40 mm and 10 × 42 mm at a minimum distance of 10 m from the nests at places of wide pedestrian flow to avoid observer effect. Observation sessions were carried out between sunrise and 10:00 h of non-rainy days. Nests were observed from 1 to 6 h each during incubation (mean ± standard deviation: 2.58 ± 1.62 h per nest) and from 1 to 14 h each during nestling period (4.09 ± 3.86 h per nest). During observations, we quantified the per cent time spent incubating the eggs (i.e. nest attentiveness) or brooding the nestlings, the frequency of nestling provisioning as the number of feeding trips to the nest, and nest sanitation as the number of faecal sacs swallowed or carried away by parents. In four nests where at least one adult was banded, nestling provisioning and nest sanitation was quantified for each adult. In these four nests, only one adult was seen incubating the eggs and brooding the nestlings, which we assumed to be the female. Therefore, we assumed that individuals that were incubating or brooding were females in all the nests, as already reported for species belonging to close-related genus (Arcos-Torres and Solano-Ugalde 2007; Freeman and Greeney 2009).

To estimate clutch size, we considered only nests found during the construction or laying phases. Eggs were measured to the nearest 0.1 mm using a manual caliper and weighed using a digital scale (± 0.1 g). We measured the nests (internal diameter, external diameter, internal height, and external height) using a rule to the nearest 0.1 cm. Nest height above ground and the height of supporting plant were measured with a graduated

pole to the nearest 0.1 m. Plant supports were identified at the lowest taxonomic level possible based on morphology.

Statistical analyses

To test whether nestling provisioning and nest sanitation rates differed between parents, we created generalised linear mixed-effects models (GLMMs) with the Poisson distribution. The number of feeding trips to the nests or the number of faecal sacs removed by each parent were set as dependent variables, with parent sex as a factor, and breeding pair ID as a random factor in both models. We also tested if nestling age (as a continuous dependent variable) affects (a) the nestling feeding rate using a GLMM with Poisson distribution, and (b) the percentage of time spent brooding (arcsine transformed) using a linear mixed-effects model, setting nest ID as a random variable in both tests. We used a log link function for the feeding rate model assuming that feeding trip frequency is constrained by energetic limitations in parental effort (Moreno 1987), and we set a negative exponential link function for the brooding model since parents are expected to completely cease nestling brooding some days before they fledge (Skutch 1954). We created a GLMM to test whether the proportion of faecal sacs carried away instead swallowed vary with nestling age. We calculated apparent nest success as a simple ratio between successful nests (i.e. nests that produced at least one fledgling) and the number of total nests. Since apparent nest success do not account for nests that failed before they could be found, we also estimated nest survival according to the Mayfield protocol (1961), which provides a more reliable estimate of nesting success based on nest exposure time. This method provides a daily survival rate (DSR) considering the number of nest failures in an interval of n nest exposure days (i.e. two nests exposed during 5 days correspond to 10 nest exposure days), through the equation DSR = 1 − [nest failures/exposure days]. We estimated separately the DSRs for incubation and nestling phases and compared them following Hensler and Nichols (1981). This comparison consisted in confronting the critical z-value at a given α to the z-value obtained from

$$z = \frac{|DSR_{egg} - S^2_{egg}|}{\sqrt{DSR_{nestling} - S^2_{nestling}}}$$

where S^2 is the variance of DSR in each nest phase. This variance, in turn, is expressed by

$$S^2 = \frac{DSR \times (1 - DSR)}{exposure\,days}$$

To obtain the estimated Mayfield survival across the entire nest cycle duration, we considered that incubation and nestling periods last 14 and 17 days, respectively (see Results). All analyses were made in the software R (R Core Team 2019) using the package 'lme4' (Bates et al. 2015), with α = 0.05. Values are reported in the text as mean ± standard deviation.

Results

We found 39 nests (eight in 2017, and 31 in 2018) between early September to middle December, with a first peak in late September, a second in late October, produced by the

cumulative effect of nests in different phases, and a third peak of new nesting attempts in middle November (Figure 1). Mean nest height above ground was 3.35 ± 1.73 m (n = 39, range 1.4–10.1 m). The height of plants used as nesting support was 6.18 ± 3.32 m (n = 27, range 2.7–5.0 m), and most of the nests were placed on exotic plants (Table 1) (Figure 2(a)). Twelve nesting attempts (30.8%) occurred in nests placed in anthropogenic supports. Both adults participated in the nest construction performing 16.5 ± 13.5 trips per hour (n = 4 h of observation in four nests). Male and female brought the material to the nest usually in synchronous trips, when each of them deposited the material and shaped the nest. The nest was a thick-walled open cup attached to the support by the bottom and laterals. Nests were internally coated with vegetal fibres and externally lined with dry leaves, seed down, rachises of compound leaves, and anthropogenic debris, such as plastic twines, pieces of sewing threads, and hygienic paper (Figure 2(b,c)). Some nests were externally covered by seed down, which conferred them a general whitish appearance. The main components of nest walls were vegetal fibres, pieces of dry grass, grass inflorescences, petioles and roots. Nest measurements (n = 5) were: internal diameter 6.90 ± 0.54 cm, external diameter 11.50 ± 1.36 cm, internal depth 4.40 ± 0.30 cm and external height 7.98 ± 2.38 cm.

Clutch size was 2.86 ± 0.38 eggs (n = 7), and eggs measured 23.3 ± 2.1 mm in length (range 20.2–29.7 mm), 17.1 ± 0.7 mm in width (range 1.56–1.81 mm) and weighed 3.42 ± 0.32 g (range 2.8–3.9 g) (n = 16 eggs from six nests). Eggs had a whitish background,
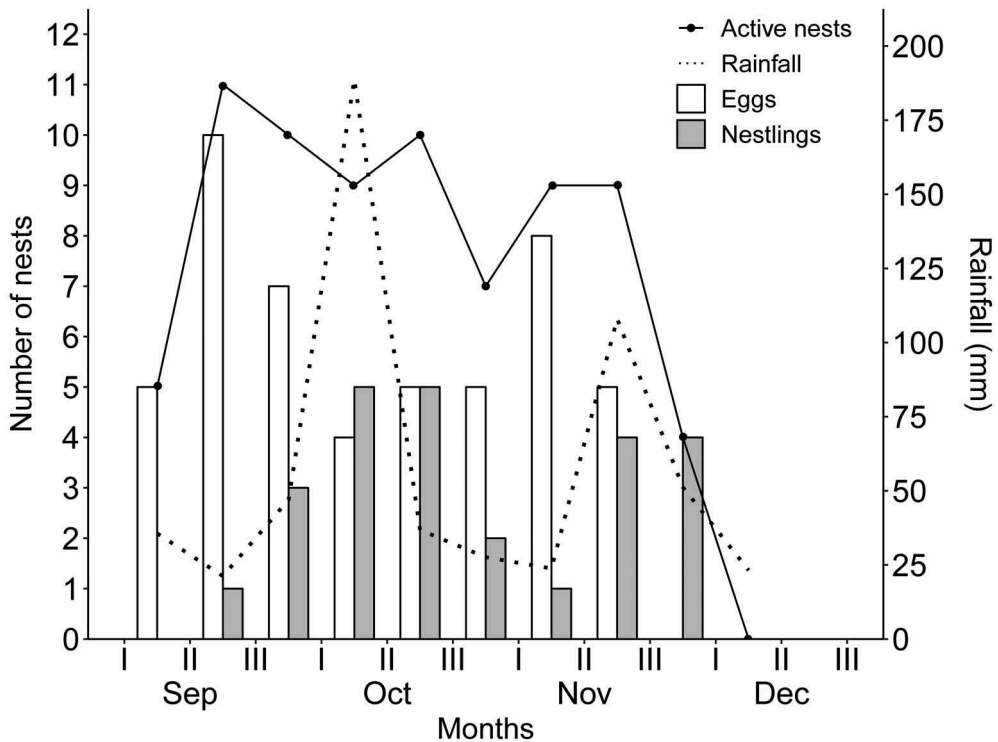

Figure 1. Number of active nests (solid line) of the Sayaca Tanager (*Thraupis sayaca*), number of nests with eggs (white bars) and nestlings (grey bars), and rainfall (dotted line) across months of the breeding season (subdivided in ten-day intervals).

Table 1. Plants used as nesting support by the Sayaca Tanager (*Thraupis sayaca*) in a periurban area of southeast Brazil, their botanical family, and the frequency of nests in each species. Asterisks indicate exotic species.

Family	Plant species	Frequency
Arecaceae	*Caryota mitis**	1
	*Phoenix roebelenii**	5
Asparagaceae	*Dracaena fragrans**	2
	*Yucca gigantea**	1
Asteraceae	*Gymnanthemum amygdalinum**	3
Bignoniaceae	*Handroanthus impetiginosus*	1
	Tabebuia roseoalba	1
Fabaceae	*Bauhinia variegata**	1
	*Delonix regia**	1
	Hymenaea courbaril	1
Lauraceae	*Nectandra megapotamica*	2
Melastomataceae	*Tibouchina granulosa*	1
Moraceae	*Morus nigra**	1
Oleaceae	*Ligustrum lucidum**	2
Podocarpaceae	*Podocarpus macrophyllus**	1
Rosaceae	*Eriobotrya japonica**	1
	*Pyrus communis**	1
Rutaceae	*Murraya paniculata**	1

abundant brown spots in patterns that varied mainly between nests, from concentrated in the blunt pole to uniformly distributed, and black marks that sometimes resembled punctures (Figure 2(d,e)). Eggs were laid in consecutive days (n = 20 eggs from seven nests), and the incubation started when the second egg was laid. Females spent 71.2 ± 17.2% of the time incubating the eggs (range 18.2–98.7%), and incubation recesses took 6.16 ± 3.05 min, ranging from 20 s to 15:22 min (n = 32 h in 12 nests). Males were never seen feeding females on the nest. The incubation period lasted 13.4 ± 0.5 days (n = 5 nests) and hatching may be synchronous or asynchronous, with two hatchings in a day and one in the subsequent day. Hatchlings had purplish dark skin, white commissures, intense pink mouth, and a dense grey down in the back, upwings and head.

During the nestling phase, females spent 37.2 ± 19.7% of the time brooding the young, and on-bouts duration decreased with nestling age (linear mixed model, t = 4.505, p < 0.001) (Figure 3(a)), so that females did not brood the nestlings in 12 of 15 h of observation when they were older than 8 days. Both parents fed the young at a rate of 13.35 ± 6.25 feeding trips per hour (n = 45 h in 11 nests), which corresponds to 5.65 ± 2.85 feeding trips per nestling/hour. The frequency of feeding trips increased with nestling age (GLMM, z = 5.072, p < 0.001) (Figure 3(b)). The frequency of nestling provisioning did not differ between parental sexes (GLMM, z = 0.900, p = 0.366; males 6.37 ± 3.08 trips per hour; females 7.74 ± 3.81 trips per hour; n = 27 h in four nests). Food items delivered to nestlings were small fruits, bites of fruit pulp (i.e. mango and avocado), and small arthropods. Both male and female were engaged on nest sanitation, usually swallowing faecal sacs (85.4% of all nest sanitation events) which the nestlings excreted immediately after being fed, and the frequency of nest sanitation did not differ between parental sexes (GLMM, z = −0.328, p = 0.743). The proportion of faecal sacs carried away instead swallowed increased with nestling age (GLMM, z = 2.015, p = 0.044). The nestling period lasted 17.4 ± 0.5 days (n = 7 nests), and siblings left the nest invariably at the same day. The fledgling plumage
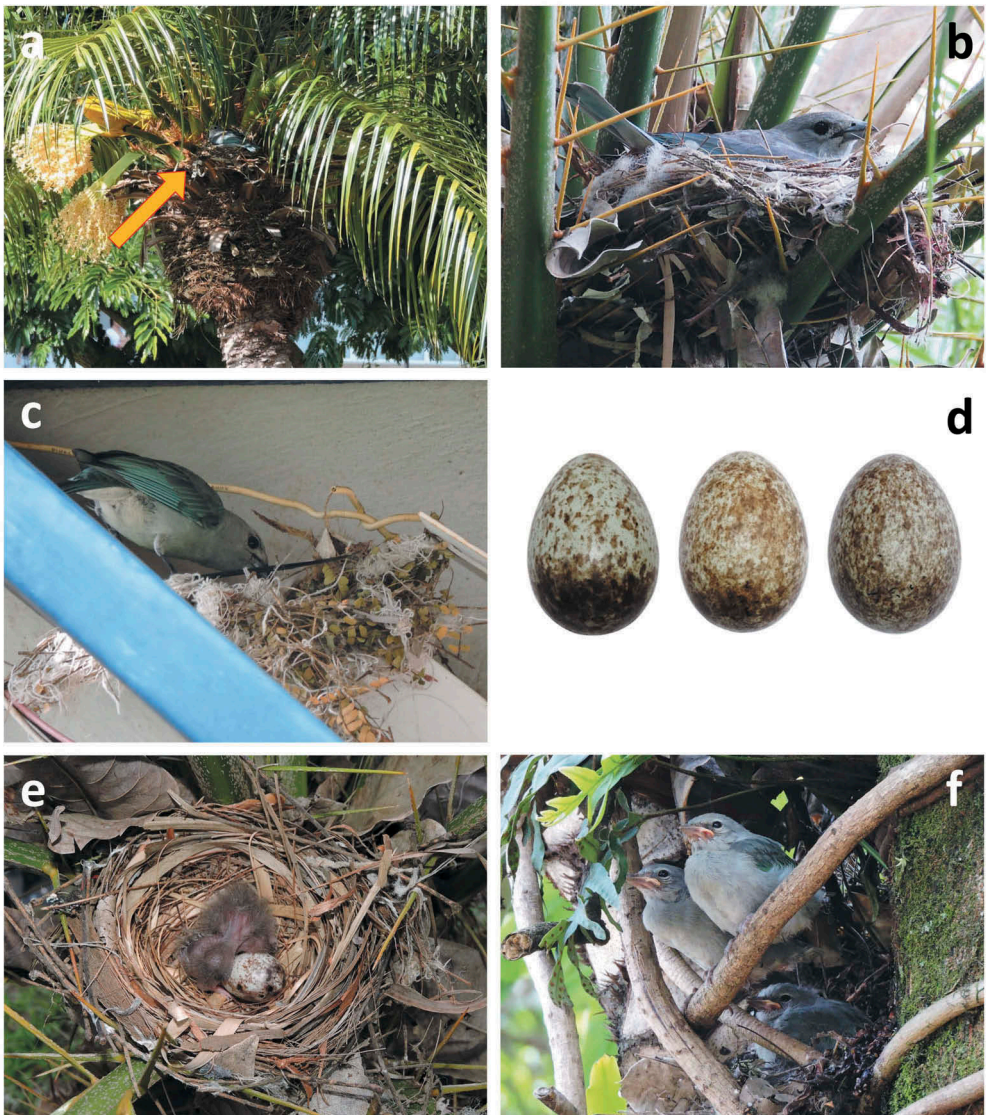
Figure 2. Nest site, nest, eggs, hatchings and fledglings of the Sayaca Tanager (*Tangara sayaca*). A nesting site under the leaves of a Phoenix palm (a), an incubating female (b), a nest externally coated with compound leaves and sewing threads in a human building structure (c), patterns of egg shell colouration (d), 1-day-old hatchling and one egg (e), and newly 17-day-old fledglings (f).

colouration was quite similar to that of adults, but without the same brightly bluish tonality in the primary wing feathers (Figure 2(f)).

Apparent nest success was 38.7% (12 successful nests in 31 monitored nesting attempts). The DSR estimated according to the Mayfield protocol did not differ between nest phases (Z = 0.966, p = 0.334), being 0.949 ± 0.132 during the egg phase (n = 235 exposure days in 26 nests), and 0.964 ± 0.013 during the nestling phase (n = 195 exposure days in 17 nests). The survival according Mayfield during the egg phase was 50.6%, and during the nestling phase 53.7%, resulting in a nest survival of 27.2% during the whole
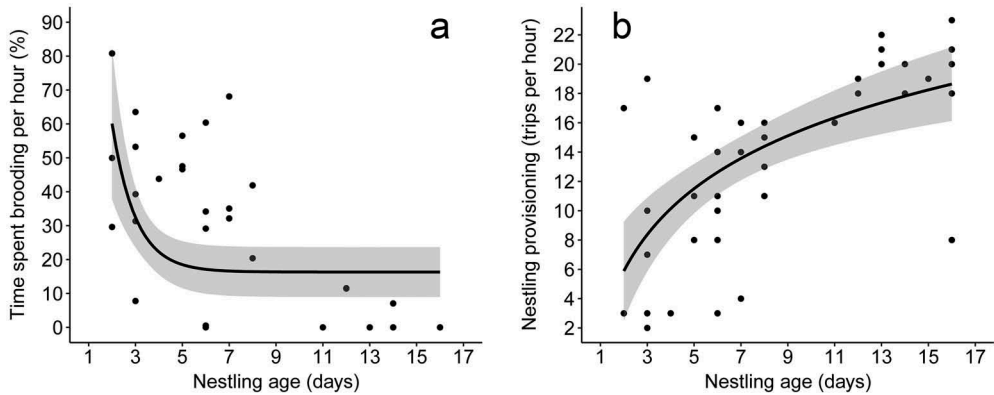
Figure 3. Percent time spent brooding the nestlings per hour (a), and the number of feeding trips per hour (b) in relation to nestling age in the Sayaca Tanager (*Thraupis sayaca*).

nesting cycle. The only nest abandonment occurred during incubation. We observed no partial brood loss during the nestling phase. Brood parasitism by *M. bonariensis* occurred in five of 24 nests (20.8%) when the nest content could be checked, and all of them contained a single cowbird egg. In the only predation event we witnessed, a Toco Toucan (*Ramphastos toco*) depredated two 8-d old nestlings of a nest placed in a *Morus nigra* tree.

We observed five events of nest-site reuse among the 39 breeding attempts. Four nesting sites (two anthropogenic and two natural supports) used in 2017 were reused in 2018, and one nest was occupied in two consecutive broods in 2018 (both successful and separated by 25 days between the fledging day of the first and the laying of the second clutch). In the four between-seasons instances of nest site reuse, birds built new nests over the old ones or in the very same place of an old, dismantled nest, while the nest used two times in 2018 was just lined between the first and the second brood. A male was seen feeding fledglings while her female incubated a new clutch. In this case, the young fledged in October 27 and the laying of a second clutch in a new nest started at November 7. These two nests of the same pair (the first an indoor nest, and the second placed in a tree) was *ca* 20 m apart from each other.

Discussion

The breeding season of tanagers is widely variable among regions and species, following local climate and its effect on food availability (Greeney and Nunnery 2006, 2006; Duca and Marini 2011; Sheldon et al. 2014). The breeding season of *T. sayaca* we recorded (early to middle rainy season) matches most tanagers in Paraguay, central, south and southeast Brazil (Andrade 1996; Willis and Oniki 2003; dos Santos and Marini 2010; Gussoni and Develey 2011; Marini et al. 2012; Hayes 2014; Veloso et al. 2018; Zima et al. 2019), although it can extend over January in south Brazil and Argentina (Di Giácomo 2005; Marques-Santos et al. 2015; de la Peña and Salvador 2016). The phenology of breeding attempts showed three peaks of active nests. Although we did not find more than two nesting attempts by the same breeding pair each breeding season, several other Neotropical passerines can make

up to three or four nesting attempts per breeding season when at least one of the first have failed (Repenning and Fontana 2016; Ferreira and Lopes 2017; Morais et al. 2019).

The mean height above ground of *T. sayaca* nests in our study was lower than in Argentina (mean 5.58 m, de la Peña and Salvador 2016) and central Brazil (mean 3.83 m, Marini et al. 2012). It was also lower than the Palm Tanager *Thraupis palmarum* (Andrade 1996) and the Burnished-buff Tanager *Stilpnia cayana* (Willis and Oniki 2003). The few robust samples of tanager nests available in the literature report a mean nest height above ground of 3.7 m for the White-rumped Tanager *Cypsnagra hirundinacea* (dos Santos and Marini 2010), 14.9 m for the Flame-faced Tanager *Tangara parzudakii* (Sheldon et al. 2014), 21 m for the Azure-rumped Tanager *Poecilostreptus cabanisi* (Eisermann et al. 2011), and less than 1 m for the grassland White-banded Tanager *Neothraupis fasciata* (Alves and Cavalcanti 1990). We found no nests <1 m height from the ground, corroborating that such nests are rare among tanagers, with exception of some grassland tanagers and some nests of the Silver-beaked Tanager *Ramphocelus carbo* (Alves and Cavalcanti 1990; Sick 2001; Batisteli and Fieker 2011).

Thraupis sayaca was largely flexible about nesting support choice, using mainly exotic plants, and being one of the few tanagers to nesting in human buildings as reported by Di Giácomo (2005), as well as for *T. parzudakii* and the Blue Tanager (*Thraupis episcopus*) (Gómez et al. 2000; Sick 2001; Sheldon et al. 2014). Exotic plants as nesting supports are punctually reported for this and several close-related species, such as the Blue-and-yellow Tanager *Thraupis bonariensis* (Di Giácomo 2005; de la Peña and Salvador 2016), *T. palmarum* (Andrade 1996), *T. episcopus* (Skutch 1954), *Tangara* spp. such as the Brassy-breasted Tanager *T. desmaresti* (Gonzaga and Castiglioni 2006), the Gilt-edged Tanager *T. cyanoventris* (Gussoni and Develey 2011), and *T. cabanisi* (Eisermann et al. 2011), and the Scrub Tanager *Stilpnia vitriolina* (Freile 2015). The use of exotic plants and anthropogenic structures as nesting supports may enhance the settlement of bird species in human-modified areas (Møller 2010; Reynolds et al. 2019). However, studies on the effect of these nesting supports on the breeding performance of adults report controversial findings, so that these alternative nesting sites may sometimes act as ecological traps (Borgmann and Rodewald 2004; Rodewald et al. 2010; Mainwaring 2015).

Information available on nest measurements for *Thraupis* and close-related tanagers are often limited to a few nests per species. The nest measurements we found matched (although around 10% deeper) those of Azure-shouldered Tanager *Thraupis cyanoptera* in Brazilian Atlantic Forest (Zima et al. 2019), *T. sayaca*, and *T. bonariensis* in Argentina (de la Peña and Salvador 2016). However, the nests we measured were in general larger than reported for the Black-capped Tanager *S. heinei* (Arcos-Torres and Solano-Ugalde 2007; Greeney et al. 2008) and five *Tangara* spp. (Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007; Sheldon and Greeney 2007; Greeney et al. 2011), with exception of *T. parzudakii* nests and a nest of the Green-and-gold Tanager *T. schrankii*, which were slightly deeper (Van Houtan and Alvarez-Loayza 2006; Sheldon et al. 2014). In comparison with two other tanagers of similar clutch size, the nests of *T. sayaca* were larger but slightly shallower than those of White-rumped Tanager *Cypsnagra hirundinaceae* (dos Santos and Marini 2010), and smaller than those of White-banded Tanager *Neothraupis fasciata* in all dimensions but external height (Alves and Cavalcanti 1990).

Thraupis sayaca nests look similar to those of congeneric species, being a relatively robust open cup firmly attached to the substrate (Sick 2001), although with some differences regarding nest composition compared to close-related species. Several *Tangara* spp., for instance, employ lichens and moss either in nest structure or lining (Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007; Sheldon and Greeney 2007; Greeney et al. 2008, 2011; Gussoni and Develey 2011; Sheldon et al. 2014), which we not observed in *T. sayaca* nests. The vegetal materials we recorded in *T. sayaca* nests are also found in nests of *Stilpnia* spp. and *Tangara* spp. (Willis and Oniki 2003; Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007; Greeney et al. 2008; Gussoni and Develey 2011; Freile 2015). Anthropogenic materials, including cloth and plastic were previously reported only in nests of *T. sayaca* and *S. vitriolina* (Almeida et al. 2012; Freile 2015), and we firstly reported the use of hygienic paper among the studies cited above. The frequent use of anthropogenic nesting material suggests that these items may resemble natural nesting materials (Batisteli et al. 2019). The pieces of sewing threads, for instance, are likely substitutes to plumose seeds regard to their white colour and malleability. The presence of anthropogenic debris on bird nests is thought to be maladaptive, since it may reduce nest survival due to increased visibility to predators and cause the death of adults and juveniles by entanglement (Borges and Marini 2010; Townsend and Barker 2014; Canal et al. 2016). Although we had not recorded any case of entanglement, we do not discard that debris had contributed to reduce nest survival in our study by increasing nest predation.

Unlikely suggested by Di Giácomo (2005), males of *T. sayaca* contribute effectively for nest construction, gathering material and modelling the nest, as in the congeneric Golden-chevroned Tanager *Thraupis ornata*, Yellow-winged Tanager *Thraupis abbas, T. cyanoptera, T. palmarum*, and *T. episcopus* (Skutch 1954; Kirwan 2009; Zima et al. 2019), besides *T. parzudakii* (Arcos-Torres and Solano-Ugalde 2007) and *S. vitriolina* (Freile 2015). In other tanagers, however, both members of the pair gather nesting material, but only the females shape the nest (reviewed in Gonzaga and Castiglioni 2006; Arcos-Torres and Solano-Ugalde 2007), or the females solely build the nest (Greeney et al. 2008; dos Santos and Marini 2010; Sheldon et al. 2014). Males were never seen feeding incubating females, unlike in some *Tangara* and *Stilpnia* species (Van Houtan and Alvarez-Loayza 2006; Arcos-Torres and Solano-Ugalde 2007; Freeman and Greeney 2009; Freile 2015). In summary, the sexual division of further breeding duties in *T. sayaca* resembles such close-related species in which females are exclusively responsible for incubation and nestling brooding, and both sexes account for nestling provisioning (Arcos-Torres and Solano-Ugalde 2007; Freeman and Greeney 2009). This pattern also occurs in other Thraupidae, such as seedeaters and finches (Franz and Fontana 2013; Vizentin-Bugoni et al. 2013; Ferreira and Lopes 2017; Rosoni et al. 2019).

Egg-laying in consecutive days as we recorded was previously reported for *T. sayaca* (Di Giácomo 2005), but is not a rule among tanagers (consecutive days: Skutch 1954; Van Houtan and Alvarez-Loayza 2006, 48 h interval: Greeney et al. 2008; Freile 2015). The eggshell background colour and spotting patterns we observed is similar to previous descriptions (Di Giácomo 2005; de la Peña and Salvador 2016). *Thraupis sayaca* eggs in our study site were larger than in Argentina (Di Giácomo 2005) and those of *S. heinei* (Greeney and Nunnery 2006; Greeney et al. 2008), *S. vitriolina* (Freile 2015), *T. parzudakii* (Sheldon et al. 2014), and Blue-and-black Tanager *Tangara vassorii*

(Greeney et al. 2011), but smaller and less elliptical than eggs of the congeneric *T. cyanoptera* (Zima et al. 2019) and *T. bonariensis* (de la Peña and Salvador 2016). Mean clutch size of *T. sayaca* in our study is higher than in Paraguay (Hayes 2014), than *T. episcopus* (Gómez et al. 2000), other *Tangara* spp. and *Stilpnia* spp. (Skutch 1954; Greeney et al. 2008; Sheldon et al. 2014), and three other syntopic tanagers in central Brazil (Alves and Cavalcanti 1990; dos Santos and Marini 2010; Veloso et al. 2018), but virtually the same mean clutch size of southern American traupids (Yom-Tov et al. 1994). The hatchlings of *T. sayaca* differ from those of the congeneric *T. cyanoptera* and *T. episcopus, S. heinei*, and *S. vitriolina* due to their purplish instead of pinkish skin (Skutch 1954; Arcos-Torres and Solano-Ugalde 2007; Freile 2015; Zima et al. 2019), and from those of *T. schrankii* due to their grey instead of white down feathers (Van Houtan and Alvarez-Loayza 2006).

Among the 29 Thraupidae species victims of brood parasitism by *M. bonariensis*, only 12 are effective hosts (i.e. successfully raise parasitic nestlings, Lowther 2018). Five victims belong to *Thraupis*, and only *T. palmarum, T. bonariensis* and *T. sayaca* are hosts for *M. bonariensis* (Lowther 2018). Brood parasitism among studied nests was low compared to other potential hosts in the study area, such as the Rufous-collared Sparrow (*Zonotrichia capensis*) and the Pale-breasted Thrush (*Turdus leucomelas*), which have >90% of their nests parasitised (Batisteli, unpublished data). In areas where *M. bonariensis* is common, such as our study site (Lessi et al. 2016), egg puncture may be an important cause of clutch reduction even in unparasitized nests (Massoni and Reboreda 2002). The scarcity of partial clutch loss during incubation suggests that *T. sayaca* nests in our study site are actually barely visited and explored by cowbirds, probably because of the predominance of certain parasitic female lineages that prefer the hosts mentioned above (Mahler et al. 2007).

Nest attentiveness by *T. sayaca* females during incubation was close to reported for the congeneric *T. episcopus* in Costa Rica (Skutch 1954), and high compared to other tanagers, such as *S. heinei* and *S. vitrolina* in Ecuador (Freeman and Greeney 2009; Freile 2015), *C. hyrundinacea* and the Swallow Tanager *Tersina viridis* in central Brazil (dos Santos and Marini 2010; Veloso et al. 2018), and several other neotropical passerines in Argentina (Auer et al. 2007), but close to other tropical tanagers (reviewed in Chalfoun and Martin 2007). However, the nest attentiveness we observed is lower than reported for other predominantly granivorous Thraupidae in southeast Brazil, such as the Double-collared Seedeater (*Sporophila caerulescens*, Francisco 2006), and the Lined Seedeater (*Sporophila lineola*, de Oliveira et al. 2010).

The incubation period of *T. sayaca* eggs we observed is close to the 14 days reported for Argentinean populations (Di Giácomo 2005; de la Peña and Salvador 2016) and relatively short compared to *Stilpnia* spp. (14–15 days, Greeney et al. 2008; Freile 2015), *Tangara schrankii* (15–17 days, Van Houtan and Alvarez-Loayza 2006), and other tanagers (15–17 days: Alves and Cavalcanti 1990; dos Santos and Marini 2010; Valdez-Juarez and Londoño 2016; 17–19 days: Veloso et al. 2018). On the other hand, the duration of nestling period we reported is longest than in *Tangara* species, which range from 13 to 17 days (Skutch 1954; Eisermann et al. 2011) and other tanagers (Alves and Cavalcanti 1990; Duca 2007; dos Santos and Marini 2010; Valdez-Juarez and Londoño 2016) with exception of the secondary cavity-nester *T. viridis* (22–24 days, Veloso et al. 2018). A long nestling period after a relatively short incubation period seems to be a remarkable difference on

the life-history traits of *T. sayaca* and the congeneric *T. episcopus* (Skutch 1954; Gómez et al. 2000) in relation to close-related species.

The rate of feeding trips per nestling we observed was higher than in most of the tanagers (Gonzaga and Castiglioni 2006; dos Santos and Marini 2010; Sheldon et al. 2014; Veloso et al. 2018), albeit lower than reported for *S. heinei* (Freeman and Greeney 2009) and Beryl-spangled Tanager *T. nigroviridis* (Sheldon and Greeney 2007). The increase in the rate of feeding trips with nestling age indicates that parents are not able to adjust completely the amount of food delivered at each feeding event to attend the growing energetic demand of nestlings. This increasingly parental activity has been reported in other Neotropical passerines (Francisco 2006; Franz and Fontana 2013; Sheldon et al. 2014; Arslan and Martin 2019), and it is expected to enhance nest detectability for visually oriented predators, reducing nest survival as predicted by Skutch (1949). Nestling brooding declined until completely ceasing in most of our observations after nestlings were 8-d old, as in *T. nigroviridis* and *T. parzudakii* (Sheldon and Greeney 2007; Sheldon et al. 2014, but see Freeman and Greeney 2009).

Our data revealed an equivalent rate of feeding trips and nest sanitation between males and females. Such inter-sexual comparisons of participation in breeding duties are rare among tanagers because sexes is often undistinguishable, but other studies reported that both members of the pair-fed the young in a quick succession, suggesting an equivalent participation of both adults (Sheldon and Greeney 2007; Freeman and Greeney 2009; Sheldon et al. 2014). In some tanagers, however, females surpass males in nest attendance, making more feeding trips or removing more faecal sacs (Van Houtan and Alvarez-Loayza 2006; Freeman and Greeney 2009; Freile 2015). Nest sanitation behaviour differed from *T. nigroviridis* and *T. parzudakii* (Sheldon and Greeney 2007; Sheldon et al. 2014), which carry away instead ingest most of faecal sacs regardless of nestling age. Although nest helpers are known for some tanager species (Alves and Cavalcanti 1990; Gelis et al. 2006; dos Santos and Marini 2010), we did not observe more than two adults attending the nests.

Nest success was higher than in other tanagers that make open-cup nests (Greeney et al. 2008; dos Santos and Marini 2010; Eisermann et al. 2011), but lower than reported for other open-cup Thraupidae (i.e. seedeaters and finches) in southeastern Brazil (Francisco 2006; de Oliveira et al. 2010; Freitas and Francisco 2012; Ferreira and Lopes 2017). The longer nest cycle including an extended nestling period in *T. sayaca* may have contributed to this relatively lower nesting success compared to finches and seedeaters. We observed five events of nest-site reuse (12.8% of all nesting attempts), of which four occurred from one breeding season to the next. Nest reuse, although rare among open-cup nesters, is known to occur in *T. schrankii* (Van Houtan and Alvarez-Loayza 2006), while nest site fidelity between consecutive breeding seasons is reported for *T. sayaca* (Di Giácomo 2005), *T. palmarum* (Andrade 1996) and *P. cabanisi* (Eisermann et al. 2011). The reasons underlying nest and nest site reuse in *T. sayaca* and other tanagers require further studies.

Our study provides a complete assessment of the breeding biology of the Sayaca Tanager, being one of the first systematic nesting biology study on this genus and one of the few on tanagers in general. We highlighted the participation of males on nest construction, the use of anthropogenic nest sites and nesting materials, the high clutch size and number of feeding trips, and the relatively long nestling period when compared to other Thraupidae.

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