ECOSYSTEMS

Drivers of nest survival in the Tawny-bellied Seedeater *Sporophila hypoxantha* (Aves: Thraupidae): time-specific factors are more related to success than ecological variables

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Abstract: Tawny-bellied Seedeater (*Sporophila hypoxantha*) is an endangered (in Brazil) grassland dependent species, whose breeding success remains poorly known hampering conservation measures on its breeding grounds. Here we analyze the nest survival of the species in relation to temporal and environmental variables over three breeding seasons in hilly dry grasslands in southern Brazil. The apparent nest success was 40%, and MARK survival 20%. Predation was the main cause of failure, affecting 55% of the unsuccessful nests, followed by desertion, infestation by *Philornis* fly larvae, cattle trampling and burning. The productivity was 1.77 young per pair. Best models include time-specific factors (nest age and time of breeding season), reflected by a gradual reduction in nest survival over the nesting cycle, accompanied by an increase in temperature, subcutaneous larvae infestation, and predation. Nest site characteristics did not influence nest survival. Predation is more prevalent in the nestling rearing period than during incubation. This tendency may be caused by an increase in the activity in the nests, as is predicted by the Skutch hypothesis. The conclusion that time-specific factors influence nest survival more than ecological variables is important to plan on seasonally dependent conservation and management measures.

Key words: breeding, nesting, predation, productivity, reproductive success.

INTRODUCTION

Nest predation is the most important single factor reducing nest success (Ricklefs 1969, Willis 1974, Roper 1992) and therefore may often be an important driver of life history evolution (Martin 2004). The higher rate of predation shown by Neotropical birds in relation to patterns in the northern hemisphere has been debated (Ricklefs 1969, Oniki 1979, Skutch 1985, Martin 1995). The simple differences in clutch size, a widely discussed and tested attribute among North and South American birds, have been well-known since the study by Moreau (1944), although variations between latitudes are in need of a major revision (Martin et al. 2000a).

Nest survival varies spatially and temporally due to differences in climate, predator community and human disturbance (Skutch 1985). Time-specific factors, such as nest age or time of breeding season may be related to variation in the nest predation risk for many species (Grant et al. 2005). An increase in predation during the nestling phase (the age-specific effect) may be due to increased activity at the nest as a consequence of feeding nestlings (the Skutch hypothesis, Skutch 1949). The selection pressure exerted by predation would force pairs to visit the nest less often and would thus restrict the potential clutch size (Martin 2011). Lack (1947) proposed an alternative to Skutch, stating that

the latitudinal difference in clutch size would actually be related to food availability and the ability of the parents to obtain it. Longer day length would allow individuals to find more food each day and, therefore, feed more nestlings. Testing Skutch's predictions, Roper & Goldstein (1997) demonstrated that the activity at a nest does not increases its chance of predation, which elucidates the need to rethink the role of predation in the evolution of tropical and temperate life histories. Indirect factors such as habitat features (i.e. whether or not variation in the nest height from the ground and support plant species favor nest concealment) influence the probability of predation and, therefore, reproductive success (Slagsvold 1982, Martin & Roper 1988).

While 80% of all passerines occur in tropical latitudes, the disproportional majority of studies that serve as a theoretical base for the understanding of behavioral ecology in birds have been conducted with north-temperate zone species (Stutchbury and Morton 2008). These authors estimate the proportion of north-temperate *vs.* tropical bird studies to be >100:1. Martin (1996) called the state of knowledge about the life history traits of tropical/southern hemisphere birds as "extremely poor." The majority of comparisons are drawn between the northern hemisphere and the tropics, and subtropical regions (south-temperate) are even more poorly studied. In addition, grassland areas are weakly represented in comparative analyses (Robinson et al. 2010). Although some studies have provided estimates of breeding success for *Sporophila* seedeaters, typical representatives of open habitats in southern South America (Silva 1999), just Repenning & Fontana (2016) inquired into the factors that are related to nest survival using modeling (on that case, for the Tropeiro Seedeater *S. beltoni*).

Here we estimate the nest survival of Tawny-bellied Seedeaters *Sporophila hypoxantha* (Aves, Thraupidae) in Brazilian subtropical grasslands and compare time-specific factors, i.e. nest age and time of the breeding season, and ecological variables (e.g. nesting traits and concealment assessments) that apparently influence nest survival. For this, we employed models that include combinations of temporal, spatial and ecological factors.

MATERIALS AND METHODS

Study site and species

The study was conducted in the *Campos de Cima da Serra* region (Brazilian Subtropical Highland Grasslands, *sensu* Iganci et al. 2011), in dry grasslands that occur along the Lava-Tudo river, in the municipalities of São Joaquim and Lages (considered two subareas in the analyses), southeastern Santa Catarina State, southern Brazil (central point: 28° 18' S, 50º 17' W). The altitude varies from 800 to 1,000 m a.s.l. among field sites and the vegetation is rich in Asteraceae shrubs, grasses such as *Sorghastrum*, *Andropogon*, *Paspalum* and *Setaria* spp. and the thorny "eryngo" *Eryngium horridum* (Apiaceae). See a detailed description of the study site in Franz & Fontana (2013).

Average monthly temperature is 13.3 °C (coldest region in Brazil) and cumulative year rainfall is 1,609 mm with no remarkable seasonality. Climatic data used in our analysis were obtained from the meteorological station of the National Institute of Meteorology (INMET), located in São Joaquim, around 33 Km from the study area.

In southern Brazil, the breeding season of the Tawny-bellied Seedeater lasts about 100 days, from the first week of November until the end of February (Franz & Fontana 2013). Females arrive a few days after the males,

which arrive in the study area the first week of November and quickly establish territories. The nest is constructed slightly above the ground (~40 cm) and is camouflaged by shrubs such as *Symphyopappus*, *Vernonanthura*, *Baccharis* and *Stevia* spp. The clutch size is two but may be three in some cases, and incubation lasts for 12 days. Nestlings are fed by the pair (the males feed nestlings once they are older) and fledge the nest after 9-10 days (Franz & Fontana 2013), which is similar to the timing in resident populations in Argentina (Di Giacomo 2005, Facchinetti et al. 2008). This grassland-dependent species is considered as endangered in Brazil (Vulnerable; ICMBio 2018).

Field procedures

During three breeding seasons (2007-2010), we conducted intensive nest-searching from the first week of November until March, in which we observed the behavior of females in territories defended by males (Martin & Geupel 1993). Each nest was marked with small biodegradable colored tape 5-10 m from the nest and a point location with GPS. In order to verify the content and determine the activity status of nests, we visited each nest every 2-6 days until it became inactive (success or predated/deserted) and eggs or nestlings were quantified. We considered incubation the period between the laying of the first egg and the hatching of the first chick (Facchinetti et al. 2008, Franz & Fontana 2013) and nestling period from the hatching of the first egg until the first nestling fledged the nest. The nests and contents were not manipulated except for a few nestlings that were banded after reaching seven days in age. For nests found during incubation, we estimated age by counting backwards from the hatching date. In nests found during the nestling period, nestlings were aged directly by morphology. We considered a nest successful if at least one nestling fledged. When

a nest was found empty before the expected fledging date or with modified content, we classified it as unsuccessful. Predated nests were those in which eggs or nestlings disappeared before reaching the completion date for each phase of development, when a predation event was documented or when the nest was found deformed. Abandoned nests were those in which incubation exceeded the expected limit for egg hatching or were no longer visited by the female during construction.

The nest site characteristics that were evaluated and measured included support plant species, support plant height, support plant cover area (greater diameter x lesser diameter in a vertical projection), nest height (from the border of the nest to the ground; these last three with a ruler) and an estimate of nest concealment (percentage of nest cover from breast height of the same observer, with 0 = completely uncovered and 100% = completely covered by plants). Whenever possible in nests with young, we verified the occurrence of subcutaneous parasites (larvae of the dipteran *Philornis seguyi*) by quickly observing the nestlings and once a nest was inactive, searching for pupae in the nest walls.

Data analysis

We employed logistic regression models to evaluate the effect of the measured variables on daily nest survival rates. For this, we used the nest survival model available on the program MARK (White & Burnham 1999). Initially, we continuously numbered each day of the reproductive period from day 1 on, which corresponds with the day in which the first nest was found with an egg during the three breeding seasons together. From the general sample of 69 nests encountered, we selected 47 nests in which we could reliably evaluate the information required for the method indicated

by Dinsmore et al. (2002) that (1) the nests be correctly aged when found, (2) the nest fates be determined with confidence, (3) inspections did not influence survival, (4) the nest fates are independent and (5) there is homogeneity in the daily nest survival rates.

We divided the analysis into two sets of candidate models and each one of the covariates or sets was utilized to represent *a priori* hypothesis and predictions. In addition to the model that assumes a constant survival (null hypothesis model), the first set included a linear time trend model and a quadratic model (polynomial model that includes both a linear and squared value). We hypothesized that the DSR may vary temporally and if so, the time trend models should be favored. Survival may vary linearly, decreasing over the reproductive period in function of a tendency for there to be greater success in early breeders (Ainley & Schlatter 1972), or curvilinearly (quadratic model), in which it may present a better pattern for the intermediate phase of the nesting season. The second set of models includes the covariates in "all combinations" (*sensu* Doherty et al. 2012) and is the set that formed the basis for choosing the models that best fit the data. Five nest-site variables were included as covariates (previously described in field procedures), which is nest height (no. of parameters [K] = 1), plant height (K = 1), plant species (K = 2), plant cover (K = 1) and nest concealment (K = 1). We tested whether nest height or support plant or plant cover influenced nesting success. One spatial variable (in which of two study sites the nest was found, K = 1) may reveal a preference for a specific area on a greater scale. The covariate year represents each of three reproductive seasons (K = 2) and the search for variations in DSR during each season. The covariate nest age (ageday1 *sensu* Rotella 2011), which represents

the day of the first egg for each nest in relation to day 1 of the reproductive period (K = 1).

We compared the values of the candidate models to the constant/null model. To run the null model, we utilized the sin link function, and for those that included the covariates, the logit link function (Dinsmore et al. 2002). Once the competing models were constructed, the support was evaluated among the set of candidate models by means of Akaike's Information Criterion, adjusted for small sample sizes (AIC$_c$; Burnham & Anderson 2002). According to these authors, only models with ΔAIC$_c$ ≤ 2 show substantial support. We tabulated all of the models that were best supported than the null model of each set of competing models and excluded the rest. We utilized the Delta method (Seber 1982) on the 'emdbook' package (Bolker 2011) of the software R version 2.14.0 (R Development Core Team 2011) to calculate and plot the product and variance from the β values of the best model adopted. We did not perform the goodness of fit because there is no reliable GOF test for MARK users on nest survival; moreover, the saturated model fit the data well in these cases (Rotella 2011).

We calculated productivity per pair based on the number of fledglings produced in relation to the number of successful nests (Beier et al. 2017), which is the same of "productivity per nest" or "annual production of fledglings per female" in this species because pairs with successful nests never re-nested in the area (Franz & Fontana 2013). We also calculated hatching rate, which is the number of eggs that hatch in relation to the number of eggs observed. In this way, we determined the frequency of occurrence of brood reduction (partial nest losses) during each phase of the nesting cycle.

To determine the correlations among the measured variables, we ran non-parametric tests for independent samples in the software

BioEstat 5.0 (Ayres et al. 2007). We presented values as means ± SD.

RESULTS

Of the 55 nests in which the final status was known (seven in 2007/2008, 26 in 2008/2009 and 22 in 2009/2010), 22 (40%) were successful, with 57%, 35% and 41% during the seasons 2007/2008, 2008/2009 and 2009/2010, respectively. Of these 22 successful nests, 39 young fledged, which represents an average productivity of 1.77 ± 0.52 young per pair per reproductive season (this species is mainly one-brooded) in successful nests. Six pairs fledged one, 15 fledged two and one fledged three young. During the incubation period, partial nest loss occurred in five nests due to predation (one egg predated in clutches of two eggs [$n = 4$], and two eggs predated in clutches of three eggs [$n = 1$]). Of the 60 eggs studied during incubation, eight did not hatch, resulting in a hatch rate of 86% (or 14% of the eggs failed to hatch). During the nestling phase, partial losses occurred in six nests (18%), always with the loss of one nestling.

The daily survival rate (MARK estimates) was 0.979 ± 0.01 during incubation and 0.878 ± 0.04 during the nestling phase. The probability of survival during the entire nesting cycle was 0.206.

Predation was the main cause of failure (55% of the unsuccessful nests), followed by abandonment (30%), infestation by *Philornis* (6%), cattle trampling (6%) and burning (3%). We observed a Brazilian Green Racer Snake (*Philodryas aestiva*, Dipsadidae) preying two three-day-old nestlings. Predated nests were generally found in two forms: intact (most common pattern) or damaged (with holes, pulled apart or totally destroyed). The causes of nest desertion were not confirmed but were likely related to intense winds and rain that caused the females to leave the nests and eggs. Although we documented parasitism by *Philornis seguyi* in 27 nests, only three young died in two nests.

The most parsimonious models found include time-specific factors such as the linear time trend and, especially, nest age (Table I). Only the temporal variables were related to daily nest survival rate. DSR was independent of the five ecological variables measured and their AIC$_c$ values were higher than that of the null model when treated without the addition of the variable of nest age (Table I, second set). Only two of the candidate models received substantial support, with Akaike weights summing 0.48 (Table I). Although the model with only the nest age variable is better than the linear + nest age model, it is necessary to consider the penalty caused by the additional parameter of the latter, even though the better model has 1.78 AIC$_c$ units less. The logistic regression equation for this best model was simply Logit (Ŝ) = 5.26 − 0.18 (nest age). However, we found that DSR decreases over the reproductive season and that it decreases rapidly with the increasing age of the nests (Figure 1).

Daily nest survival values were negatively correlated with maximum daily temperature in the study area ($P = 0.001$), which gradually increases between November (monthly average 19.9 ± 4.2 °C) and February (monthly average = 22.9 ± 2.54 °C).

DISCUSSION

We found that nest age was the most relevant factor to survival in *Sporophila hypoxantha* nests, with DSR sharply falling over the nesting cycle (Figure 1a). In this species, the frequency of visits to the nest are considerably higher during the

Table I. Model for DSR indicating (a) time trend and (b) the determinants of daily survival for nests of Tawny-bellied Seedeaters *Sporophila hypoxantha* in southern Brazilian grasslands, over three breeding seasons (2007-2010). AIC represents Akaike´s Information Criterion corrected for small sample sizes. We excluded models with performance worse than the null model. [a]AIC_c = 114.33. [b]AIC_c = 107.81. ΔAIC_c = difference between AIC_c of each model and the top model; K = number of parameters; w_i = Akaike weight; T = linear time trend; TT = quadratic time trend; *(.)* = null model. Notations follow Dinsmore et al. (2002).

Model	ΔAIC_c	w_i	K	Deviance
(a) Time trend				
S_T	0.00[a]	0.49	2	110.30
S_{TT}	1.00	0.29	3	109.27
$S_{(.)}$	1.74	0.20	1	114.06
(b) Linear trend + covariates				
S_{age}	0.00[b]	0.34	2	103.78
$S_{T + age}$	1.78	0.14	3	103.53
$S_{T + age + study\ site}$	2.19	0.11	4	101.90
$S_{T + age + nest\ concealment}$	3.51	0.05	4	103.22
$S_{T + age + nest\ height}$	3.52	0.05	4	103.23
$S_{T + age + plant\ height}$	3.75	0.05	4	103.46
$S_{T + age + plant\ cover}$	3.82	0.05	4	103.53
$S_{T + age + year}$	4.19	0.04	5	101.85
$S_{T + age + study\ site + nest\ concealment}$	4.21	0.04	5	101.88
$S_{T + age + year + study\ site}$	4.57	0.03	6	100.17
$S_{T + age + plant\ species}$	4.74	0.03	5	102.40
$S_{T + age + year + study\ site + nest\ concealment}$	6.62	0.01	7	100.15
$S_{T + age + year + plant\ species}$	7.99	0	7	101.52
S_{global}	11.59	0	11	96.74
S_T	19.27	0	2	123.05
$S_{T + study\ site}$	19.87	0	3	121.62
$S_{(.)}$	20.70	0	1	126.50

nestling feeding period than during incubation (4-9 visits hr⁻¹ and 2 visits hr⁻¹, respectively; Franz & Fontana 2013). Furthermore, provisioning visits per hour increase as nestlings develop and males care for the young particularly when they are more developed, after they reach four to five days of age (Facchinetti et al. 2008, Franz & Fontana 2013). Therefore, nest activities clearly increase along the nesting cycle, which could aid diurnal predators to find the nests. This pattern is in agreement with the amply debated and partially tested Skutch hypothesis (see Introduction). Various studies have shown this tendency. Recently, Di Giacomo et al. (2011) found this condition in Strange-tailed Tyrants (*Alectrurus risora*) in open savannas of the eastern Chaco, Argentina. Both Brawn et al. (2011) and Auer et al. (2007), which studied various
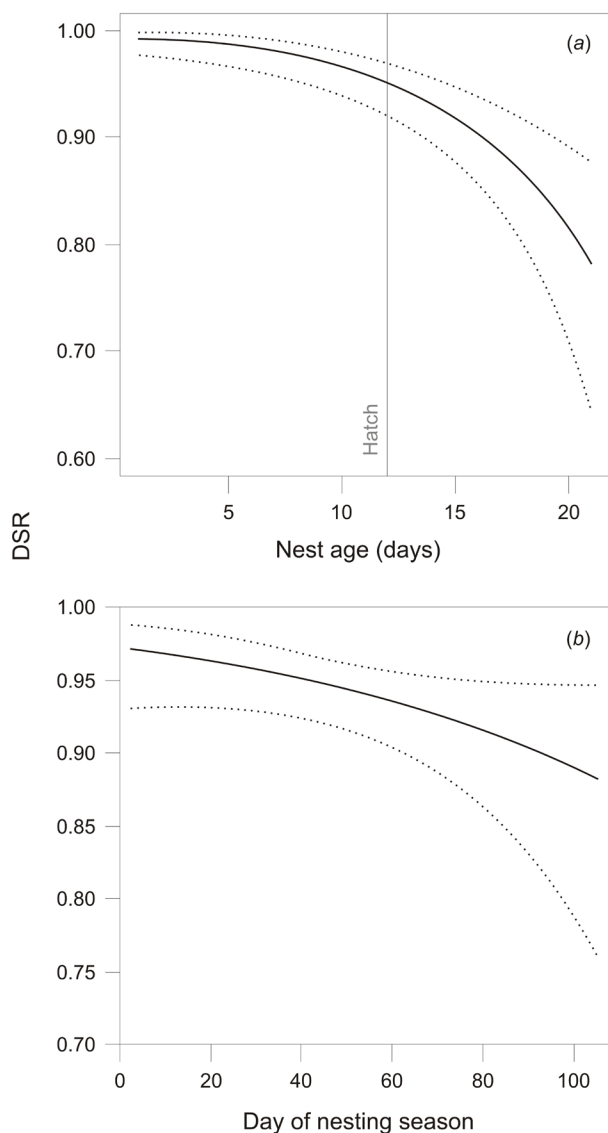
Figure 1. Estimated daily survival rates (DSR) of nests of the Tawny-bellied Seedeaters *Sporophila hypoxanta* during three breeding seasons (2007-2010), according to nest age (a; through the 21-days nesting cycle: 12 of incubation and 9 of nestling) and day of nesting season (b; respecting a linear time trend), calculated with program MARK by means of candidate models that include each predictor variable. Dashed lines represent 95% confidence limits.

passerine species in Panama and Argentina, respectively, found lower rates of survival during the nestling period than during incubation for some of the studied representatives (but see Segura & Reboreda 2012). França & Marini

(2009), in the first study modeling survival of nests of Brazilian birds, reported the decrease in survival over the nesting cycle of Chapada Flycatchers (*Suiriri islerorum*). DSR in the Black-bellied Seedeater was also time dependent, but also was influenced by nest site characteristics (Rovedder 2011). Similarly, Lined and Double-collared Seedeater nests have a higher probability of survival during the incubation period than during nestling rearing (Francisco 2006, Oliveira et al. 2010). Rosoni et al. (2019) found a similar pattern for the Rusty-collared Seedeater (*Sporophila collaris*) in grasslands of southern Brazil, with DSR decreasing with nest age. Although some studies support Skutch's theory (Martin et al. 2000b, Muchai & Du Plessis 2005), others search for alternatives (Segura & Reboreda 2012). Roper & Goldstein (1997) argued against the theory based on an experiment in which they demonstrated that predation does not increase with increased nest activity and the principal predators are nocturnal and not visually oriented.

The Linear time trend model was the temporal model that best explained our data and indicated that the DSR decreases over the breeding season (Figure 1b). This pattern can be seen in many species. Grant et al. (2005) monitored the nests of two passerine species in North Dakota and found a better model for both species that considers only nest age (but with a cubic effect) and a second best model that also included a linear time trend. *Sporophila melanogaster* (Rovedder 2011), Stripe-tailed Yellow-finches (*Sicalis citrina*; Gressler 2007) and *Alectrurus risora* (Di Giacomo et al. 2011) also reflected this linear effect on DSR. *Sporophila collaris* also presented a linear time trend, but with DSR increasing over the breading season (Rosoni et al. 2019). In the present study, we exclude the ideas that this pattern is due to the occurrence of renesting

because this rarely occurs with this species in the study area (Franz & Fontana 2013) or a decrease in protective cover (Davis 2005), since the shrubs and surrounding vegetation do not change during the months of study. Alterations in the predator community (Grant et al. 2005) and food resource availability were not tested. As seen, temperature increases throughout the season and, consequently, so does intensity of nestling parasitism by subcutaneous *Philornis* larvae. This could potentially reduce the DSR as the end of the breeding season approaches (Skutch 1985, Grant et al. 2005).

We included in the experimental design the hypothesis that the daily survival rates of Tawny-bellied Seedeater nests was not influenced by height above ground, support plant species and nest concealment which is possibly caused by low amount of variation in the measured values of these variables. Nests are higher than 25 cm and lower than 60 cm (Franz & Fontana 2013), and perhaps this variation is not sufficient in providing an effect on the differential access capacity to nests by predators. The same theory could serve for the support plants, which are structurally similar (more than 80% of the nests were in the shrubs *Vernonanthura chamaedrys* e *Symphyopappus compressus*; Franz & Fontana 2013), and thus vary little with respect to nest concealment.

The estimated reproductive success for Tawny-bellied Seedeaters in southern Brazil (40% of apparent success and 20% of MARK survival) is similar to that found in other species of *Sporophila* seedeaters, although only a few studies are available. In the only study of reproductive success in the "capuchinos group" (a clade of small and colorful seedeaters composed by our study species and 11 others), Rovedder (2011) obtained an apparent reproductive success of 42% and a Mayfield success of 21% (*n* = 64) for the Black-bellied

Seedeater (*S. melanogaster*), which is also found in Brazilian subtropical grasslands. Francisco (2006) found an apparent success of 36% (*n* = 41) for the Double-collared Seedeater (*S. caerulescens*) in southeastern Brazil. In this same region, the apparent success of Lined Seedeaters (*S. lineola*) was higher (56%, *n* = 41; Oliveira et al. 2010). Blue-black Grassquits (*Volatinia jacarina*), a closely related species that nests in open areas, had a lower success (24%, *n* = 81) in central Brazil (Aguilar et al. 2008). Skutch (1985) found a success of 54.5% (*n* = 44) in nests of the Variable Seedeater (*S.* ["aurita"] *corvina*), in Costa Rica. Chestnut-throated Seedeaters (*S. telasco*) had a success of 37% (*n* = 190) in Equador (Marchant 1960). The 40% success found for *S. hypoxantha* (between 36% and 56% for *Sporophila* seedeaters studied up to today) can be considered median, within the normal range and close to the average for tropical birds.

As expected, predation was the principal cause of nest failure and affected 55% of the unsuccessful nests (33% of the total). The rate of predation is more closely related to the pattern found in birds of north-temperate zones (40-60%, Martin 1993) than with the high predation pressure exerted on tropical zones (55-85%; Stutchbury & Morton 2001 but see Oniki 1979). This apparent reduced predation rate may be related to the efficient camouflage of the nests in general compared to syntopic species. In the same area, nests of other shrub-nesting species such as the Bearded Tachuri (*Polystictus pectoralis*) that are more visible in the vegetation have higher rates of predation (Fontana et al. unpubl. data). Characteristics of the vegetation near nests influence the probability of predation (Martin & Roper 1988, Martin 1993, Roper 2000, Fontaine et al. 2007). Additionally, behavioral adjustments due to the risk of predation (Fontaine & Martin 2006)

seem to be efficient and cause nesting activities to be more inconspicuous. Roper et al. (2010) state that individuals that are under lower than average predation risks may be favored in the selection that leads to lower predation rates.

All cases of nest desertion occurred during the incubation period (n = 7) or nest construction (n = 3), and this is the second most important cause of nest failure, affecting 30% of unsuccessful nests. Desertion is likely related to the locally frequent rainstorms, but may also include lack of food resources (Ricklefs 1969), or parents' perceiving risk of predation (Berger-Tal et al. 2010, Zanette et al. 2011).

Parasitism by *Philornis seguyi* (Diptera) may importantly influence survival as it occurred in 61% of nests with Tawny-bellied Seedeaters nestlings. *Philornis seguyi* is known to have negative effects of infestations on chick survival and nestling growth of other birds (Rabuffetti & Reboreda 2007, Segura & Reboreda 2011). In Tawny-bellied Seedeaters, mortality occurred in only three nestlings (two of them had 24 and 26 larvae; Franz & Fontana 2013) suggesting that infestations of more than 20 larvae per nestling may be lethal as we documented that nestlings with between five and 17 larvae fledged successfully. *Philornis* may also influence survival of other seedeater species such as *S. americana*, *S. lineola*, *S. angolensis*, *S. nigricollis*, *S. angolensis*, *S. bouvreuil*, *S. intermedia* and *S. caerulescens* (Gross 1952, Dodge & Aitken 1968, Löwenberg-Neto 2008) for which other *Philornis* species have been reported.

Analyzing the nest survival of the Tawny-bellied Seedeater in relation to temporal and environmental variables over three breeding seasons in Brazilian subtropical grasslands we show that best models include time-specific factors as nest age and time of breeding season, reflected by a gradual reduction in nest survival over the nesting cycle, accompanied by an increase in temperature, subcutaneous larvae infestation, and predation. This conclusion is important to plan on seasonally dependent conservation and management measures in a region facing harmful land-use and climate changing. We consider the study areas to be of utmost importance in the conservation of this species and others that reproduce in or utilize the region as a stopover during migration. Finally, we suggest more studies with grassland-dependent South American birds, especially those endangered species with medium-low breeding success and productivity, in order to identify their ecological and biological requirements.

Acknowledgments

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Ismael Franz was responsible for the funding acquisition, project conceptualization, field data collection, analysis, figure production, writing and review. Carla S. Fontana was responsible for the funding acquisition, project conceptualization, writing and review.