JOURNAL OF
AVIAN BIOLOGY

Research article

Anthropogenic nesting substrates increase parental fitness in a Neotropical songbird, the pale-breasted thrush *Turdus leucomelas*

Augusto Florisvaldo Batisteli[1], **Hugo Sarmento**[2] and **Marco Aurélio Pizo**[3]

[1]Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos–SP, Brazil
[2]Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos–SP, Brazil
[3]Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista Júlio de Mesquita Filho, Rio Claro–SP, Brazil

Correspondence: Augusto Florisvaldo Batisteli (augustofb@gmail.com)

Journal of Avian Biology
2024: e03240
doi: 10.1111/jav.03240
Subject Editor: Elisa Perez Badas
Editor-in-Chief: Staffan Bensch
Accepted 08 May 2024

The failure of breeding attempts is a major hindrance to bird reproduction, making nest site choice under strong selective pressure. Urbanization may offer lower risk of nest predation to certain bird species, but the impact of using anthropogenic structures as nesting sites on parental fitness is seldom studied. We studied the effect of anthropogenic substrates and brood parasitism by the shiny cowbird *Molothrus bonariensis* on the nest success of a Neotropical songbird, the pale-breasted thrush *Turdus leucomelas*. We monitored 263 nesting attempts between 2017 and 2020 to estimate daily survival rate (DSR), which represents the probability of a given nest surviving until the next day. DSR was modelled as a response variable in function of substrate type (plants as 'natural' or human buildings as 'artificial') and brood parasitism as fixed factors, using as covariates year, a linear and a quadratic seasonal trends. Additionally, we tested the effect of these same explanatory variables on the number of fledglings per nest using a generalized linear mixed-effects model. Most nests (78.7%) were placed in artificial substrates and apparent nest success (i.e. the percentage of nesting attempts that produced at least one thrush fledgling) was higher in artificial (50.2%) than in natural substrates (37.5%). DSR was higher for nests in artificial than in natural substrates regardless of cowbird parasitism, whereas the number of fledglings per nest was higher both in artificial substrates and for nests without cowbird parasitism. We highlight that nesting in buildings significantly increases parental fitness in pale-breasted thrushes, which may favor their settlement in cities and potentially drive the evolution of this breeding behavior in urban birds.

Keywords: Breeding behavior, nest success, Turdidae, urban bird

Introduction

The failure of breeding attempts, often referred to simply as nest failure, is a major determinant of avian breeding performance (Martin 1993). Thus, behavioral traits that enhance brood survival are generally under strong selective pressure. For

---

NORDIC SOCIETY OIKOS
www.avianbiology.org

instance, parents actively select the site of nest construction to maximize their reproductive success (Ardia et al. 2006, Camprodon et al. 2008). Nest site can affect parental fitness in several ways, such as promoting an adequate microclimate for incubation and chick development (Ardia et al. 2006), reducing the predation risk of the incubating adult and its clutch (Gómez-Serrano and López-López 2014) and the risk of brood parasitism (Fiorini et al. 2009). Nest site preferences vary among species so that some birds prefer one or a few plant species to support their nests, such as the Brazilian endemic black-bellied seedeater *Sporophila melanogaster* (Rovedder and Fontana 2012) and the Chilean elaenia *Elaenia chilensis* (Gorosito et al. 2024). Other species adapted to human-modified habitats worldwide use a variety of native or exotic plant species and even artificial structures belonging to human buildings as nesting substrates. In this group are passerines such as the Eurasian blackbird *Turdus merula* (Wang et al. 2015) and the Neotropical creamy-bellied thrush *T. amaurochalinus* (Batisteli et al. 2020) and large-bodied species such as raptors and gulls (Soldatini et al. 2008, Wallace et al. 2016). However, several studies have failed to find a clear relationship between nest site features and offspring survival because it depends on morphological and behavioral traits of each species, and the main causes of nest failure at a local scale (e.g. clutch predation; brood parasitism; nestling starvation; Weidinger 2002, Borgmann and Conway 2015, Deeming and Reynolds 2015).

Predation is the commonest cause of nest failure and the list of potential nest predators comprises reptiles, mammals and birds, which differ markedly from each other regarding nest-searching behavior and cognitive abilities (Menezes and Marini 2017). Nest placement, which includes the characteristics of substrates, determines the accessibility of nests to different types of predators, such as aerial/terrestrial and visually/olfactorily-oriented predators (Colombelli-Négrel and Kleindorfer 2009). Thus, depending on the predominant nest predators of a given locality, birds can alter their nest site preferences to reduce predation risk (Lomáscolo et al. 2010). Brood parasitism is another important cause of hatching failure and nestling mortality, for instance, by food competition with host chicks (Massoni and Reboreda 2002). Hatching failure caused by brood parasitic birds involves egg puncturing during nest inspections, heat competition with host eggs and damage to host eggs caused by the thick shell of parasite eggs (Tuero et al. 2007, López et al. 2018). The relative importance of these and other factors that account for nest failure vary broadly among species, nest phases and environmental contexts (Stanley 2000, Okada et al. 2017).

Nest survival rates in human-modified environments vary widely so that some studies reported urban areas as 'safe nesting zones' because of high nest success (Gering and Blair 1999, Ibáñez-Álamo and Soler 2010), whereas others showed that urbanization increases nesting failure (Jokimäki and Huhta 2000). Furthermore, nest success varies broadly between and within urban areas depending on main nest predators, which can differ among regions and across urbanization gradients (Jokimäki et al. 2005, Rodewald and Kearns 2011, Rivera-López and MacGregor-Fors 2016). Similarly, the incidence of brood parasitism is affected by anthropogenic land uses, and on a smaller scale by nest site characteristics (Saunders et al. 2003, Burhans and Thompson 2006, Fiorini et al. 2009). Nevertheless, there are relatively few studies showing how nest site choices influence the patterns of nest survival and brood parasitism in urban areas (Borgmann and Rodewald 2004, Muñoz et al. 2008, Mikula et al. 2014).

The typical nest site features of conspecifics or closely related species are shaped by natural selection in response to the main drivers of nest success and adult survival (Nilsson 1984, Gómez-Serrano and López-López 2014), but nest placement is somewhat flexible so that individuals can exert their own choices under those evolutive constraints (Lomáscolo et al. 2010, Mainwaring 2017). Once a given choice increases parental fitness, it tends to spread within the population, by either genetic inheritance or social learning (Møller 2010, Slagsvold et al. 2013). In this sense, differences in nest site preference among individuals allow population-level responses to environmental variations and the colonization of new areas (Yeh 2007, Lomáscolo et al. 2010).

Some bird species are considered urban adapters, being able to use a variety of anthropogenic resources, such as food and nesting sites (McKinney 2002, Wang et al. 2015). The use of artificial substrates for nesting is widespread among urban birds (Wang et al. 2015, Pizo 2018, Reynolds et al. 2019), but the impacts of the use of such nesting sites on individual fitness have been rarely estimated, and with controversial findings (Mainwaring 2015). For instance, the use of anthropogenic nesting substrates and indoor breeding may increase nest survival (Møller 2010, da Silva et al. 2018; but see Muñoz et al. 2008), while nest proximity to human habitations and indoor nests reduce the chance of brood parasitism (Liang et al. 2013, Møller et al. 2016). However, anthropogenic nesting substrates may act as ecological traps by decreasing the breeding performance of birds (Schlaepfer and Sherman 2002, Sumasgutner et al. 2014).

In this study, we assessed the effect of nesting substrate (natural versus anthropogenic) and brood parasitism on the nest success of a Neotropical songbird, the pale-breasted thrush *T. leucomelas* in an urban area of southeastern Brazil. We predicted that breeding success, expressed by survival rates and the number of fledglings produced, would be greater for nests placed on anthropogenic substrates due to the protective effect of artificial structures. Nests placed on human buildings probably benefit from reduced nest detectability and nest accessibility for both aerial and terrestrial (climbing) predators and brood parasitic birds. We also predicted a lower number of fledglings in nests parasitized by cowbirds regardless of substrate type.

Material and methods

Study area

This study was carried out in two university campuses in São Paulo State, southeast of Brazil: the campus of the

Universidade Estadual Júlio de Mesquita Filho (UNESP), in Rio Claro municipality (22°23′43″S, 47°32′46″W, 115.5 ha), and the campus of the Universidade Federal de São Carlos (UFSCar), in São Carlos municipality (21°59′02″S, 47°52′58″W, 645 ha). The campuses are 57 km apart from each other and the climate in both sites is humid subtropical with dry winters and hot summers (Cwa) according to Köppen classification, with mean monthly temperature varying from 16.2°C to 23°C and annual rainfall of approximately 1344 mm in Rio Claro and 1435 mm in São Carlos (Alvares et al. 2013). The study areas are in the transition between Atlantic Forest and Cerrado domains, and both campuses are well-arborized periurban areas with remnants of native vegetation (semideciduous seasonal forest and savannas). Their urbanized portion contains sparse human buildings surrounded by lawns and managed vegetation with mixed exotic and native plant species.

Study species

The pale-breasted thrush occurs from northern South America to Paraguay and Argentina, inhabiting a variety of habitats from forests to urbanized areas (Collar and Garcia 2020). Breeding season ranges from August to late December, and pairs can have up to three breeding attempts a year (Batisteli et al. 2021a). Only the female builds the nest and incubates the eggs, while both parents rear the chicks (Davanço et al. 2013). In the study area, clutch size is usually three eggs, with incubation and nestling phases lasting 13 and 16 days, respectively (Haddad et al. 2024). The potential predators of eggs and nestlings in the study area are birds, such as raptors (*Caracara planchus*, *Milvago chimachima*, *Rupornis magnirostris* and *Ictinia plumbea*), owls (*Athene cunicularia*, *Tyto furcata* and *Megaschops choliba*), the Toco toucan *Ramphastos toco*, and jays (*Cyanocorax cristatellus* and *C. chrysops*), besides mammals, such as opossums *Didelphis* spp., rodents (*Mus musculus* and *Rattus* spp.) and domestic cats *Felis catus*. Similar to other Neotropical thrushes, the pale-breasted thrush is parasitized by the shiny cowbird (*Molothrus bonariensis*) (Batisteli et al. 2021a). Although cowbirds rarely remove host eggs, they usually puncture host eggs in parasitized and non-parasitized nests, thus being treated as a potential source of breeding failure for hosts (Massoni and Reboreda 2002).

Field procedures

We monitored nests during four breeding seasons (2017–2020) in both Rio Claro and São Carlos. Nests were found by inspecting all potential nesting sites (human buildings or plants) and following adults carrying nesting material or food to the nestlings. We checked the nests using a pole with a mirror every 1–3 days to determine the nest status and content (the number of eggs or nestlings), hatching date and nest fate. For successful nesting attempts, the number of fledglings at the nest at the last nest checking was assumed as the number of fledglings. Recognition of brood parasitism was based on the visual discrimination of eggs and nestlings of the cowbird, as cowbirds eggs are smaller than thrush eggs and their nestlings present black down, rosy skin and red mouth, while thrush nestlings have yellowish down, a more pallid skin and yellow mouth. Predation was assigned when all the eggs or nestlings disappear from the nest before the expected fledgling date, which matches with the circumstances of most failed nests. More rarely, a nest was classified as abandoned when none of the parents was seen in the nest vicinity in three consecutive nest monitoring days or when nestlings were found dead in the nest. For the purpose of this study, predation, abandonment and other likely instances were indistinctly treated as nest failure.

We classified each nest support as natural (plants, usually trees) or artificial, i.e. man-made structures such as concrete columns, metallic rails, lamps, air conditioners, windows, supporting structures of metallic roofs and other structures belonging to buildings.

Statistical analyses

We estimated apparent nest success from the ratio between successful nesting attempts (i.e. those that produced at least one fledgling) and the total number of nesting attempts monitored. We tested whether the frequency of brood parasitism differed between nesting substrates using a Chi-square test. To investigate for likely differential effects of particular artificial structures, the number of successful and failed nesting attempts in the most used man-made structures was compared by means of a Chi-square test before being pooled together as nests in artificial substrates.

Some of the nests were found later in the nesting cycle. To control for a possible methodological bias regarding the influence of nest age on nest survival estimates, we tested whether there was a difference in the timing of nest discovery between nest substrate types (natural or artificial) using a Wilcoxon ranked test. Although most of the nests had been found during laying, some of them were found later during incubation or nestling phases. Thus, the percentage of successful nests might be overestimated as some nests may have failed before being encountered. To account for this imprecision, we used a traditional approach of nest survival estimate following Mayfield (1961). This protocol considers nest fate as nest-day units (i.e. a nest-day is a period of 24 h exposure of a given nest) to calculate daily nest survival rate (DSR) as 1.0 minus the quotient between the number of nest failures and the sum of nest-days in the population (Batisteli et al. 2019a), representing therefore the probability of a given nest surviving until the next day. DSR was modelled as a response variable with the package 'RMark' (Laake et al. 2019), an interface of the program MARK (White and Burnham 1999) in the software R (www.r-project.org), which runs nest survival models and allows testing of the effect of covariables and fixed factors. Modelling nest survival in RMark requires informing, for each nesting attempt, its fate as a binary variable (0 = success, 1 = failure) and three parameters provided as days of the breeding season: 1) the date the nest was found,

2) the last date the nest content was alive and 3) the last date the nest was checked. These dates were determined considering day 1 as the day the first egg was found in a given breeding season.

Due to the high number of potential candidate models, we conducted a two-step hierarchical model selection based on the Akaike information criterion corrected for small sample sizes (ΔAICc) (Burnham and Anderson 2002). Models were considered supported when $\Delta AICc < 2.0$ (Anderson 2008), unless they were more complex derivations of better-ranked models. First, we tested for potential trends of DSR within (i.e. seasonal) and between (i.e. interannual) breeding seasons. We therefore included three temporal trends in the candidate models, namely a linear seasonal trend ('Time'), a quadratic seasonal trend ('$Time^2$') and a linear interannual trend ('Year') using all possible combinations of these variables. Two supported models were retained (see Results), one containing 'Time' and 'Year' and another containing only 'Time', and both were used as baselines to the second step of model selection. In this second step, we included in the candidate models nest age (age 1 = the day the first egg was laid), site (Rio Claro/São Carlos), substrate type (artificial/natural), cowbird parasitism (yes/no) and the interaction between substrate and cowbird parasitism, considering all possible combinations of these variables for each of the two baseline models.

We tested whether the DSR differed between egg (DSR_{egg}) and nestling phases ($DSR_{nestling}$) following Hensler and Nichols (1981). DSR_{egg} was estimated as a subset of DSR considering only nest-days during the egg stage, i.e. without any hatchling in the nest, and nest fate was attributed as successful when at least one thrush egg hatched and failed otherwise. Similarly, $DSR_{nestling}$ considered only nest-days during the nestling stage, from the first hatching onwards, and a nest was successful when at least one thrush egg fledged from the nest, or failed otherwise.

When reporting percentages of nest survival across different phases from DSR, we considered the egg phase as the 14-day period between the laying of the first egg and the hatching of the first nestling, although females effectively start incubating from the second egg onwards. Nestling phase encompasses the 16-day interval between the first hatching and the first nestling fledged from the nest (fledging of thrush siblings usually occurs on the same day), resulting in a complete nesting cycle of 30 days. Therefore, estimated nest survival for egg and nestling phases were obtained by the DSR_{egg}^{14} and $DSR_{nestling}^{16}$, respectively, and their product returned nest survival during a nesting cycle.

Because the Mayfield method described above considers nest fate as a binary variable (failed or successful), we conducted a complementary analysis using the number of fledglings produced per nesting attempt as a response variable to a more direct assessment of parental fitness. Number of fledglings can be strongly influenced by clutch size, which in turn depends on female fitness prior to egg laying. In our study species, however, clutch size has low variation, and using the proportion of fledglings (i.e. fledgling number divided by clutch size) led to the same results (Supporting information), but nests found during the nestling phase should be discarded, reducing the sample size and the robustness of results. Therefore, we opted for using the number of fledglings as a response variable to include both the nests found before and after hatching. The number of fledglings per nesting attempt was used as response variable in a generalized linear mixed-effects model (GLMM) with negative binomial error distribution using the packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017) of the software R (www.r-project.org). Similarly to the DSR approach, the explanatory variables in this GLMM were site (Rio Claro/São Carlos), substrate type (artificial/natural), cowbird parasitism (yes/no), day of breeding season ('Time') and year. Nests were frequently reused in our study populations (Batisteli et al. 2021a), so that we set nest identity as a random factor. The interaction between substrate and cowbird parasitism was assessed but it did not improve significantly the model and was dropped off ($p = 0.504$).

Because clutch size could limit the number of fledglings, we created another negative binomial GLMM to test whether the number of thrush eggs per nesting attempt varies with site (Rio Claro/São Carlos), substrate type (artificial/natural), cowbird parasitism (yes/no), day of breeding season and year. Again, nest identity was set as a random factor and we tested for the interaction between substrate and cowbird parasitism, but it did not improve the model significantly ($p = 0.762$).

Results

We gathered data for 263 nesting attempts, 207 on artificial and 56 on natural substrates, most of them (69.2%) found during or before egg laying. The most used artificial structures were concrete columns ($n = 31$), metallic rails ($n = 25$), lamps ($n = 22$), windows ($n = 21$), supporting structures of metallic roofs ($n = 18$) and air conditioners ($n = 15$), which comprised 63.8% out of the nesting attempts in artificial substrates (Fig. 1). Nest fate as a binary variable did not differ among these kind of structures ($\chi^2 = 7.894$, $p = 0.162$), so they were pooled together as nests in artificial substrates.

Nesting attempts were discovered on average 4.2 ± 5.9 days after initiation (mean ± standard deviation), and were similar between nests placed on natural and on artificial substrates (Wilcoxon ranked test, $W = 5246.5$, $p = 0.243$). Apparent nest success was 47.5%, being higher for nests in artificial (50.2%) than in natural substrates (37.5%). Brood parasitism by the shiny cowbird occurred in 81.7% of the nests, being similar between nests placed in natural (83.9%) and in artificial substrates (81.1%), ($\chi^2 = 0.079$, $p = 0.779$). The DSR did not differ between egg phase (0.958 ± 0.003, 3272 exposure days) and nestling phase (0.956 ± 0.004, 3144 exposure days) ($z = 0.979$, $p = 0.327$). Nesting survival according to the Mayfield method was 54.7% during egg phase and 48.8% during the nestling phase, resulting in an overall survival of 26.7% for the entire nesting cycle.

The global DSR estimated by the null model was 0.978 ± 0.002 (mean ± standard error). The first step of model

Figure 1. The use of man-made structures as nest supports by the pale-breasted thrush *Turdus leucomelas* in southeast Brazil, depicting nests attached to the top, behind or on the side of concrete columns (A), metallic rails (B), lamps (C), air conditioners (D), windows (E) and supporting structures of metallic roofs (F).

selection revealed that two models were equally supported: one of them contained 'Time' and 'Year' and a second model contained only 'Time'. A third model with AICc < 2.0 was not considered as being a more complex version of the best ranked model (Table 1). We therefore retained these two models as alternative baselines for the next step of DSR modelling. In the second step, the best ranked was the unique supported model and included the linear seasonal trend (estimate ± standard error: −0.005 ± 0.004) and year (estimate ± standard error: −0.223 ± 0.001), both corresponding to a progressive decreasing of DSR (Fig. 2), besides nest age and substrate (Table 1). According to that model, DSR decreased with nest age (estimate ± standard error: −0.047 ± 0.010) and was higher for nests placed on artificial substrates (estimate ± standard error: −0.457 ± 0.213) (Fig. 3). A second model was not supported despite having AICc < 2.0 as it was a more complex version of the best ranked model, with the additional presence of 'cowbird parasitism' among the explanatory variables.

The mean number of eggs per nesting attempt was 2.28 ± 0.74 (mean ± standard error, n = 255) and did not differ

Table 1. Results of the hierarchical model selection for nest survival in the pale-breasted thrush *Turdus leucomelas* (n = 263 nesting attempts) based on the Akaike criterion corrected for small sample sizes (ΔAICc). Supported models are in bold (ΔAICc < 2.0, unless they were more complex derivations of best ranked models). Time: linear seasonal trend, Time^2: quadratic seasonal trend, Year: 2017 to 2020, Age: nest age, Subs: substrate (natural or artificial), CB: parasitism by the shiny cowbird *Molothrus bonariensis*. Candidate models with AICc higher than the AICc of the null model not shown.

Model	Parameters	AICc	ΔAICc	Weight	Deviance
Step 1					
S(~Time + Year)	**3**	**927.184**	**0.000**	**0.344**	**921.179**
S(~Time + Time^2 + Year)	4	927.548	0.365	0.287	919.540
S(~Time)	**2**	**928.781**	**1.597**	**0.155**	**924.779**
S(~Time + Time^2)	3	929.919	2.735	0.088	923.914
S(~Time^2)	2	930.120	2.936	0.079	926.117
S(~Year)	2	931.986	4.803	0.031	927.984
S(~1)	1	933.408	6.224	0.015	931.407
Step 2					
S(~Time + Year + Age + Sub)	**5**	**907.741**	**0.000**	**0.362**	**897.730**
S(~Time + Year + Age + Sub + CB)	6	908.975	1.234	0.195	896.959
S(~Time + Year + Age + Sub + CB + Sub:CB)	7	909.827	2.085	0.128	895.805
S(~Time + Year + Age)	4	910.052	2.310	0.114	902.044
S(~Time + Year + Age + CB)	5	910.977	3.236	0.072	900.966
S(~Time + Age + Sub)	4	911.555	3.814	0.054	903.547
S(~Time + Age + Sub + CB)	5	912.533	4.792	0.033	902.521
S(~Time + Age + Sub + CB + Sub:CB)	6	913.886	6.145	0.017	901.870
S(~Time + Age)	3	914.066	6.325	0.015	908.061
S(~Time + Age + CB)	4	914.766	7.024	0.011	906.758
S(~1)	1	933.408	25.666	0.000	931.407

between nesting substrates, neither it was affected by any of the other variables tested (Table 2). The number of fledglings in successful nests averaged 2.24 + 0.43 (n = 257), and the GLMM revealed that nests placed in artificial substrates (Fig. 4A) and those without cowbird parasitism (Fig. 4B) produced more fledglings than those placed in natural substrates, while year, day of breeding season and site had no effect (Table 2).

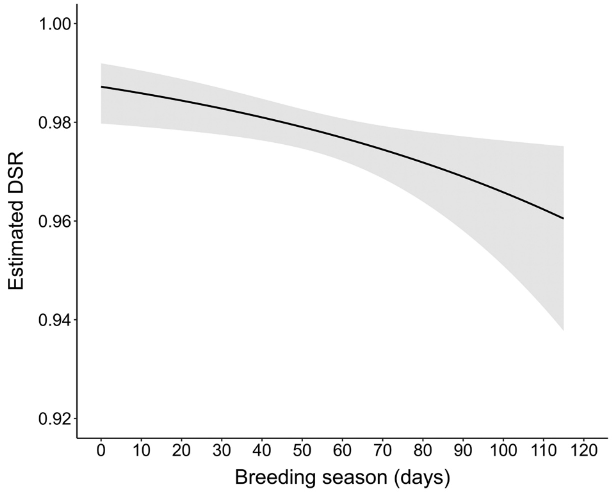

Figure 2. Seasonal variation of daily survival rate (DSR) in 263 pale-breasted thrush *Turdus leucomelas* nests monitored between 2017 and 2020 in two periurban settings in southeast Brazil, where breeding season ranges from late August to late December (day 1 = the day the first egg was laid in each breeding season). The solid line represents the linear trend while the gray envelope represents the standard error.

Discussion

Corroborating our main hypothesis, we found that clutches in nests placed on buildings had greater survival and produced more fledglings than those in nests constructed on natural substrates (Table 1, Fig. 4). Most potential predators of thrush nests in the Neotropics are birds, which are mostly diurnal and visually oriented (Menezes and Marini 2017),

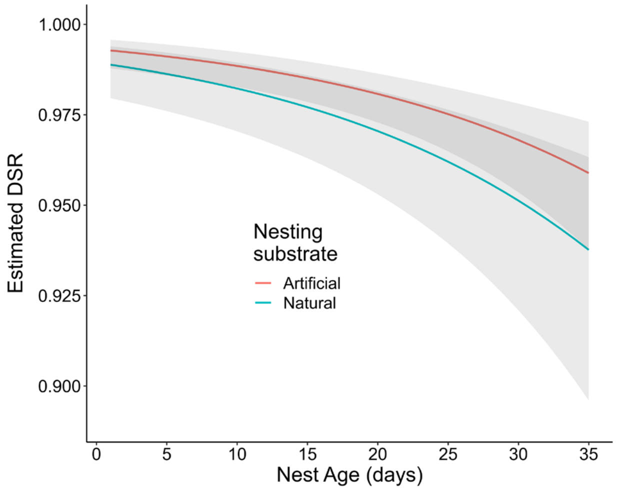

Figure 3. Daily survival rates (DSR) of pale-breasted thrush *Turdus leucomelas* nests placed on artificial and natural substrates (human buildings and plants, respectively) in relation to nest age (day 1 = laying of the first egg), monitored from 2017 to 2020 in two periurban settings of southeast Brazil (n = 263 nesting attempts). Depicted are the tendency lines enveloped by their standard error (shaded areas).

Table 2. Results of generalized linear mixed-effects models assessing the number of eggs and the number of fledglings in nests of the pale-breasted thrush *Turdus leucomelas* ($n=255$ and 257 nesting attempts, respectively) from 2017 to 2020 in two study sites of southeast Brazil. Site: Rio Claro/São Carlos, Time: linear trend within breeding season, Substrate (natural or artificial), CB parasitism: presence of the brood parasitic shiny cowbird *Molothrus bonariensis*. Asterisks indicate statistical significance at $\alpha=0.05$.

	Estimate	Std. error	z	p
Number of eggs				
Intercept	0.902	0.263	3.427	0.001*
Site	−0.026	0.088	−0.297	0.767
CB parasitism	0.132	0.104	1.272	0.203
Substrate	0.022	0.106	0.211	0.833
Year	−0.021	0.037	−0.557	0.577
Time	0.001	0.002	0.381	0.703
Number of fledglings				
Intercept	−0.896	0.545	−1.644	0.100
Site	0.134	0.188	0.710	0.478
CB parasitism	0.733	0.184	3.987	<0.001*
Substrate	0.555	0.232	2.389	0.017*
Year	−0.071	0.075	−0.952	0.341
Time	0.004	0.003	1.226	0.220

but nests in buildings are also likely safe from climbing predators such as opossums. In addition, we suspect that some major avian nest predators in our study area, such as corvids, avoid proximity to or entering into buildings even if they are able to locate the nests, as also reported for European corvids (Møller 2010). Therefore, nests in buildings had lower chance of failure probably because the anthropogenic structures around them restrict their visual exposure or limit the ability of some predators to reach them.

Our data did not support higher survival rates during the egg than the nestling phase, unlike common reports for passerine species (Auer et al. 2007). Parental activity at the nest usually increases from hatching onwards, and constant parental arrivals and departures from the nest enhance its detectability by predators (Skutch 1949, Şahin Arslan and Martin 2024). Additionally, begging calls and odor of nestlings provide additional sensorial cues for predators, enhancing nest location (Colombelli-Négrel and Kleindorfer 2009, Husby 2019). During the egg phase, on the other hand, nest attentiveness is higher, and the presence of parents around the nest or covering the eggs can repel opportunistic nest predators to some extent (Evans and Stutchbury 2012, Hu et al. 2017). Although our finding contradicts the general expectation, similar daily survival rates during egg and nestling phases are reported for other urban passerine populations in the study region, namely the sayaca tanager *Thraupis sayaca* and the creamy-bellied thrush (Batisteli et al. 2019a, 2020), indicating that it may arise from regional aspects such as the characteristics of the main nest predators. Future studies that address predator identity in these areas can help to understand their particular role in egg and nestling survival.

In line with our prediction, the number of fledglings was lower in parasitized nests (Table 2), which may result from egg damage by adult cowbirds and competition for food between cowbird and thrush nestlings. Pale-breasted thrush nestlings have larger body size compared to the shiny cowbird nestmates (i.e. 48.1 versus 27.8 g, respectively, when they are approximately 10 days old, unpubl.), so that we could expect a weak nestling–nestling competition. Indeed, the presence of cowbird chicks did not compromise the survival of thrush chicks for the sympatric creamy-bellied thrush (Astié and Reboreda 2006). Therefore, egg puncturing by adult cowbirds is probably the main negative impact of these parasites on the breeding success of our study species. This egg damaging behavior is a strategy to reduce competition with host chicks for food and thereby to promote parasitic chick survival (Fiorini et al. 2014). We did not find, however, an effect of cowbird parasitism in nest daily survival rates, which indicates that parasitized and non-parasitized nests had the same chance of total failure as in another Neotropical thrush, the creamy-bellied thrush (Astié and Reboreda 2006).

We found that nest survival decreased with the progress of the breeding season (Table 1, Fig. 2), a pattern commonly reported for passerines that may result from biotic and abiotic factors. For instance, climate conditions may worsen as the breeding season progresses, bringing limitations imposed by heavy rains and warmer temperatures (Franz and Fontana 2021). Second, a high number of simultaneous active nests

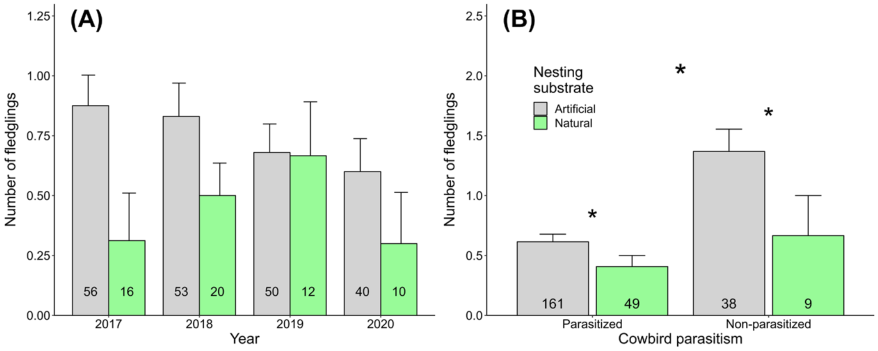

Figure 4. Number of fledglings of pale-breasted thrush *Turdus leucomelas* in nests placed on artificial and natural substrates (human buildings and plants, respectively) across years (A) and in relation to the parasitism by shiny cowbird *Molothrus bonariensis* (B) in southeast Brazil. Numbers inside bars represent sample size ($n=263$ nesting attempts in total), bars represent the mean, whiskers indicate standard errors and asterisks denote statistical significance at $\alpha=0.05$.

during the early breeding season may help to create a dilution effect that makes nests less likely to be predated or parasitized (Gorosito et al. 2023). Nest density in our study species reduces as breeding season progresses because pairs give up making further attempts after a successful clutch (Batisteli et al. 2021a), increasing the chance of predation for each nest. Third, predators may use short-term memory to improve their nest searching abilities, becoming more efficient later in the breeding season as predicted by the 'predator search image' hypothesis (Duca et al. 2019).

Similarly, there was a decreasing trend of nesting survival across study years (Table 1). This trend correlates to an annual increasing of brood parasitism by the shiny cowbird in Rio Claro, where parasitized thrush nests gradually increased from 76.4% in 2017 to a peak of 95.6% in 2019, even without marked changes in the parasite's population size (unpubl.). One can argue that cowbird parasitism should not be evoked to explain a decrease in nest survival rates as it was not part of the best-ranked nest survival model. However, egg puncturing may be as frequent in non-parasitized as in parasitized nests as a way to obligate potential hosts to renest, thus providing a new opportunity for brood parasitism to cowbirds ('farming hypothesis', Massoni and Reboreda 2002, Swan et al. 2015). The increase in brood parasitism across years may be related to host shift by cowbird females, since the shiny cowbird is a generalist parasite that exploits over 100 different host species (Lowther 2023), though there are lineages of cowbird females that prefer certain hosts (Mahler 2007). Decreasing population trends in their preferred hosts might lead to increased parasitism of alternative hosts, but we have no data to test this possibility.

The use of anthropogenic resources, such as nesting substrates and artificial nesting material, has been thought of as a simple consequence of their higher availability in relation to natural elements in the breeding territory of urban birds (Wang et al. 2009, 2015). However, these behaviors are probably more intricate as the use of anthropogenic nesting materials can differ between species exposed to the same availability of human debris (Batisteli et al. 2019b). Moreover, some birds are more inclined to use anthropogenic materials triggered by characteristics such as nest architecture and sexual dimorphism (Jagiello et al. 2023). Likewise, nest site selection may involve complex decision-making processes that include a genetic component, phenotypic plasticity and individual lifetime experiences (Mennerat et al. 2009, Slagsvold et al. 2013), which call for further studies to unravel the factors behind the selection of artificial nesting sites by birds. Although the causes underlying the selection for buildings as nesting sites for the pale-breasted thrush remain unclear, it does not lessen the significance of the finding that pairs willing to use buildings as nesting substrates have increased fitness, expressed by both higher nest survival rates and higher number of fledglings per nesting attempt.

In conclusion, our data do not support the idea that anthropogenic nesting substrates could act as ecological traps regarding their effects on clutch survival, in accordance with other studies that report higher breeding success for nests placed in artificial substrates (Wallace et al. 2016, da Silva et al. 2018). Instead, the choice of anthropogenic nesting substrates increased parental fitness in our study population. Considering the genetic and cognitive aspects of nest site selection (Slagsvold et al. 2013), we might infer that the use of buildings for nesting should be positively selected for in this population (Møller 2010). Furthermore, previous studies have indicated potential benefits related to the use of buildings as nesting sites by the pale-breasted thrush. The protection to nest structures conferred by buildings enables their reuse across years, which allows earlier initiation of breeding (Batisteli et al. 2021a) and a relaxed incubation budget due to better thermal insulation (Batisteli et al. 2021b). We stress, however, that the use of buildings as nesting substrates may have costs that were not evaluated in this study, such as the physiological stress caused by the proximity to certain building equipment (e.g. air conditioners) that are particular sources of chronic anthropogenic noise in the urban environment (Kleist et al. 2018). Nevertheless, we highlight that the use of anthropogenic nesting substrates may favor the settlement of certain bird species in urban areas and potentially induce adaptive (and non-adaptive) responses in the nesting behavior of urban birds.

Acknowledgements – We are grateful to Talita P. Soares and other field assistants, to the reviewers for their valuable comments, to the subject editor Elisa P. Badas and to other members of the editorial board for the careful handling of our manuscript. We thank Prof. Mercival R. Francisco, Prof. Augusto J. Piratelli, Dr César Cestari and Dr Matheus G. Reis for their comments on a first draft. We declare no conflict of interest.

Funding – This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. MAP receives a research grant from the Brazilian Research Council (CNPq, grant no. 304742/2019-8).

Permits – All the steps of this study were previously approved by federal environmental institutions (ICMBio/SISBIO no. 59414-1) and the ethical committee of the Universidade Federal de São Carlos (CEUA no. 1958100718).

Author contributions

Augusto Florisvaldo Batisteli: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Hugo Sarmento**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Marco Aurélio Pizo**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/jav.03240.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0k6djhb63 (Batisteli et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alvares, C. A., Stape, J. L., Sentelhas, P. C., De Moraes Gonçalves, J. L. and Sparovek, G. 2013. Köppen's climate classification map for Brazil. – Meteorol. Z. 22: 711–728.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. – Springer Science & Business Media.

Ardia, D. R., Pérez, J. H. and Clotfelter, E. D. 2006. Nest box orientation affects internal temperature and nest site selection by tree swallows. – J. Field Ornithol. 77: 339–344.

Astié, A. A. and Reboreda, J. C. 2006. Costs of egg punctures and parasitism by shiny cowbirds (*Molothrus bonariensis*) at creamy-bellied thrush (*Turdus amaurochalinus*) nests. – Auk 123: 23–32.

Auer, S. K., Bassar, R. D., Fontaine, J. J. and Martin, T. E. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. – Condor 109: 321–333.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Batisteli, A. F., da Silva Neto, E. N. S., Soares, T. P., Pizo, M. A. and Sarmento, H. 2019a. Breeding biology of the Sayaca tanager (*Thraupis sayaca*) in southeast Brazil. – J. Nat. Hist. 53: 2397–2412.

Batisteli, A. F., Guilhermo-Ferreira, R. and Sarmento, H. 2019b. Abundance and prevalence of plastic twine in nests of Neotropical farmland birds. – Wilson J. Ornithol. 131: 201–205.

Batisteli, A. F., Costiuc, M. Y., Santieff, I. Z., Costa, R. O., Sarmento, H. and Pizo, M. A. 2020. Breeding biology of the creamy-bellied thrush (*Turdus amaurochalinus*) in southeast Brazil. – Stud. Neotrop. Fauna Environ. 55: 233–241.

Batisteli, A. F., Sarmento, H. and Pizo, M. A. 2021a. Nest reuse by pale-breasted thrushes reduces the chance of cowbird parasitism and allows earlier initiation of breeding. – J. Field Ornithol. 92: 105–114.

Batisteli, A. F., De Souza, L. B., Santieff, I. Z., Gomes, G., Soares, T. P., Pini, M., Guillermo-Ferreira, R., Pizo, M. A. Sarmento, H., Pizo, M. A. and Sarmento, H. 2021b. Buildings promote higher incubation temperatures and reduce nest attentiveness in a Neotropical thrush. – Ibis 163: 79–89.

Batisteli, A. F., Sarmento, H. and Pizo, M. A. 2024. Anthropogenic nesting substrates increase parental fitness in a Neotropical songbird, the pale-breasted thrush (*Turdus leucomelas*). – Dryad Digital Repository, https://doi.org/10.5061/dryad.0k6djhb63.

Borgmann, K. L. and Rodewald, A. D. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. – Ecol. Appl. 14: 1757–1765.

Borgmann, K. L. and Conway, C. J. 2015. The nest-concealment hypothesis: new insights from a comparative analysis. – Wilson J. Ornithol. 127: 646–660.

Burhans, D. E. and Thompson, F. R. III 2006. Songbird abundance and parasitism differ between urban and rural shrublands. – Ecol. Appl. 16: 394–405.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer-Verlag.

Camprodon, J., Salvanyà, J. and Soler-Zurita, J. 2008. The abundance and suitability of tree cavities and their impact on hole-nesting bird populations in beech forests of NE Iberian Peninsula. – Acta Ornithol. 43: 17–31.

Collar, N. and Garcia, E. F. J. 2020. Pale-breasted thrush (*Turdus leucomelas*), ver. 1.0. – In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. and de Juana, E. (eds), Birds of the world. Cornell Lab of Ornithology.

Colombelli-Négrel, D. and Kleindorfer, S. 2009. Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). – Ecol. Res. 24: 921–928.

Da Silva, T. L., Cabral, R. B. G., Andrade, L. A. S., Nogueira, N. F., Oliveira, M. S. and Ferreira, I. 2018. Comparison of breeding biology aspects of *Fluvicola nengeta* (Aves: Tyrannidae) between two nesting sites. – J. Nat. Hist. 52: 225–235.

Davanço, P. V., Oliveira, L. S., Sousa, L. M. and Francisco, M. R. 2013. Breeding life-history traits of the pale-breasted thrush (*Turdus leucomelas*) in southeastern Brazil. – Ornitol. Neotrop. 24: 401–411.

Deeming, D. C. and Reynolds, S. J. 2015. Perspectives on avian nests and eggs. – In: Nests, eggs, and incubation: new ideas about avian reproduction. Oxford Univ. Press, pp. 221–225.

Duca, C., Brunelli, W. A. AND Doherty Jr, P. F. 2019. Predator search image and the dilution effect: when is the best time to nest? – Auk Ornithol. Adv. 136: ukz009.

Evans, M. L. and Stutchbury, B. J. 2012. Nest attendance and reproductive success in the wood thrush. – Condor 114: 401–406.

Fiorini, V. D., D. T., Tuero, A. J. and Reboreda, C. 2009. Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by shiny cowbirds on chalk-browed mockingbirds. – Behaviour 146: 1387–1403.

Fiorini, V. D., Gloag, R., Kacelnik, A. and Reboreda, J. C. 2014. Strategic egg destruction by brood-parasitic cowbirds? – Anim. Behav. 93: 229–235.

Franz, I. and Fontana, C. S. 2021. Drivers of nest survival in the tawny-bellied seedeater *Sporophila hypoxantha* (Aves: Thraupidae): time-specific factors are more related to success than ecological variables. – An. Acad. Bras. Cienc. 93 Supplement 3: e20191458.

Gering, J. C. and Blair, R. B. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? – Ecography 22: 532–541.

Gómez-Serrano, M. Á. and López-López, P. 2014. Nest site selection by Kentish plover suggests a trade-off between nest-crypsis and predator detection strategies. – PLoS One 9: e107121.

Gorosito, C. A., Tuero, D. T. and Cueto, V. R. 2023. More is better: predator dilution effect increases Chilean Elaenia (*Elaenia chilensis*) nest survival. – J. Ornithol. 165: 147–155.

Gorosito, C. A., Tuero, D. T. and Cueto, V. R. 2024. Does predation drive Chilean elaenia (*Elaenia chilensis*) nest-site selection in the temperate forest of southern South America? – J. Ornithol.: https://doi.org/10.1007/s10336-024-02163-2.

Haddad, R. N. M., Batisteli, A. F., Ibáñez-Álamo, J. D. and Pizo, M. A. 2024. Sexual division of nestling parental care in the pale-breasted thrush (*Turdus leucomelas*). – J. Ornithol. 165: 193–202.

Hensler, G. L. and Nichols, J. D. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. – Wilson Bull. 93: 42–53.

Hu, Y. B., Zhao, Q. S., Lou, Y. Q., Chen, L. J., González, M. A. and Sun, Y. H. 2017. Parental attendance of chestnut thrush reduces nest predation during the incubation period: compensation for low nest concealment? – J. Ornithol. 158: 1111–1117.

Husby, M. 2019. Nestling begging calls increase predation risk by corvids. – Anim. Biol. 69: 137–155.

Ibáñez-Álamo, J. D. and Soler, M. 2010. Does urbanization affect selective pressures and life-history strategies in the common blackbird (*Turdus merula* L.)? – Biol. J. Linn. Soc. 101: 759–766.

Jagiello, Z., Reynolds, S. J., Nagy, J., Mainwaring, M. C. and Ibáñez-Álamo, J. D. 2023. Why do some bird species incorporate more anthropogenic materials into their nests than others? – Philos. Trans. R. Soc. B 378: 20220156.

Jokimäki, J. and Huhta, E. 2000. Artificial nest predation and abundance of birds along an urban gradient. – Condor 102: 838–847.

Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Sorace, A., Fernández-Juricic, E., Rodriguez-Prieto, I. and Jimenez, M. D. 2005. Evaluation of the "safe nesting zone" hypothesis across an urban gradient: a multi-scale study. – Ecography 28: 59–70.

Kleist, N. J., Guralnick, R. P., Cruz, A., Lowry, C. A. and Francis, C. D. 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. – Proc. Natl Acad. Sci. USA 115: E648–E657.

Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.

Laake, J., Rakhimberdiev, B. A., Turek, D. and Mcclintock, B. 2019. Package 'RMark'. – R Code for Mark Analysis.

Liang, W., Yang, C., Wang, L. and Møller, A. P. 2013. Avoiding parasitism by breeding indoors: cuckoo parasitism of hirundines and rejection of eggs. – Behav. Ecol. Sociobiol. 67: 913–918.

Lomáscolo, S. B., Monmany, A. C., Malizia, A. and Martin, T. E. 2010. Flexibility in nest-site choice and nesting success of *Turdus rufiventris* (Turdidae) in a montane forest in northwestern Argentina. – Wilson J. Ornithol. 122: 674–680.

López, A. V., Fiorini, V. D., Ellison, K. and Peer, B. D. 2018. Thick eggshells of brood parasitic cowbirds protect their eggs and damage host eggs during laying. – Behav. Ecol. 29: 965–973.

Lowther, P. E. 2023. Lists of victims and hosts of the parasitic cowbirds, version 16 Oct 2023. – The Field Museum, https://www.datocms-assets.com/44232/1698688185-host-list-molothrus-ver-16oct2023.pdf.

Mahler, B., Confalonieri, V. A., Lovette, I. J. and Reboreda, J. C. 2007. Partial host fidelity in nest selection by the shiny cowbird (*Molothrus bonariensis*), a highly generalist avian brood parasite. – J. Evol. Biol. 20: 1918–1923.

Mainwaring, M. C. 2015. The use of man-made structures as nesting sites by birds: a review of the costs and benefits. – J. Nat. Conserv. 25: 17–22.

Mainwaring, M. C. 2017. Causes and consequences of intraspecific variation in nesting behaviors: insights from blue tits and great tits. – Front. Ecol. Evol. 5: 39.

Martin, T. E. 1993. Nest predation and nest sites. – BioScience 43: 523–532.

Massoni, V. and Reboreda, J. C. 2002. A neglected cost of brood parasitism: egg punctures by shiny cowbirds during inspection of potential host nests. – Condor 104: 407–412.

Mayfield, H. 1961. Nesting success calculated from exposure. – Wilson Bull. 73: 255–261.

Mckinney, M. L. 2002. Urbanization, biodiversity, and Conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. – BioScience 52: 883–890.

Menezes, J. C. and Marini, M. Â. 2017. Predators of bird nests in the Neotropics: a review. – J. Field Ornithol. 88: 99–114.

Mennerat, A., Perret, P. and Lambrechts, M. M. 2009. Local individual preferences for nest materials in a passerine bird. – PLoS One 4: e5104.

Mikula, P., Hromada, M., Albrecht, T. and Tryjanowski, P. 2014. Nest site selection and breeding success in three *Turdus* thrush species coexisting in an urban environment. – Acta Ornithol. 49: 83–92.

Møller, A. P. 2010. The fitness benefit of association with humans: elevated success of birds breeding indoors. – Behav. Ecol. 21: 913–918.

Møller, A. P., Díaz, M. and Liang, W. 2016. Brood parasitism and proximity to human habitation. – Behav. Ecol. 27: 1314–1319.

Muñoz, A. M., Mccleery, R. A., Lopez, R. R. and Silvy, N. J. 2008. Nesting ecology of mourning doves in an urban landscape. – Urban Ecosyst. 11: 257–267.

Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. – Ornis Scand. 15: 167–175.

Okada, S., Lindenmayer, D. B., Wood, J. T., Crane, M. J. and Pierson, J. C. 2017. How does a transforming landscape influence bird breeding success? – Landsc. Ecol. 32: 1039–1048.

Pizo, M. A. 2018. A narrow-billed woodcreeper, *Lepidocolaptes angustirostris*, nesting in a mailbox. – Rev. Bras. Ornitol. 26: 189–191.

Reynolds, S. J., Ibáñez-Álamo, J. D., Sumasgutner, P. and Mainwaring, M. C. 2019. Urbanisation and nest building in birds: a review of threats and opportunities. – J. Ornithol. 160: 841–860.

Rivera-López, A. and Macgregor-Fors, I. 2016. Urban predation: a case study assessing artificial nest survival in a Neotropical city. – Urban Ecosyst. 19: 649–655.

Rodewald, A. D. and Kearns, L. J. 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. – Condor 113: 899–906.

Rovedder, C. E. and Fontana, C. S. 2012. Nest, eggs, and nest placement of the Brazilian endemic black-bellied seedeater (*Sporophila melanogaster*). – Wilson J. Ornithol. 124: 173–176.

Şahin Arslan, N. and Martin, T. E. 2024. Visual predators and diurnal nest predation provide support for the Skutch Hypothesis and explain evolved incubation behaviors in a montane tropical bird community. – Ornithology 141: ukad047.

Saunders, C. A., Arcese, P. and O'connor, K. D. 2003. Nest site characteristics in the song sparrow and parasitism by brown-headed cowbirds. – Wilson Bull. 115: 24–28.

Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. 2002. Ecological and evolutionary traps. – Trends Ecol. Evol. 17: 474–480.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? – Ibis 91: 430–455.

Slagsvold, T., wigdahl Kleiven, K. W., Eriksen, A. and Johannessen, L. E. 2013. Vertical and horizontal transmission of nest site preferences in titmice. – Anim. Behav. 85: 323–328.

Soldatini, C., Albores-Barajas, Y. V., Mainardi, D. and Monaghan, P. 2008. Roof nesting by gulls for better or worse? – Ital. J. Zool. 75: 295–303.

Stanley, T. R. 2000. Modeling and estimation of stage-specific daily survival probabilities of nests. – Ecology 81: 2048–2053.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H. W. and Gamauf, A. 2014. Hard times in the city–attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. – Front. Zool. 11: 48.

Swan, D. C., Zanette, L. Y. and Clinchy, M. 2015. Brood parasites manipulate their hosts: experimental evidence for the farming hypothesis. – Anim. Behav. 105: 29–35.

Tuero, D. T., Fiorini, V. D. and Reboreda, J. C. 2007. Effects of shiny cowbird *Molothrus bonariensis* parasitism on different components of house wren *Troglodytes aedon* reproductive success. – Ibis 149: 521–529.

Wallace, Z. P., Kennedy, P. L., Squires, J. R., Olson, L. E. and Oakleaf, R. J. 2016. Human-made structures, vegetation, and weather influence ferruginous hawk breeding performance. – J. Wildl. Manage. 80: 78–90.

Wang, Y., Huang, Q., Lan, S., Zhang, Q. and Chen, S. 2015. Common blackbirds *Turdus merula* use anthropogenic structures as nesting sites in an urbanized landscape. – Curr. Zool. 61: 435–443.

Wang, Y., Chen, S., Blair, R. B., Jiang, P. and Ding, P. 2009. Nest composition adjustments by Chinese bulbuls *Pycnonotus sinensis* in an urbanized landscape of Hangzhou (E China). – Acta Ornithol. 44: 185–192.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. – J. Anim. Ecol. 71: 424–437.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird St. 46: 120–139.

Yeh, P. J., Hauber, M. E. and Price, T. D. 2007. Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. – Oikos 116: 1473–1480.