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Nest reuse by Pale-breasted Thrushes reduces the chance of cowbird parasitism and allows earlier initiation of breeding

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ABSTRACT. Selection of safe nest sites is a first step toward improving the chances of breeding successfully. Reusing old nests can save time and energy for breeding birds, but nest reuse is rare among open-cup nesting songbirds and the factors contributing to this behavior and its consequences for reproductive output remain little known. We studied an urban population of Pale-breasted Thrushes (*Turdus leucomelas*) in southeastern Brazil to determine whether nest reuse (1) was more likely after a successful nesting attempt both within and between breeding seasons, (2) affected the number of fledglings in the next nesting attempt, (3) reduced the chances of nest parasitism by Shiny Cowbirds (*Molothrus bonariensis*), and (4) was associated with earlier initiation of nests at the beginning of breeding seasons and shorter re-nesting intervals within breeding seasons. We monitored 266 nests from 2010 to 2019 and obtained data on 130 re-nesting events by individually marked birds. Nest reuse was more frequent after successful nesting attempts within breeding seasons. New nests were more likely to be parasitized by cowbirds, which had a negative effect on the number of fledglings per clutch. Reusing nests allowed earlier initiation of breeding at the start of breeding seasons, but did not shorten re-nesting intervals within seasons. Nest reuse by Pale-breasted Thrushes followed the win-stay lose-switch strategy and corroborated the time-saving hypothesis. Our results suggest that nest reuse may increase the fitness of Pale-breasted Thrushes by reducing the likelihood of cowbird parasitism.

RESUMEN. **La reutilización de nidos en *Turdus leucomelas* reduce la probabilidad de parasitismo por *Molothrus bonariensis* y permite una iniciación más temprana de la reproducción**

La selección de sitios seguros para la anidación es un primer paso hacia el incremento en la probabilidad de una reproducción exitosa. La reutilización de nidos viejos puede ahorrar tiempo y energía para las aves en la reproducción, pero la reutilización de los nidos, entre las especies passeriformes con nidos de copa abiertas, es poco frecuente y los factores que contribuyen a este comportamiento y sus consecuencias para la reproducción son poco conocidas. Estudiamos una población urbana de *Turdus leucomelas* en el sureste de Brasil para determinar si la reutilización de los nidos (1) era más probable después de un intento de anidación exitoso, tanto dentro de la misma temporada como en diferentes temporadas de reproducción, (2) afecta el número de pichones en el siguiente intento de anidación, (3) reduce la probabilidad de ser parasitado por *Molothrus bonariensis* y (4) estuvo asociado con una iniciación más temprana de los nidos al inicio de las temporadas de reproducción e intervalos de re-anidación más cortos dentro de la misma temporada. Monitoreamos 266 nidos desde 2010 hasta 2019 y obtuvimos datos de 130 eventos de re-anidación por individuos marcados. Los nidos nuevos fueron parasitados por *Molothrus bonariensis* con mayor probabilidad, lo cual a su vez tuvo un efecto negativo sobre el número de pichones en la nidada. La reutilización de los nidos permitió una iniciación más temprana de la reproducción al inicio de la temporada reproductiva, pero no redujo los intervalos de re-anidación dentro de la misma temporada. La reutilización de nidos por *Turdus leucomelas* siguió la estrategia quedarse-ganar cambiar-perder y corrobora la hipótesis de ahorro de tiempo. Nuestros resultados sugieren que la reutilización de los nidos puede incrementar la aptitud en *Turdus leucomelas* mediante la reducción de la probabilidad de parasitismo por *Molothrus bonariensis*.

Key words: cowbird parasitism, breeding behavior, nest site selection, *Turdus*, win-stay lose-switch

Animal reproductive strategies, such as the selection of a safe site for breeding, evolve in response to complex trade-offs between offspring production and the energetic investment in reproduction (Alcock and Rubenstein 2019). For birds, nest failure is a major barrier for successful breeding, with potential impacts on bird population dynamic and avian community structuring (Martin 1988, Thompson 2007). The most common

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cause of nest failure in a variety of species and ecosystems is nest predation (Auer et al. 2007, Marini 2017), but brood-parasitic birds also have a negative effect on nesting success by damaging host eggs and through nestling-nestling competition (Kilner 2003, Astié and Reboreda 2006). Strong evolutionary pressure for nesting success favors parental behaviors that increase the chances of nest success, and this begins with selecting nest sites safe from predators and brood parasites (Lima 2009).

Birds use specific features of potential nest sites, such as the degree of concealment and habitat structure, to lower the risk of both nest predation and brood parasitism (Fiorini et al. 2009, Young et al. 2017). However, selecting safe nest sites is a complex behavioral decision based on multiple microhabitat features because the effectiveness of different nesting strategies in avoiding nest predation depends on the behavior and cognitive abilities of local nest predators, which vary with space and time (Jokimäki et al. 2005, Sperry et al. 2008). To cope with such changes in environmental pressures, individuals can use flexible behavioral responses to manage predation risk, using information from previous breeding attempts to decide where to build nests (Chalfoun and Martin 2010). Thus, nest-site selection is a complex process in which birds integrate innate and acquired information (Slagsvold et al. 2013).

Some individuals or pairs may use old nests to save time and energy (time/energy saving hypothesis, Cancellieri and Murphy 2013). Possible benefits of re-using old nests include earlier clutch initiation (Cavitt et al. 1999), increased nest success (McIvor and Healy 2017), and shorter intervals between successive nesting attempts (Cancellieri and Murphy 2013). Nest reuse, however, is rare among open-cup nesting songbirds, in part because nests tend to degrade over time when exposed to the elements, but also because open-cup nests are especially vulnerable to predators, and changing nest locations allows birds to avoid repeated nest failures due to short-term predator memory (Weidinger and Kočvara 2010). Positive breeding outcomes (i.e., a successful nest) might be expected to favor nest-site fidelity, whereas nest failure should induce a change in nest site (the “win-stay, lose-switch” strategy) (Chalfoun and Martin 2010).

Among the few studies of nest reuse to date, Wysocki (2004) found that nest reuse was more likely after successful nesting attempts by Eurasian Blackbirds (*Turdus merula*), but the number of fledglings was similar for reused and new nests. Ellison (2008) reported that nest reuse by Vermilion Flycatchers (*Pyrocephalus rubinus*) was restricted to previously successful nests and that reused nests had higher daily survival rates. However, additional studies are needed to further examine the relationship between nest reuse and aspects that affect parental fitness, such as nest predation, brood parasitism, and the timing of breeding, and to better understand why nest reuse is rare among open-cup nesting birds. We studied an urban population of Pale-breasted Thrushes (*Turdus leucomelas*) with an unusually high rate of nest reuse to determine whether reuse (1) was influenced by the fate of a nesting attempt (win-stay, lose-switch strategy) both within and between breeding seasons, (2) affected nest success, (3) reduced the chance of brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*), and (4) allowed earlier initiation of nesting in the next breeding season or reduced the interval between consecutive nesting attempts in a given breeding season.

METHODS

Our study was conducted at the campus of the Universidade Estadual Paulista Júlio de Mesquisa Filho (UNESP) in Rio Claro, São Paulo state, Brazil (22°23′43″S, 47°32′46″W, 628 m a.s.l.), between 2010 and 2019. The campus is a periurban area of ~ 115 ha, of which ~ 52 ha consists of an urban area rich in unpaved spaces, such as lawns, gardens with exotic shrubs and trees, and small (< 1 ha) woodlands of native vegetation of the semideciduous seasonal forest of the Atlantic Forest domain.

Study species. Pale-breasted Thrushes are socially monogamous and resident Neotropical songbirds (Sick 1997). Adults (~ 23.4 cm in length) are monomorphic in plumage and weigh ~ 69.1 g, and females are slightly heavier than males (Moraes et al. 2018). This species inhabits habitats ranging from riparian forests to green urban areas, where it benefits from exotic plants as food sources and buildings as nesting substrates

(Gasperin and Pizo 2009, Batisteli et al. 2021). In our study area, Pale-breasted Thrushes typically breed from September to December, and pairs have up to three nesting attempts per breeding season, but no more than two successful broods a year (Davanço et al. 2013). Nests are robust low cups ~ 13.2 cm in external diameter and 10.2 cm in height, composed by a mix of vegetal material (mainly roots, moss, and fibers) and mud (Ruiz et al. 2017), usually placed on forks of tree trunks or in or on buildings (Batisteli et al. 2021). Clutch size is usually three eggs (range = 1–4; Davanço et al. 2013). As with other Neotropical thrushes, Pale-breasted Thrushes are hosts of brood-parasitic Shiny Cowbirds (Lowther 2018).

Field procedures. We focused our nest searching efforts on the urbanized portion of the campus to ensure that we thoroughly documented the reproductive histories of birds in our population. We conducted nest searches every other day from mid-August to late December and found nests by following adult thrushes and inspecting potential nest sites (trees and buildings). Nests in buildings were placed on concrete columns, air conditioners, metallic ducts, structures under metal roofing, and polyvinyl chloride (PVC) tubes and were surrounded laterally by concrete or metallic barriers and from above by roofs of concrete, PVC or clay tiles (Fig. S1).

During each year beginning in 2010, we captured adult thrushes with mist-nets and marked them with a metal band and a unique combination of colored leg bands to allow individual identification. Nestlings were also banded beginning in 2014. Data from nesting attempts from 2010 to 2012 provided us with information about a number of known breeding pairs and their territories at the beginning of the 2013 breeding seasons. However, we discarded data from these first three years when examining nest reuse and its possible effect on the number of fledglings and likelihood of brood parasitism due to irregular nest monitoring and uncertainty about nest success. Data from all breeding seasons (from 2010 to 2019) were used to estimate the effect of nest reuse in the timing of initiation of breeding at the beginning of breeding seasons and renesting intervals. We collected blood samples using the toenail clip method (Owen 2011) and used the samples to sex birds in an outsourced laboratory (UNIGEN—Biologia pelo DNA, São Paulo, Brazil) using sex-specific genetic markers.

We assigned each nest a numeric code when discovered. During the non-breeding season, some old nests were either removed by university staff or fell to the ground. If birds returned to use one of these vacated nest sites, we assigned a new number to the new nest. Thus, we only classified nests as reused when at least one banded individual made consecutive breeding attempts in the same nest structure. This definition allowed us to assign nest reuse independently of divorce. Nests of unbanded pairs, although used for estimating the effect of nest reuse on nest initiation dates and renesting intervals, were excluded from our analyses of nest survival and brood parasitism due to the assumed individual variation in the ability to avoid brood parasitism and nest predation.

Nests not located at the start of a breeding season might inflate laying date estimates if we incorrectly assigned a second clutch as a first one. To reduce this potential issue, we only considered nests found during the first 30 days after the start of a breeding season when analyzing the effect of old and new nests on laying date. We chose this threshold because only two of 43 known second clutches had laying dates within the first 30 days of the start of a breeding season.

We checked nests every 1–3 days to record the number of eggs and nestlings and daily near the expected fledging date to obtain a more reliable assignment of nest outcome. Eggs of Shiny Cowbirds and Pale-breasted Thrushes could be identified based on differences in size, shape, and eggshell coloration, and cowbird hatchlings could be identified by the presence of black down feathers on their back and rosier skin. For each nest, we recorded laying date as the date when the first egg was laid (hereafter, laying date), assuming that females laid one egg per day. For nests found after clutch completion, we estimated laying dates by backdating from hatching day, assuming a 14-day interval between laying of the first egg and hatching date. For each breeding season, we assigned the earliest laying date of all nests as day 1 of the breeding season. Renesting intervals were calculated as the difference between either the estimated fledging date or the day a nest failed and the laying date of the next nesting attempt by the same female.

A nest was considered successful when at least one nestling (either thrush or cowbird) survived until fledging. Nests were considered to have failed when eggs or nestlings disappeared before the expected fledging date (likely due to nest predation), when nestlings died in the nest, or eggs remained in a nest with no indication of adult presence for three consecutive monitoring visits.

Statistical analyses. We compared the frequency of nest reuse and the apparent success (i.e., the percentage of nests that fledged young) for nests in trees and buildings with Fisher's exact test and a chi-square test, respectively. Because our data contained repeated observations of breeding pairs and nests, we built linear mixed-effects models (LMMs) and generalized mixed-effects models (GLMMs) to test our predictions. We built a binomial GLMM to test whether nest reuse was triggered by the outcome of the last nest as a binary variable (0 = failed, 1 = successful), inter-nest interval (0 = within, 1 = between breeding seasons), and the interaction between these binary variables using individual identity as a random factor.

Prior to examining the effect of nest reuse on the number of fledglings, we compared the clutch sizes of reused and new nests. Because 93% of nests had two or three eggs, we excluded nests with either one or four eggs per clutch and built a GLMM with clutch size as a categorical response variable (two or three eggs), nest reuse, inter-nest interval and their interaction as binary explanatory variables, and female identity and nest number as random factors. Because newly formed pairs produce fewer fledglings (M. A. Pizo, unpubl. data), we only used data of pairs with prior experience in a LMM to test whether fledging success (i.e., the number of fledglings per clutch; square-root-transformed) was affected by nest reuse, inter-nest interval (0 = within, 1 = between breeding seasons) and their interaction, setting parasitism by cowbirds as another explanatory binary variable, clutch size as a covariate and pair identity and nest number as random factors. We applied a stepwise backward selection to eliminate non-significant terms, comparing nested models with a chi-square test (Zuur et al. 2009).

We used a GLMM to examine possible seasonal variation in parasitism by cowbirds (a binary response variable), setting the date of clutch imitation as a continuous explanatory variable and nest identity as a random factor. We also used a GLMM to determine whether brood parasitism by cowbirds was less common in reused nests both within and between breeding seasons (all binary variables), with adult identity and nest number as random factors. Finally, to determine whether females that reused nests initiated egg laying earlier than those building new nests at the beginning of breeding seasons, as predicted by the time/energy saving hypothesis, we built LMMs using laying date and renesting interval as continuous response variables (both square-root-transformed). Nest type (0 = old, 1 = new) and year were set as categorical explanatory variables, whereas adult identity and nest number were set as random factors in both models. Because post-fledging parental care after successful nesting attempts could delay the initiation of a new nest, we also included the fate of the last nest as a binary explanatory variable in the model assessing the effect of old nests on renesting intervals.

In models where interaction terms were significant, we conducted pairwise comparisons by means of a Tukey post hoc test. All analyses were conducted in the software R (R Development Core Team 2019) using the packages "lme4" (Bates et al. 2014) and "lmerTest" (Kuznetsova et al. 2015), with $\alpha = 0.05$. Values are provided as means ± 1 SD.

RESULTS

We banded 469 individuals (323 adults and 146 nestlings), with 96 (52 males and 44 females) recorded as breeding during our study. Among pairs where both birds were banded, only nine of 45 males and 10 of 35 females were observed with more than one mate. Of 266 monitored nests, 169 had at least one banded adult and, from these, we obtained data on 130 re-nesting events. Ten re-nesting events were not included in our analyses because they occurred in non-consecutive breeding seasons so we may have failed to detect additional nesting attempts.

Nest reuse tended to be less common for nests in trees (4 of 14 = 28.6% of renesting events) than for those in or on buildings (38 of 68 = 55.9%; Fisher's exact test, $P = 0.058$). In most cases of nest reuse, nests remained relatively intact through several breeding seasons because of the protection provided by buildings. Most nests in trees either disappeared or were in various stages of deterioration during a single nonbreeding season. Given their reduced likelihood of reuse, we excluded nests in trees from the model assessing factors underlying nest reuse.

We found 87 first, 40 second and 14 third nests. Most pairs with a third nesting attempt had either one ($N = 6$) or two ($N = 5$) previous failed nests. Apparent success was 51.1% ($N = 266$) and was similar for parasitized (55.8%) and non-parasitized nests (52.9%) ($\chi^2 = 0.1$, $P = 0.75$). Cowbirds parasitized 35.7% of all nests (95 of 266), and the effect of date of clutch initiation on the chance of cowbird parasitism was only marginally significant (GLMM, $P = 0.051$). Considering data from nests of banded females found prior to hatching, mean clutch sizes of first, second, and third clutches were 2.5 ± 0.8 ($N = 83$), 2.5 ± 0.6 ($N = 38$), and 2.7 ± 0.7 ($N = 12$), respectively. Overall, the mean number of fledglings for first, second, and third nesting attempts was 1.0 ± 1.1 ($N = 83$), 1.1 ± 1.2 ($N = 40$), and 0.6 ± 1.1 ($N = 11$), respectively, and, considering only successful nests, 1.9 ± 0.7 ($N = 44$), 2.2 ± 0.8 ($N = 20$), and 2.3 ± 0.6 ($N = 3$), respectively.

Nests were reused for consecutive nesting attempts as frequently within as between breeding seasons, and reuse was more frequent after successful nesting attempts ($N = 106$ clutches in 59 nests, Table 1). However, the higher frequency of nest reuse after a successful nesting attempt was only for consecutive clutches in the same breeding season (last nest outcome × inter-nest interval in Table 1, Fig. 1A).

Nest reuse had no effect on clutch size, independently of inter-nest interval (Table 1). Similarly, the number of fledglings per clutch did not differ between reused and new nests either within or between breeding seasons, regardless of clutch size (Table 2). However, the number of fledglings was lower for nests parasitized by cowbirds (Table 2, Fig. 1B). Cowbird parasitism, in turn, was less frequent in reused nests ($N = 112$ clutches in 67 nests; Fig. 2). Although the likelihood of cowbird parasitism did not differ between consecutive nesting attempts within and between breeding seasons, the interaction between inter-clutch time and nest reuse was significant, and a post hoc test revealed that only the reuse of nests within breeding seasons contributed to a reduction in cowbird parasitism (Table 1, Fig. 2).

Table 1. Results of generalized linear mixed-effects models assessing the effect of the outcome of the last nesting attempt (failure/success) on nest reuse by Pale-breasted Thrushes, and the relationship between nest reuse and clutch size and brood parasitism by Shiny Cowbirds, considering consecutive nesting attempts within and between breeding seasons (inter-nest interval).

	Estimate	SE	*z*	*P**
Nest reuse				
Intercept	1.006	0.328	3.1	0.002*
Last nest outcome	−1.230	0.389	−3.2	0.002*
Inter-nest interval	−0.341	0.455	−0.8	0.45
Inter-nest interval × Last nest outcome	1.192	0.601	2.0	0.047*
Clutch size				
Intercept	1.308	0.519	2.5	0.012*
Nest reuse	−0.546	0.570	−1.0	0.34
Inter-nest interval	−0.545	0.517	−1.0	0.29
Inter-nest interval × Nest reuse				0.37
Brood parasitism				
Intercept	−1.482	0.495	−3.0	0.003*
Nest reuse	2.219	0.616	3.6	<0.001*
Inter-nest interval	1.348	0.717	1.9	0.06
Inter-nest interval × Nest reuse	−1.749	0.873	−2.0	0.045*

*Statistically significant *P*-values at $\alpha = 0.05$.

Laying dates for first nesting attempts of each breeding season averaged 5.9 days earlier for females using old nests, and this trend was consistent throughout our study (Table 2, Fig. 3A) ($N = 78$ clutches of 25

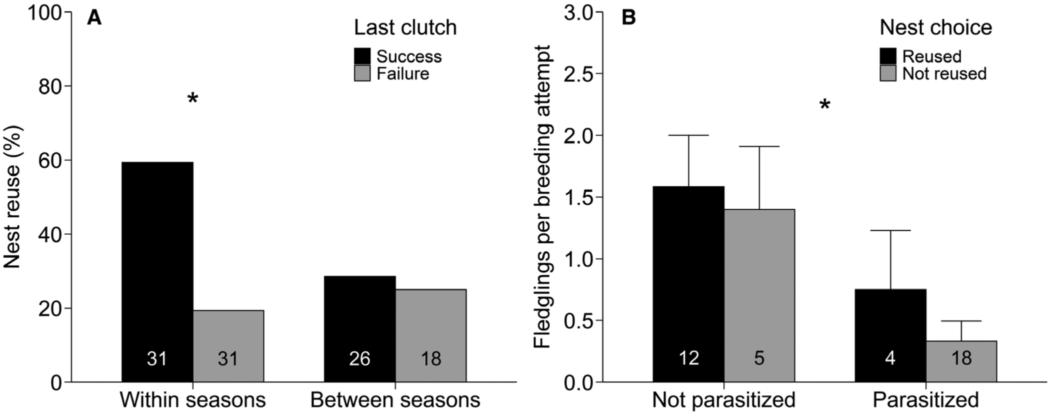

Fig. 1. (A) Frequency of nest reuse within and between breeding seasons after failed and successful nesting attempts and (B) number of fledglings per clutch in relation to brood parasitism by Shiny Cowbirds and nest reuse by an urban population of Pale-breasted Thrushes. Numbers inside bars represent sample sizes, whiskers denote standard errors, and asterisks indicate statistical significance at α = 0.05.

Table 2. Results of linear mixed-effects models assessing the effect of nest reuse on the number of fledglings per nesting attempt and the consequence of using old nests on the laying dates and renesting intervals of Pale-breasted Thrushes during the 2010 to 2019 breeding seasons.

	Estimate	SE	df	*t*	*P**
Number of fledglings					
Intercept	0.839	0.500	33.817	1.7	0.10
Clutch size	0.093	0.172	33.536	0.5	0.59
Nest reuse[b]	−0.076	0.271	33.855	−0.3	0.78
Inter-nest interval[c]	−0.189	0.225	29.399	−0.8	0.41
Brood parasitism[d]	−0.588	0.260	33.901	−2.3	0.03*
Nest reuse × Inter-nest interval					0.67
Laying date					
Intercept	−94.151	146.201	5.413	−0.6	0.55
Nest type[e]	−1.218	0.371	66.934	−3.3	0.001*
Year	0.049	0.072	5.437	0.7	0.53
Renesting interval					
Intercept	210.231	143.379	34.972	1.5	0.15
Nest type	−0.103	0.071	34.973	1.4	0.16
Year	−0.243	0.275	33.428	−0.9	0.38
Last nest outcome[f]	0.181	0.262	33.248	0.7	0.49

*Statistically significant *P*-values α = 0.05.
[b] Nest reuse = same/other nest in consecutive clutches.
[c] Inter-nest interval = consecutive nesting attempts within/between breeding seasons
[d] Brood parasitism = presence/absence of cowbird parasitism.
[e] Nest type = old/new.
[f] Last nest outcome = failure/success.

banded females in 63 nests). Renesting intervals did not, however, differ between old and new nests (Table 2, Fig. 3B), either after successful or failed nesting attempts or among years (*N* = 40 clutches of 18 banded females in 34 different nests). Laying dates of second clutches were similar for reused (53.6 ± 12.6 days after the beginning of the breeding season, *N* = 20) and new nests (53.1 ± 12.0 days, *N* = 11).

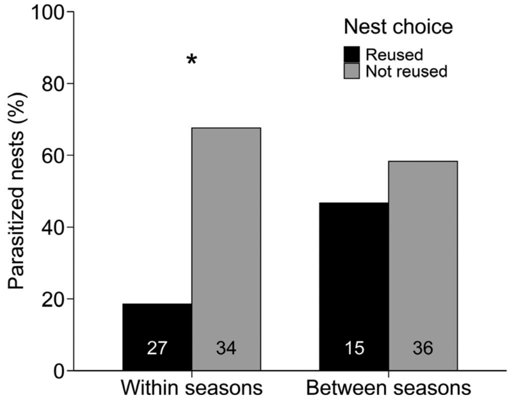

Fig. 2. Frequency of nests parasitized by Shiny Cowbirds in relation to nest reuse within and between breeding seasons in an urban population of Pale-breasted Thrushes. Numbers inside bars represent sample sizes and an asterisk indicates statistical significance at $\alpha = 0.05$.

DISCUSSION

We found that nest reuse within a breeding season was more frequent after a successful nesting attempt and reuse benefited Pale-breasted Thrushes by reducing the likelihood of brood parasitism by cowbirds, thus indirectly contributing to greater breeding success. Moreover, nest reuse resulted in a nearly six day earlier start to laying of initial clutches at the beginning of breeding seasons, a period comparable to that of nest construction in this species (i.e., ~ 7 days). Earlier initiation of nesting by females reusing nests has also been reported for other species of birds (Cavitt et al. 1999, Antonov and Atanasova 2003, Wysocki 2004). For example, females reusing nests initiated breeding an average of 6.5 days earlier than females building new nests by an average of 6.5 days in Eurasian Magpies (*Pica pica*; Antonov and Atanasova 2003) and by an average of 17.4 days in Brown Thrashers (*Toxostoma rufum*; Cavitt et al. 1999).

Nests of most open-cup nesting passerines typically do not last long enough to be reused between seasons, and thus, reuse occurs mainly during the same breeding season (Aguilar and Marini 2007, Ellison 2008, but see Cavitt et al. 1999). Nest reuse between consecutive years requires that nests be protected to avoid being dismantled by the weather (Wysocki 2004). Consequently, nests in buildings in our study were more likely to be reused because they were generally better protected from the elements than nests in trees. In addition, however, nests in buildings may be reused because they provide other benefits, e.g., providing a more favorable (warmer) microclimate for developing embryos and nestlings and better protection of nest contents from the elements. In fact, nest integrity is not enough to induce nest reuse, as also reported for Eurasian Blackcaps

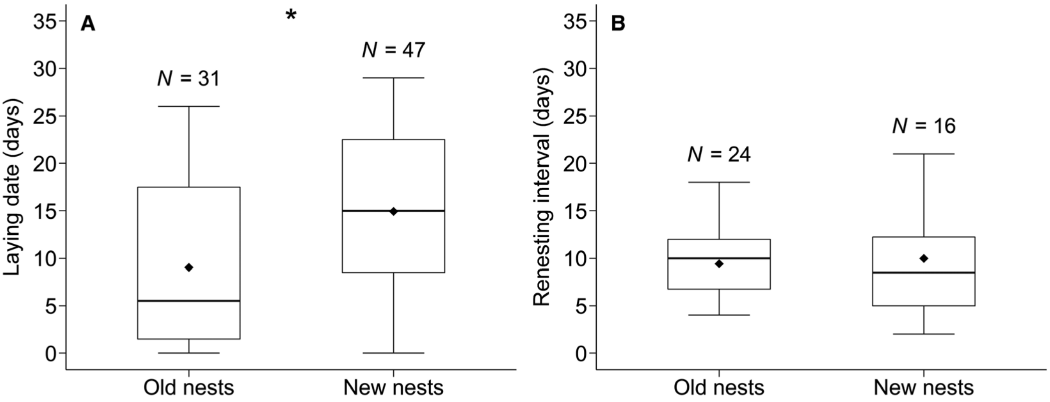

Fig. 3. Effect of nest reuse on date of initiation of egg laying (i.e., laying date, with 0 representing the earliest date that a female initiated egg laying) for first nesting attempts in a breeding season (A) and on the renesting interval between consecutive clutches during the same breeding season (B) for an urban population of Pale-breasted Thrushes. Boxes = interquartile range, whiskers = minimum and maximum, horizontal lines = median, diamonds = mean. Asterisk indicates statistical significance at $\alpha = 0.05$.

(*Sylvia atricapilla*, Zieliński 2012), because other factors such as the fate of the last nesting attempt and whether consecutive nesting attempts occurred within or between breeding seasons also influence the likelihood of nest reuse, as found in our study.

We found that nests were reused more often after successful nesting attempts in agreement with the "win-stay, lose-switch" strategy (see also Wysocki 2004 for Eurasian Blackbirds), but this was limited to consecutive nesting attempts in the same breeding season, likely because the repeatability of nest fate at a given nest-site depends on a short time interval between successive nesting attempts (Weidinger and Kočvara 2010). However, reuse after a successful nesting attempt did not ensure success for the next nesting attempt, which, with rare exceptions (e.g., Ellison 2008), corroborates the results of previous studies (Antonov and Atanasova 2003, Wysocki 2004, Styrsky 2005). In the Neotropics, nest predators and their nest-searching methods are highly diverse (Menezes and Marini 2017), which presumably helps explain the unrelated fates of consecutive nesting attempts in reused nests (Weidinger and Kočvara 2010).

We found that the likelihood of cowbird parasitism was lower only when nests were reused during the same breeding season. The results of previous studies suggest that host activity near nests increases the likelihood of brood parasitism by cowbirds (Fiorini and Reboreda 2006, Svageli et al. 2009). The higher incidence of parasitism of new nests in our study suggests that cowbirds locate nests by monitoring parental behavior rather than revisiting previously parasitized nests. Moreover, this difference suggests that cowbirds probably rely on specific host behaviors to locate nests, such as nest-site inspection (i.e., when an adult thrush repeatedly visits potential nesting sites) and nest building (Batisteli, pers. obs.). The reduced likelihood of parasitism in reused nests may be related to the reduced time needed to add nest lining compared to building an entirely new nest, with construction of a new nest providing cowbirds with more opportunities to find nests because of the greater number of nest visits.

Nest reuse, although rare among open-cup nesting birds, can allow earlier initiation of egg laying at the start of a breeding season and shorter intervals between consecutive nesting attempts during the same breeding season (Cavitt et al. 1999, Antonov and Atanasova 2003). However, as also reported for Eurasian Blackbirds (Wysocki 2005), nest reuse did not shorten re-nesting intervals within breeding seasons in our study. Nest reuse also did not allow earlier initiation of second clutches. One likely explanation for this is that re-nesting intervals can be influenced by several factors that we did not take into account, such as adult experience (Roper 2005), parental condition and time remaining for breeding in a breeding season (Nilsson 2000), and the duration of post-fledging care (Tarwater and Brawn 2010).

We also found limited evidence that initiating nests earlier in the breeding season reduced the likelihood of cowbird parasitism, with this relationship being only marginally significant. However, earlier nesting may allow more time for renesting during a breeding season and may also provide fledglings with more time to develop skills that can increase their likelihood of survival during the non-breeding season (Barba et al. 1995, Nilsson 2000). Renesting intervals within the same breeding season were similar for successful and failed nesting attempts, and the fact that males usually care for fledglings while females initiate new nests (Davanço et al. 2013) may have contributed to this result.

As in other studies, nest reuse in our study did not provide other potential advantages, such as larger clutches (Redmond et al. 2007, Cancellieri and Murphy 2013) or more nesting attempts (Styrsky 2005). In fact, nest reuse cannot save enough time to allow an extra nesting attempt in a breeding season because the time saved by reusing nests is about only 20% of the duration of a complete nesting cycle of Pale-breasted Thrushes (Davanço et al. 2013). Laying dates for the second or third clutches likely depend more on the fate of the first nesting attempts than nest reuse. Therefore, the possibility of a third nesting attempt appears to depend primarily on the extra time made available by the failure of at least one of the first two nesting attempts (11 of 14 cases).

In conclusion, we found that reuse of nests by Pale-breasted Thrushes was more likely after successful nesting attempts, allowed earlier initiation of egg laying at the beginning of breeding seasons, and reduced the likelihood of cowbird parasitism. Additional studies of other urban populations of open-cup nesting birds, especially those able to nest in or on buildings, are needed to better understand the potential advantages and, perhaps, disadvantages of reusing nests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Fig. S1. Examples of structures in or on buildings used as nesting sites of Pale-breasted Thrushes (*Turdus leucomelas*) in a periurban area of southeastern Brazil.