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ASOCIACIÓN ESPAÑOLA DE ECOLOGÍA TERRESTRE

Ecosistemas 31(1):2196 [Enero-Abril 2022]
https://doi.org/10.7818/ECOS.2196

MONOGRAPHIC: Urban Ecology: A Growing Discipline

Editors: Juan Diego Ibáñez Álamo and Mercedes Molina Morales

RESEARCH ARTICLE

ecosistemas
REVISTA CIENTÍFICA DE ECOLOGÍA Y MEDIO AMBIENTE

ISSN 1697-2473
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disponible en www.revistaecosistemas.net

The location of thrush nests on buildings affects the chance of cowbird parasitism

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> Recibido el 20 de marzo de 2021 - Aceptado el 11 de febrero de 2022

How to cite: Batisteli, A. F., Pizo, M. A. 2022. The location of thrush nests on buildings affects the chance of cowbird parasitism. *Ecosistemas* 31(1): 2196 https://doi.org/10.7818/ECOS.2196

The location of thrush nests on buildings affects the chance of cowbird parasitism

Abstract: Nest site placement is a critical choice among passerines, being an important factor that affects their breeding success. In urban areas, human buildings offer suitable nesting sites usually less exposed to predators and brood parasitic birds and readily available to be reused for several breeding seasons. However, the extent to which the features of nest placement sites in buildings contribute to reduce nest detectability by predators and brood parasites is still unknown. Here, we tested whether the features of the nesting site (i.e., lateral concealment, distance to the building ceiling, and height above ground) affect the chance of brood parasitism by Shiny Cowbirds (*Molothrus bonariensi*s) in Pale-breasted Thrushes (*Turdus leucomelas*) nests placed on buildings in a Brazilian suburban area from 2013 to 2019. Cowbird parasitism increased throughout the study years, and nests closer to ceilings, supposedly better concealed, were more likely to be parasitized. Laying date, height above ground, and lateral concealment were not related to the probability of cowbird parasitism. We suggest that less concealed nests enhance vicinity monitoring by parents, allowing a faster agonistic response to the presence of cowbirds near the nest. Our results indicate that nest site location in cities may have consequences for the breeding success of cowbird hosts.

Keywords: anthropogenic nesting sites; *Molothrus bonariensis*; nest concealment; urban bird

La ubicación de los nidos de zorzal en los edificios afecta a la posibilidad de parasitismo del tordo

Resumen: La ubicación del nido es una elección crítica entre los paseriformes, ya que es un factor importante que afecta a su éxito reproductivo. En las áreas urbanas, los edificios ofrecen sitios de nidificación adecuados, generalmente menos expuestos a depredadores y a aves parásitas de cría y fácilmente disponibles para ser reutilizados durante varias temporadas de cría. Sin embargo, aún se desconoce hasta qué punto las características de los sitios de colocación de nidos en los edificios contribuyen a reducir la detectabilidad de los nidos por parte de depredadores y parásitos reproductores. Aquí, analizamos si las características del sitio de nidificación tienen un efecto en la probabilidad de parasitar por los tordos renegridos (*Molothrus bonariensis*) en nidos de zorzal sabiá (*Turdus leucomelas*) colocados en edificios en un área suburbana brasileña. El parasitismo de los tordos aumentó a lo largo de los años de estudio, y los nidos más cercanos a los techos, supuestamente mejor escondidos, tenían más probabilidad de ser parasitados. La fecha de puesta, la altura sobre el suelo y la ocultación lateral no se relacionaron con la probabilidad de parasitismo por tordos. Los resultados sugieren que los nidos menos ocultos mejoran la vigilancia de las inmediaciones por parte de los padres, lo que permite una respuesta agonística más rápida a la presencia de tordos cerca del nido. Nuestros resultados indicaron que la elección de la ubicación del nido en los edificios por parte de los huéspedes potenciales del tordo puede tener consecuencias para su éxito reproductivo en las ciudades.

Palabras clave: sitios antropogénicos de nidificación; *Molothrus bonariensis*; ocultación del nido; ave urbana

Introduction

The selection of a safe site for breeding is a widespread strategy to increase offspring survival in a variety of organisms. Among altricial birds, nest site selection is a behavioral process by which birds can passively reduce the risk of threats to an initially sessile offspring and thus increase its survivorship (Lima 2009; Ibáñez-Álamo et al. 2015).

The pattern of nest site selection is in general well conserved in phylogeny, so that each group of species exhibits typical nest site features (Collias 1997; Brightsmith 2005). However, there is certain inter- and intraspecific level of flexibility in this behavior, and local fluctuations in the abundance or identity of the main nest predators, as well as changes in environmental pressures, may incur in different nest placement choices (Lima 2009). Moreover, birds can use information gathered in previous breeding attempts to select breeding sites, which are safer from threats represented by predators and weather elements (Chen et al. 2011; Bressler et al. 2020). Such plasticity in nest site selection allows rapid adjustments of reproductive strategies at individual and population level, contributing to the occupation of new environments such as urban habitats (Bressler et al. 2020).

Urban areas exhibit a particular set of environmental pressures, acting as a severe biological filter to the regional pool of bird species

(Croci et al. 2008; Clucas and Marzluff 2016). Species more inclined to tolerate human proximity and explore the resources provided by humans tend to perform better in the city (Møller 2010a; Galbraith et al. 2017). For instance, several bird species from different continents use human structures to breed, which facilitates the settlement of urban bird populations (Mainwaring 2015; Reynolds et al. 2019). There is evidence that the use of anthropogenic structures as nesting sites potentially increases parental fitness by greater offspring survival and lower nest attentiveness during incubation (Møller 2010b; Wallace et al. 2016; Batisteli et al. 2021a), while the proximity with human buildings can also reduce nest susceptibility to brood parasitism (Liang et al. 2013; Møller et al. 2016), which accounts for considerable offspring losses in several species (Arcese et al. 1996; Massoni and Reboreda 2002).

Around 1% of all the bird species evolved the complex behavior of laying their eggs exclusively in nests of foster species – the so-called obligate brood parasites (Robert and Sorci 2001). Instead of the typical parental tasks of nest building, nest defense and offspring rearing, adult obligate brood parasites (hereafter simply “brood parasites”) perform behaviors to increase the chance of hatching and survival of their eggs until fledge, for instance by removing, ingesting or puncturing host eggs (Payne and Sorensen 2005; Svagelj et al. 2009). Brood parasites can employ two major, complementary tactics to find host nests: following behavioral cues of potential hosts, such as nest building and territorial defense (the host activity hypothesis) or inspecting potential nesting sites (the habitat search hypothesis) (Robinson and Robinson 2001; Jelínek et al. 2014). In the specific case of cowbirds (*Molothrus* spp.), host parental activity is necessary or increases drastically the frequency of parasitism (Robinson and Robinson 2001; Svagelj et al. 2009). On the other hand, there are evidences showing that certain nest site features, such as the degree of nest concealment, may also predict the risk of brood parasitism by cowbirds – more concealed nests were less likely to be parasitized (Burhans 1997; Larison et al. 1998; Saunders et al. 2003; but see Fiorini et al. 2009), suggesting that they can locate nests independently of host parental activity. However, despite the potential relationship between the features of nest sites provided by human buildings and the action of parasitic birds, there is no study testing whether the characteristics of nest location in buildings can affect the chance of brood parasitism in urban areas.

Here, we studied the effect of microhabitat features of nests placed on buildings on the occurrence of brood parasitism by the Shiny Cowbird *Molothrus bonariensis* on the Pale-breasted Thrush *Turdus leucomelas* in a suburban area in Brazil. We hypothesized that the degree of nest concealment, estimated by the lateral concealment and the distance to the building ceiling, would affect the probability of cowbird parasitism in active nests. Particularly, we expect that more exposed nests will be more parasitized according to the habitat search hypothesis.

Material and methods

Study area

We carried out this study at the campus of Universidade Estadual Paulista “Júlio de Mesquita Filho”, a green urban area in the periphery of Rio Claro municipality, southeastern Brazil (22º23′43″S, 47º32′46″W, 628 m a.s.l.). The regional climate is subtropical with dry winters and hot summers, with annual rainfall around 1344 mm concentrated between October and March and mean monthly temperatures ranging from 16.5 to 23 ºC (Alvares et al. 2013).

The study site corresponds to the Atlantic Forest domain, and the original vegetation was semidecidual forest, currently highly modified into urban areas, pastures and monocultures. The urbanized portion of the campus, where the study was conducted, is characterized by sparse buildings surrounded by lawns and gardens composed by native and exotic vegetation, besides small forest patches (i.e. unmanaged vegetation).

Study species

The Pale-breasted Thrush is a medium-sized omnivore passerine that inhabits from undisturbed gallery forests to urban centers (Sick 2001). In the study region, the breeding season of this monomorphic and resident species concentrates between September and December; clutch size is usually three, and each pair has up to three nesting attempts a year (Davanço et al. 2013). Pale-breasted Thrush nests are low cups (external diameter: 13.2 cm, external height: 10.2 cm) made mainly from roots and other vegetal fibers firmly cemented with mud (Ruiz et al. 2017). The robust nest structure may resist from one year to another if sheltered from rain as is the case of nests on or in buildings, and pairs frequently reuse nest sites or nest structures from previous breeding seasons in our study population (Batisteli et al. 2021b). The nests are usually placed on the lowest bifurcations of tree trunks, but this species also exploit anthropogenic structures such as concrete columns, PVC tubes, and metallic rails as nesting sites in urban areas (Batisteli et al. 2021b). Like other Neotropical thrushes the Pale-breasted Thrush is parasitized by the Shiny Cowbird (Lowther 2018).

Field procedures

Nest searching and monitoring – We monitored 223 nesting attempts of the Pale-breasted Thrush between 2013 and 2019, of which 192 were made on buildings. Nests were located by following adults or inspecting all potential nest sites. We checked the nest content every 1-3 days with the aid of a mirror attached to a pole to determine laying dates and the presence of cowbird eggs, which were discernible by size, shape and color. Thrush eggs have a greenish or bluish background and are larger and more elliptical than cowbird eggs, which may have a wide variation in the coloration of the eggshell background, including whitish and rosy ones (De la Peña 2013).

We considered the day when the earliest Pale-breasted Thrush egg was laid as the day 1 of each breeding season. Laying date for the rest of the nests was estimated by the difference between the day of the first egg of a given clutch and the day 1 of that season. For nests found after clutch completion, we assigned a laying date by backdating 14 days (the average incubation period) from the hatching day, defined as the earliest day when nestlings were recorded in a clutch, with a precision of ± 1 day (Batisteli et al. 2021a).

Within-season nest reuse is associated to a lower probability of cowbird parasitism in our study population (Batisteli et al. 2021b), then, these cases were discarded from our analyses (n = 39 out of 192). Some other nesting attempts with missing data were excluded due to uncertainty on the presence of cowbird eggs (n = 9), imprecision on laying date (n = 4), or because nest sites were inaccessible and could not be characterized (n = 8). Finally, we retained data on 132 clutches (13 in 2013, 14 in 2014, 24 in 2015, 22 in 2016, 21 in 2017, 23 in 2018 and 15 in 2019).

Bird capturing and banding – We used mist nets to capture and marked adult thrushes throughout the study period. Each captured bird received a metallic ring and a unique combination of colored leg bands. Nestlings were also ringed from 2014 onwards. To determine the sex of individuals, we collected blood samples of all adults and nestlings following the toenail clip method (Owen 2011). Molecular sexing was made by an outsourced laboratory (“UNIGEN - Biologia pelo DNA”, São Paulo) through the Polymerase Chain Reaction (PCR) method.

Nest site characterization – Each monitored nest was characterized regarding lateral concealment, distance to the ceiling, and height above ground. Nest concealment was assessed visually at six distances (1, 2, 4, 8, 16, and 32 m) in each of the four cardinal directions at a horizontal plan from the nest, totalizing 24 sampling points. In each sampling point, we assigned 1 when the nest was visible or 0 when the nest was visually obstructed by any structure belonging to buildings. We focused on building structures because, despite the vegetation in nest surroundings could also provide concealment, this is restricted to a few sampling points. Furthermore, the vegetation that may partially obstruct the view of the nest can also constitute perches for cowbirds from which potential host nests could be found (Larison et al. 1998), acting as a permeable barrier. On the contrary, structures belonging to human buildings, such as walls, represent a true barrier to nest visibility that has to be circumvented to access the nests. The percentage of points from where a given nest was visible (i.e., the sum of visible points divided by 24 sampling points) was used as an estimation of the lateral concealment. The distance between the nest and the ceiling and the nest height above ground were estimated to the nearest 0.1 m using a graduated pole.

Statistical analyses

To test the relationship between nest location and the probability of cowbird parasitism, we first built a generalized mixed-effects model (GLMM) with a binomial response variable (presence or absence of cowbird eggs), setting as candidate explanatory variables (all continuous) lateral concealment, distance to the ceiling, height above ground, laying date, and year. Lateral concealment was transformed in log (x + 1) taken into account the cases of zero visibility. Because some nest sites were used in multiple breeding seasons, we set nest site as a random factor. Then, we conducted a stepwise backward procedure based on likelihood-ratio tests following Zuur et al. (2009) to find the minimal adequate model. We also used likelihood-ratio tests to address the inclusion of male and female identity as random factors using the subset of clutches to which this information was available (80 nesting attempts from 36 marked males, 95 from 36 marked females, and 67 from 26 marked pairs). As the inclusion of male or female identity as random factors did not improve significantly the final models ($p = 0.418$ and $p = 0.826$, respectively), we retained only nest site as a random factor and used the entire dataset, including nesting attempts from unbanded pairs. We also analyzed data from new nests (i.e., the first time each nest site was used) and events of nest site reuse (hereafter "reused nests") separately using the same modeling approach described above. All analyses were conducted in the software R (R Core Team 2020) assuming $\alpha = 0.05$, and values are presented as mean ± standard deviation.

Results

The overall frequency of brood parasitism by cowbirds was 42.6% among the 183 monitored nesting attempts on buildings to which this information was available. Excluding within-years events of nest site reuse and nesting attempts with other missing data, brood parasitism was 49.2% (65 parasitized clutches out of 132). These nesting attempts were made on 63 different nest sites, so that 69 out of these 132 clutches consisted in between-seasons nest site reuse instances. Most of the 63 nest sites were used in one (n = 28) or two breeding seasons (n = 17), whereas few nest sites were used in three (n = 6), four (n = 9), five (n = 2), or six (n = 1) seasons.

Among the 63 nest sites, lateral concealment ranged from 0% (n = 9), when there were barriers closer than 1 m from the nest in all cardinal directions, to 79.2%, averaging 16.5 ± 15.8 %. Out of the 63 nest sites, 34 (54.0%) were adjacent to corners formed by building structures (**Fig. 1A**), which implied that nests in these places were immediately concealed in three of the four cardinal directions. Another 25 nests were built close to walls or windows, being completely concealed from two of the four cardinal directions (**Fig. 1B**). Distance to ceiling varied from 0.1 to 1.8 m (mean 0.37 ± 0.32 m), but most (80.9%) nest sites were right close to the ceiling, between 0.2 m and 0.4 m. Nest height above ground averaged 2.84 ± 0.71 m, ranging from 1.6 to 7.0 m.

Distance to ceiling affected the probability of cowbird parasitism, with nests closer to the ceiling being more parasitized (**Table 1**). However, this effect is restricted to the first time the nests were used, being not significant when reused nests were analyzed separately (**Table 1**). The effect of lateral concealment in cowbird parasitism was marginally significant when considering all nests, but not significant when the subsets of new or reused nests were analyzed separately (**Table 1**). Height above ground did not affect the probability of cowbird parasitism in any model, and there was no temporal trend of brood parasitism within breeding seasons either for new or reused nests (**Table 1**). However, the frequency of parasitism by cowbirds increased drastically during the study years (**Table 1**; **Fig. 2**), from 23.1% in 2013 to 93.3% in 2019.

Figure 1. *Typical nesting sites of the Pale-breasted Thrush (Turdus leucomelas) on human buildings: a nest adjacent to a corner formed by building structures* ***(A)****, and an adult thrush with a Shiny Cowbird (Molothrus bonariensis) nestling in a nest placed on a metallic downspout close to the wall* ***(B)****.*

Figura 1*. Sitios de anidación típicos zorzal sabiá (Turdus leucomelas) en edificios humanos: un nido adyacente a una esquina formada por estructuras de construcción* ***(A)*** *y un tordo adulto con un tordo renegrido (Molothrus bonariensis) pichón en un nido colocado en una bajante metálica cerca de la pared* ***(B)****.*

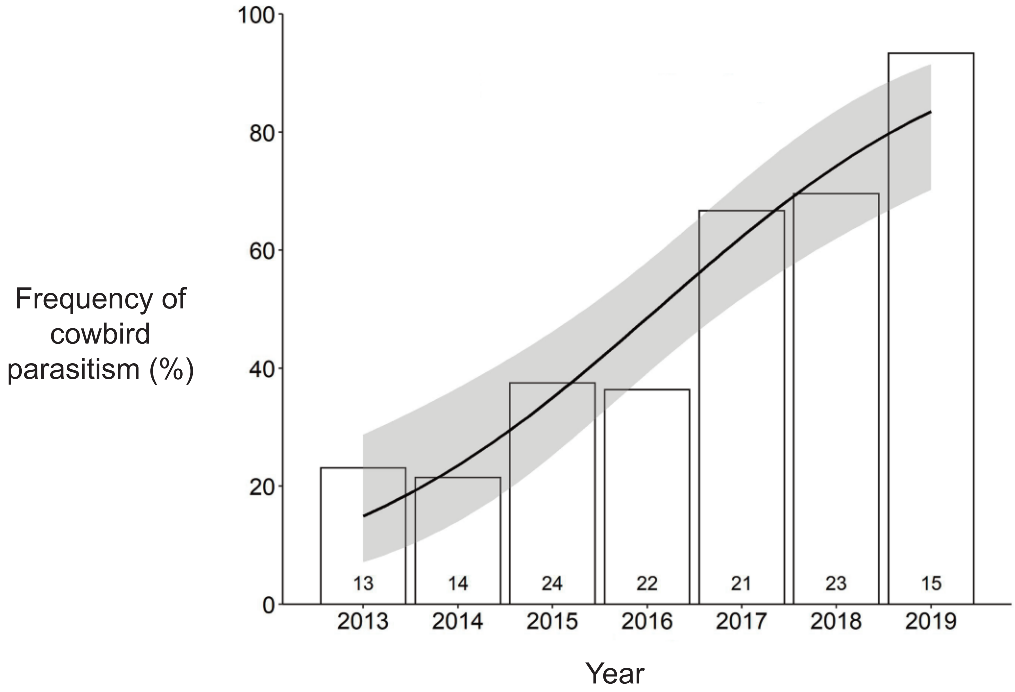

Figure 2. *Frequency of parasitism by Shiny Cowbirds (Molothrus bonariensis) in nests of Pale-breasted Thrush (Turdus leucomelas) placed on buildings in relation to year (2013–2019 breeding seasons). Numbers inside bars indicate sample size, columns show the frequency of parasitized nests per year, and the curve represents a significant logistic trend (with the 95% confidence interval depicted as the grey band) of increasing brood parasitism across years.*

Figura 2. *Frecuencia de parasitismo por tordo renegrido (Molothrus bonariensis) en nidos de zorzal sabiá (Turdus leucomelas) colocados en edificios humanos en relación al año (temporadas de reproducción 2013-2019). Los números dentro de las barras indican el tamaño de muestra, las columnas muestran la frecuencia de nidos parasitados por año y la curva representa una tendencia logística significativa (con el intervalo de confianza del 95% representado como la banda gris) de aumento del parasitismo de cría a lo largo de los años.*

Table 1. *Best Generalized Linear Models selected assessing the probability of parasitism by Shiny Cowbirds Molothrus bonariensis in nests of Pale-breasted Thrush Turdus leucomelas in relation to year (2013–2019), distance to the ceiling, lateral concealment, height above ground and laying date. Data was analyzed separately from the first time each nest was used ("New nests only"), events of nest reuse ("Reused nests only") and all nests pooled together ("All nests"). Estimate, standard error and z-value are not shown for terms excluded from the final models after backward stepwise selection based on likelihood-ratio tests.*

Tabla 1. *Mejores modelos lineales generalizados evaluando la posibilidad de parasitismo por el tordo renegrido Molothrus bonariensis en nidos de zorzal sabiá Turdus leucomelas en relación con el año (2013-2019), distancia al techo, ocultación lateral, altura sobre el suelo y fecha de puesta. Los datos se analizaron por separado desde la primera vez que se utilizó cada nido ("New nests only"), los eventos de reutilización de nidos ("Reused nests only") y todos los agrupados ("All nests"). Estimador, error estándar y valor z no mostrados para los términos excluidos de los modelos finales después de una selección paso a paso hacia atrás basada en pruebas de razón de verosimilitud.*

	Estimate	Std. Error	z	p
All nests				
Intercept	-1.201.000	4.479	-268.221	<0.001*
Year	0.596	0.002	269.040	<0.001*
Distance to the ceiling	-2.179	1.146	-1.901	0.057
Lateral concealment				0.074
Height above ground				0.786
Laying date				0.876
New nests only				
Intercept	-1.022.000	5.172	-197.641	<0.001*
Year	0.508	0.003	198.860	<0.001*
Distance to the ceiling	-3.888	1.807	-2.152	0.031*
Lateral concealment				0.126
Height above ground				0.879
Laying date				0.167
Reused nests only				
Intercept	-1.789.000	7.384	-242.300	<0.001*
Year	0.887	0.004	242.200	<0.001*
Distance to the ceiling				0.576
Lateral concealment				0.230
Height above ground				0.436
Laying date				0.299

Discussion

We found weak support for the habitat search hypothesis, i.e. that anthropogenic structures around Pale-breasted Thrush nests placed on buildings affect the probability of brood parasitism by the Shiny Cowbird. This is based on the marginally significant effect of lateral concealment and that nests closer to the ceiling had a higher probability of being parasitized, although only for the first time each nest site was used. Several studies indicated that cowbirds can actively search for host nests (Burhans 1997; Larison et al. 1998; Saunders et al. 2003; Fiorini and Reboreda 2006; Fiorini et al. 2009; Svagelj et al. 2009). However, the same studies also reported that parental activity enhance the encounter of host nests by cowbirds Furthermore, we found no association between nest height above ground and cowbird parasitism, in line with previous studies (Saunders et al. 2003; Fiorini et al. 2009).

One likely explanation for our unexpected result is that nests more distant to the ceiling allowed a greater visibility of the surroundings for the host parents, either at the nest or while perched in nearby trees. Both these aspects should enhance an early visual detection of cowbirds by thrushes, which perceive them as a threat and frequently chase them away from active nests (Reboreda et al. 2013; Batisteli pers. obs.), reducing the occurrence of cowbird parasitism in more exposed nests. One could argue that following the same thought lateral concealment should have affected cowbird parasitism as well, but there are at least two plausible reasons that could explain these unexpected results. First, we might suspect that the range of lateral concealment is too narrow to allow a detectable difference in cowbird parasitism, because most nests in buildings were at least 50% visually obstructed if attached to a wall, and 75% when at the corners formed by buildings structures. Second, Shiny Cowbirds may have some preference for host nests, relegating more exposed nests to a second choice, for instance, due to their increased risk of predation, as suggested by Fiorini et al. (2009).

The inverse relationship between distance to the ceiling and cowbird parasitism was restricted to new nests. Cowbirds usually found potential host nests by following parents during nest building (Fiorini et al. 2019), and reused nests take presumably less time to lining than new nests that have to be entirely built. Thus, nest reuse could potentially reduce the opportunities of locating a potential host nest for cowbirds. We found this pattern within the breeding season but not between years (Batisteli et al. 2021b). In accordance, nests of the Eastern Phoebe *Sayornis phoebe* parasitized by the Brown-headed Cowbird *Molothrus ater* are even more likely to be parasitized again in the next breeding season (Hauber 2001). This difference corroborates that cowbirds can use multiple tactics to find suitable host nests as reported for Common Cuckoos *Cuculus canorus* (Jelínek et al. 2014), including revisiting nests parasitized in previous years – but not within breeding seasons, which deserves further studies.

The occurrence of brood parasitism by cowbirds often increases throughout the breeding season (Sackmann and Reboreda 2003; Fiorini et al. 2009; but see Hauber 2001), but we found no such temporal trend. The presence of other favored host species (e.g. the Rufous-collared Sparrow *Zonotrichia capensis*) that extend their breeding period beyond that of thrushes allows cowbirds to explore other potential hosts. The presence of multiple hosts with different breeding periods during the same season may have contributed to the absence of a within-season temporal variation on the frequency of cowbird parasitism in the Pale-breasted Thrush, but we have no data to test this assumption.

We found a noticeable increase in the frequency of brood parasitism across the study years, reaching 93.3% of the clutches in the 2019´s breeding season. Data from point-counts and mist-net captures in the study area do not support a similar growing trend in cowbird abundance, which presented no large variation during the study period (M. A. Pizo, unpubl. data). Therefore, the growth on the parasitism pressure on Pale-breasted Thrush nests demands alternative explanations, such as those related to cowbird behavior or that of the thrushes themselves. Despite the existence of lineages of Shiny Cowbird females with host preferences (Mahler et al. 2007), this species is generalist on choosing the nests they parasitize (Fiorini et al. 2019). It is likely, therefore, that the number of parasitized clutches has increased due to the flexibility of cowbird females in response to the decrease of other potential host nests at local scale. We do not discard that the increase in cowbird parasitism within the study period relates to the observer effect to some extent because of the disturbance caused by the field procedures (Smith-Castro and Rodewald 2010). Most parent thrushes usually attacks the observer and emit alert vocalizations during nest monitoring, which could help cowbirds to discover host nests.

Conclusions

We concluded that the presence of anthropogenic structures above the nests of the Pale-breasted thrush can affect the probability of brood parasitism by cowbirds to some extent, with nests close to ceilings being more parasitized. However, we found weak support to the habitat search hypothesis overall, indicating that some nest site features, such as nest lateral concealment and nest height above ground, may have a negligible power in predicting cowbird parasitism for thrush nests placed on buildings.

Author contributions

Augusto Florisvaldo Batisteli: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review and Editing. Marco Aurélio Pizo: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Review and Editing.

Acknowledgments

We are grateful to field assistants. MAP receives a research grant from the Brazilian Research Council (CNPq; 304742/2019-8). We declare no conflict of interest. We received no funding for this study.

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