



Female neophobia predicts the use of buildings as nesting sites in a Neotropical songbird

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Neophobia (i.e. the degree of avoidance to novel situations) is a personality trait that may predict the ability to exploit new resources, which potentially affects the success of settlement of urban animal populations. Despite the increasing amount of information on birds using artificial structures as nesting supports, the hypothesis that the propensity to nest on buildings is related to parental personality has never been tested. In a field experiment, we addressed the relationship between female neophobia and the use of buildings as nesting sites in an urban population of the pale-breasted thrush, *Turdus leucomelas*, in southeast Brazil. We placed novel objects near active nests placed on buildings ($N = 16$) and trees ($N = 12$) and measured the latency of incubating females to resume incubation. Using linear mixed-effects models, we estimated the individual repeatability of this behavioural response and tested whether latency times differed between neophobia and control tests within nesting substrate types. We found significant repeatability for the latency to resume incubation during neophobia tests ($r = 0.353$), indicating that this behaviour was consistent at the individual level as expected for personality-mediated responses. Latency was higher in neophobia than in control tests, but only among females that nested on trees. Previous studies suggest that less neophobic individuals tend to express more exploratory and innovative behaviours, which may have enhanced the use of buildings as nesting sites by fearless females. We conclude that less neophobic females are more prone to nest on buildings in the pale-breasted thrush. Our study is the first to link bird neophobia and the use of buildings as nesting substrates, evidencing that the exploitation of artificial resources may be associated with the predominance of certain animal personalities in anthropic environments.

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Animal behaviours evolve towards maximizing the outcome between the potential risks and benefits of decisions. These trade-offs usually depend on individual physiological state and environmental context, because the gains and risks are related to intrinsic factors, such as body condition (Moiron et al., 2019; Moschilla et al., 2018), and external factors, such as resource availability and predation risk (Heithaus & Dill, 2002; Verdolin, 2006). However, behavioural responses in similar contexts can vary among conspecifics because personality traits impose on each individual different baselines of expected responses in a given situation (Wolf & Weissing, 2012). Unlike ephemeral alterations in behavioural patterns caused by positive or negative stimuli (Dugatkin, 1997; Fuxjager & Marler, 2010), personality-mediated behaviours induce consistent individual responses through time (Castanheira et al.,

2013; Fratkin et al., 2013; Kelleher et al., 2018). The persistence of individuals with different reaction norms within populations is thought to be sustained by assortative mating and fluctuations in environmental pressures across time and space (Groothuis & Carere, 2005; Niemelä et al., 2013), as predicted by the game theory (Smith & Price, 1973). Nevertheless, in particular contexts, extremes of personality traits may be favoured and become predominant (Samia et al., 2015).

Anthropogenic disturbance is a known driver of changes in animal behaviour (Ditchkoff et al., 2006), ultimately promoting the selection of specific personalities (Lapiedra et al., 2017; Samia et al., 2015). Urbanization, for instance, induces behavioural differences between urban and rural populations in several animal groups (Bókony et al., 2012; Lapiedra et al., 2017; Samia et al., 2015), probably because urban dwellers repeatedly face novel resources, threats and disturbances, and lineages able to deal with such abnormal experiences should prosper in cities (Samia et al., 2015; Tryjanowski et al., 2015). Neophobia, the degree of fear of facing an

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unknown situation, is an important dimension of personality and can predict the ability of an individual to solve problems and discover new resources (Sol et al., 2011; Webster & Lefebvre, 2001), which in turn enhances its persistence in highly mutable environments, such as urban areas (Sol et al., 2011).

Although birds are successful in colonizing urban areas worldwide, urban avifauna has a narrow species composition, and the performance of each species in urban habitats depends on biological traits as diet, social structure and migratory status (Crocchi et al., 2008; Kark et al., 2007). More recently, behavioural aspects related to individual personality have also been the focus of studies comparing conspecifics from urban and rural bird populations (e.g. Bókonyi et al., 2012; Minias et al., 2018). Urban bird colonization is usually associated with the persistence of certain phenotypes, such as more aggressive, sedentary, human-tolerant and less neophobic individuals (Minias et al., 2018; Miranda et al., 2013; Møller et al., 2014; Weaver et al., 2018). Tolerance to human proximity and lower neophobia levels are thought to enhance innovative behaviours (Greenberg, 2003; Sol et al., 2011), such as the exploitation of unusual nesting places, but the relationship between bird personality and nest site choices is rarely studied.

Nest site selection has important fitness consequences for breeding birds, being their major response against the risk of offspring predation and adverse weather (Mainwaring et al., 2015). The main characteristics of a potential nest site are relatively well conserved phylogenetically, by which most avian taxa are associated with typical nest site features (Sheldon & Winkler, 1999). Although such patterns result primarily from vertical transmission, individuals can exert their own preferences on nest site selection according to lifetime experiences and personality (Morinay, Forsman, Doligez, 2020; Morinay, Forsman, Germain, Doligez, 2020; Seltmann et al., 2014; Slagsvold et al., 2013). Nesting substrate (i.e. the plant or surface where the nest is attached) is key to nest site selection, directly affecting clutch survival (Donazar et al., 1994; Rodewald et al., 2010). Some bird species rely on one or a few plant species to support their nests, while others are able to nest in a wide variety of anthropogenic substrates (Reynolds et al., 2019). However, despite increasing information on the use of anthropogenic nesting sites by urban birds (see the reviews by Mainwaring, 2015; Reynolds et al., 2019), to the best of our knowledge no study has addressed differences in the personality of individuals nesting in natural and anthropogenic substrates.

Here, we asked whether the use of anthropogenic nesting substrates relates to the neophobia level in females of the pale-breasted thrush, *Turdus leucomelas* Vieillot, 1818, a Neotropical open-cup nesting passerine. In field experiments, we tested whether the latency to re-engage in parental tasks (i.e. return to nest vicinity, perch on the nest rim and resume incubation) differ between incubating females in nests placed on buildings and on trees in the same urban setting. We predicted that females nesting on buildings would be less neophobic, since they choose to nest in novel substrates closer to other artificial structures. In addition, such nesting sites are probably more exposed to pedestrian flow and further sources of anthropogenic disturbance, which are apparently more intense in the pathways around buildings than in the unpaved spaces that surround the trees in our study site.

METHODS

Study Area

This study took place at the campus of the Federal University of São Carlos (21°59'02"S, 47°52'58"W), São Carlos municipality, São Paulo State, Brazil. The regional climate is subtropical, with mean

monthly temperatures between 16.2 and 22.4 °C, and annual rainfall around 1435 mm (Alvares et al., 2013). São Carlos is located on the southern portion of the cerrado domain (Brazilian savanna), and the campus (645 ha) occupies a periurban area, representing an environmental context where both trees and buildings are available as nesting substrates. The campus comprises a mosaic of unmanaged vegetation types (cerrado stricto sensu, riparian forests, *Eucalyptus* and *Pinus* stands and anthropogenic fields dominated by invasive grasses) and urbanized areas (ca. 96 ha) where we conducted this study. Such areas include relatively sparse buildings surrounded by lawns, with abundant native and exotic vegetation.

Study Species

The pale-breasted thrush is a medium-sized omnivore passerine (22 cm, 63 g) that occurs from northern South America to Paraguay and Argentina (Collar & Garcia, 2016; Moraes et al., 2018). This monomorphic resident species inhabits a range of habitats, from undisturbed native vegetation to urban areas (Sick, 2001). The nest is a bulky low cup measuring 13.2 ± 1.3 cm in external diameter and 10.2 ± 2.3 cm in external height, built with roots firmly cemented with mud (Ruiz et al., 2017). Breeding attempts in the study region are concentrated in September–December, and clutch size is usually three eggs (Davanço et al., 2013). Both parents raise the nestlings, but the female is solely responsible for nest construction, incubation and nestling brooding (Ruiz et al., 2017). The nest is usually attached to a large, lower tree trunk bifurcation, but this species also use buildings as nesting substrates (Davanço, 2009; Ruiz et al., 2017) (Fig. 1).

Field Procedures

We mist-netted adult thrushes weekly from September 2017 to August 2019. To minimize the stress of captured birds, we transferred them to a dark cloth bag where they were kept for a maximum of a few minutes and released soon after being ringed. Captured birds received a metallic ring and a unique combination of coloured bands. Individuals were sexed through field observations during the breeding period, assuming that singing and incubation are performed exclusively by the male and female, respectively. We searched for nests by following adults and inspecting all trees and buildings. Once located, nests were monitored every other day using a pole with a mirror to determine laying date, assuming that one egg was laid per day. Females in the study area were presumably habituated to the perturbation caused by nest monitoring, which has been conducted since 2017 as part of other studies.

Neophobia Experiment

During the 2019 and 2020 breeding seasons, we conducted neophobia experiments to assess the neophobia of incubating females. The experiment consisted of two rounds of paired trials (a neophobia test and a control) per nest. Paired trials were conducted on the same morning (0900–1200 hours) on sunny days 2 h apart to reduce the interference of the female's reaction to the first trial in the next trial. Rounds in each nest were spaced 2–3 days apart, depending on weather conditions, to test whether female responses were consistent through time. Because the cumulative value of a clutch increases across incubation, we chose not adopt a larger interval to avoid differences in female behaviour. As novel objects, we chose a textured yellow ball (5 cm diameter) and a magic cube (5 cm edge). For each nest, we randomized the order of treatments within rounds (neophobia or control) and of the novel



Figure 1. Nests and nesting sites of the pale-breasted thrush, *Turdus leucomelas*, in a periurban area in southeast Brazil. (a–c) Use of artificial structures (buildings) as nesting substrates with adult individuals at the nest. (d, e) Typical natural nesting placement of this species in forks of tree trunks, with incubating females. Arrows in (a), (b) and (d) indicate nest locations.

object in the neophobia tests (magic cube or ball). To assure that nests were independent replicates, we excluded those attended by unbanded females unless they were active simultaneously or located at least 200 m apart. Females were tested between day 4 and day 8 of the incubation cycle (14 days) in nests of known age.

We measured neophobia of females from 28 nests, 16 placed on buildings and 12 on trees. This proportion is representative of the nest site choices in the study site since most of them (105 out of 164 nests found between 2017 and 2020) were placed on buildings even though there were many trees in the vicinity. Immediately before the beginning of the trials, we made sure that females were on the nests. In neophobia tests, while females incubated, one of us (A.F.B.) walked directly to the nest from its most visible angle holding the pole used in nest monitoring, placed a novel object 30 cm away from the nest and then moved 20 m away from the nest to a hidden place. We attached a receptacle in the empty extremity of the pole to aid placing the novel object near the nest. Control trials were conducted in the same manner, but no object was left near the nest, being thus similar to a routine nest check.

Considering the lack of a standardized protocol to measure neophobia of incubating females, we estimated three latencies per trial, all starting from the moment the female flushed from the nest until she (1) returned to nest vicinity (i.e. a 2 m radius from the nest), (2) perched on the nest rim and (3) resumed incubation. Nest vicinity was defined based on observations of female trips when returning to the nest during a previous study on incubation behaviour in this species (Batisteli et al., 2021). We recorded no nest abandonment during this experiment. The experiment was conducted under federal banding licences (SISBIO 59414-1, CEMAVE 4216/1), and our field protocol was previously approved by the ethical committee of animal research of the Universidade Federal de São Carlos, São Carlos, São Paulo, Brazil (code 1958100718).

Statistical Analyses

To assess individual consistency in neophobia responses, as expected for personality-mediated behaviours, we performed repeatability tests using the function ‘rptGaussian’ in the R package

'rptR' (Stoffel et al., 2017). This function uses linear mixed-effects modelling to provide a repeatability estimate and its confidence interval calculated using parametric bootstrapping and Bayesian methods, and it tests whether the repeatability estimate differs from zero (i.e. inconsistent behavioural responses at the individual level) through a likelihood ratio test. Using only data from neophobia tests, we estimated the repeatability level for each of the three latency measures, setting the latency to return to nest vicinity, perch on nest rim and resume incubation as response variables (all were square-root transformed to achieve normality) in separate procedures. In all models, we set 1000 iterations for the parametric bootstrapping, included female identity as a random effect, and nesting substrate (buildings versus trees) and the object used in neophobia tests (magic cube versus ball) as fixed effects to control for these potential confounding factors during repeatability estimation (Stoffel et al., 2017). Using the same procedures, we also estimated separately the repeatability for latencies during control trials.

To test for behavioural differences in neophobia and control tests between females nesting in trees and buildings, we used a linear mixed-effects model (LMM). Because the three latencies were highly correlated among each other (see Results), we discarded two of them, and tested our hypothesis using only the latency to resume incubation, since it is the parental task the females were performing before being flushed. We used the latency to resume incubation from both neophobia and control tests as a response variable (square-root transformed), setting treatment (neophobia versus control), nesting substrate (building versus tree), and the interaction treatment \times nesting substrate as categorical explanatory variables, and female identity as a random factor. To control for a potential habituation effect, we also included as explanatory variables in the model the order of treatments (neophobia or control first) and round number (first or second). As the interaction term was significant, we ran a Tukey post hoc test comparing latency times between treatments within nesting substrates. All analyses were conducted in R (R Core Team, 2018) using the packages 'rptR', 'lme4' (Bates et al., 2007), 'lmerTest' (Kuznetsova et al., 2015) and 'emmeans' (Lenth et al., 2018), assuming $\alpha = 0.05$. Repeatability estimates are followed by standard errors and confidence intervals (CI), and further values are presented as means \pm standard deviation unless noted otherwise.

RESULTS

We found different levels of repeatability for each behaviour studied. Repeatability in neophobia tests was 0.474 ± 0.142 (CI: 0.180–0.737) for return to nest vicinity and 0.353 ± 0.161 (CI: 0.021–0.664) for resuming incubation, both significantly different from zero in likelihood ratio tests (return to nest vicinity: $\chi^2 = 6.65$, $P = 0.005$; resume incubation: $\chi^2 = 3.36$, $P = 0.033$). On the other hand, the latency to perch on the nest rim showed no repeatability (0.274 ± 1.64 , CI: 0–0.598), not differing from zero ($\chi^2 = 1.91$, $P = 0.084$). The studied behaviours also showed repeatability at the individual level during control trials (return to nest vicinity: 0.592 ± 0.124 , CI: 0.317–0.787, $\chi^2 = 10.9$, $P < 0.001$; perch on nest rim: 0.419 ± 0.154 , CI: 0.098–0.688, $\chi^2 = 4.57$, $P = 0.016$; resume incubation: 0.367 ± 0.162 , CI: 0.012–0.648, $\chi^2 = 3.32$, $P = 0.034$).

The three latencies were highly correlated with each other (all $r > 0.936$ and $P < 0.001$), thus we retained only the latency to resume incubation as a response variable. This latency differed significantly between treatments. Females took significantly less time to resume incubation in control trials than in neophobia tests (313.3 ± 212.1 s versus 437.1 ± 330.1 s, respectively) (Table 1), which implies that novel objects actually inhibited the females. However, we found a significant interaction between treatment

Table 1

Results of a linear mixed-effects model assessing the latency of incubating females of the pale-breasted thrush, *T. leucomelas*, in different nesting substrates (trees, $N = 12$; buildings, $N = 16$) to resume incubation during two rounds of neophobia tests and control trials ('treatment'), the interaction between nesting substrate and treatment, the order of treatments and round number (1 or 2)

	Estimate	SE	df	t ratio	P
Intercept	13.575	2.562	77.742	5.298	<0.001
Nesting substrate	2.120	2.272	41.308	0.933	0.356
Treatment	5.857	1.658	81.000	3.533	0.001
Nesting substrate \times Treatment	-5.163	2.193	81.000	-2.354	0.021
Order of treatments	0.483	1.975	25.000	0.244	0.809
Round number	1.007	1.085	81.000	0.928	0.356

and nesting substrate (Table 1). The post hoc test revealed that the higher latency in neophobia than in control tests was restricted to females that nested on trees (Fig. 2, Table 2). There was no difference in latency to resume incubation between nesting substrates in the controls (Table 1), indicating that all females were similarly prone to resume incubation in neutral situations.

DISCUSSION

We found different levels of neophobia between females nesting on trees and on buildings in an urban habitat, supporting the hypothesis that female neophobia and nest site choice are related in the pale-breasted thrush. In line with our prediction, females that placed nests on trees had longer latencies in neophobia tests than in control trials, whereas females that placed nests on buildings behaved similarly in both treatments. These results indicate that a novel object near the nest did not inhibit certain females (e.g. those that nested on buildings) from resuming incubation. The repeatability of latency measurements for returning to the nest vicinity and resuming incubation indicated that these responses were consistent at the individual level, suggesting that our neophobia tests provided a reliable differentiation between female behavioural profiles.

Individuals with lower neophobia levels usually show more exploratory and innovative behaviours (Biondi et al., 2020; Ducatez et al., 2017; Greenberg, 2003; Overington et al., 2011), which should have contributed to less neophobic females selecting suitable

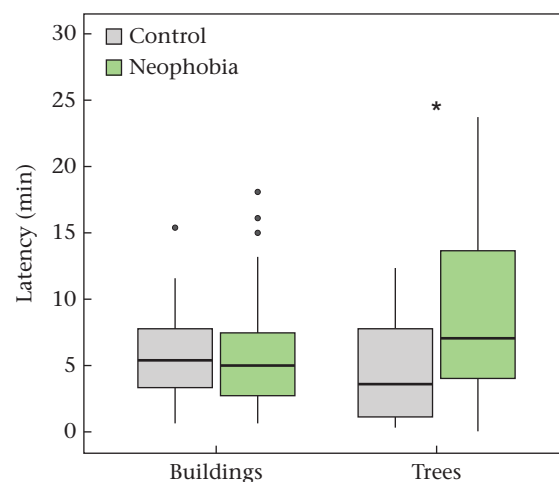


Figure 2. Latency to resume incubation in females of an urban population of the pale-breasted thrush, *Turdus leucomelas*, that nested in buildings ($N = 16$) and trees ($N = 12$) during neophobia and control tests. Whiskers: minimum and maximum values; boxes: interquartile ranges; horizontal segments: medians; dots: outliers; asterisk: statistical significance at $\alpha = 0.05$.

Table 2

Pairwise comparisons by Tukey post hoc tests assessing the latency to resume incubation in females of the pale-breasted thrush, *T. leucomelas*, that nested in different substrates (trees, $N = 12$; buildings, $N = 16$) during neophobia tests and control trials

Pairwise comparisons (treatment/substrate)	Estimate (SE)	df	t ratio	$P_{adj.}$
Control/Tree vs Neophobia/Tree	-5.857 (1.660)	81.0	-3.533	0.004
Control/Tree vs Control/Building	-2.120 (2.270)	41.3	-0.933	0.787
Neophobia/Tree vs Neophobia/Building	3.043 (2.270)	41.3	1.339	0.544
Control/Building vs Neophobia/Building	-0.694 (1.440)	81.0	-0.484	0.962

nesting sites in buildings. Females that nested on buildings showed similar latency in neophobia tests and control trials, which is uncommon (see studies cited below). One likely reason for these unexpected similar responses is that novel objects are usually presented near a source of food (e.g. Apfelbeck & Raess, 2008; Audet et al., 2015; Bókony et al., 2012; Boogert et al., 2006; Fox & Millam, 2007; Miranda et al., 2013), while our neophobia tests were conducted near active nests. Thus, unlike simply losing a foraging opportunity, the studied females probably took into account the value of the current offspring in terms of invested energy.

Individuals of urban bird populations are usually less neophobic than their counterparts in rural or natural habitats (Biondi et al., 2020; Bókony et al., 2012; Ducatez et al., 2017), although some studies have found an opposite trend (Audet et al., 2015; Miranda et al., 2013). We found considerable variation in neophobia among females in the same urban population, and previous studies have reported how individuals that exhibit certain behavioural profiles can benefit more from living close to humans (reviewed in Sol et al., 2013). Less neophobic individuals, for instance, are more prone to exploit novel food sources (An et al., 2011). Additionally, higher tolerance to human proximity is typical among vertebrate populations in urban and other human-disturbed habitats (Samia et al., 2015) and may lead to greater protection for adult birds and their nests against predators and brood parasites (Møller, 2010, 2012; Møller et al., 2016). Although we did not measure other potential benefits, less neophobic females in this study benefited at least from having access to additional nesting sites in anthropogenic structures. Furthermore, pale-breasted thrush females in our study population that nest on buildings enjoy higher nest temperatures and thus need to devote less time to incubating (Batisteli et al., 2021), besides having higher nest survival rates (A. F. Batisteli, personal observation). Thus, the potential benefits provided by anthropogenic resources such as nesting substrates are probably heterogeneously experienced by individuals within a bird population according to their personality traits.

Parental personality in birds affects the engagement in breeding tasks, with direct impacts on reproductive performance (Barnett et al., 2012; Colchester & Harrison, 2016; Li et al., 2020). In urban environments, parents suffer repeated human perturbation, and those who show lower latencies to resume parental tasks should have higher breeding success. Recent studies have reported that the personality of breeding adults affects nest site preferences and offspring survival, because the parental ability to deal with nest threats interacts with the risk of predation associated with nest site characteristics (Seltmann et al., 2014; Zhao et al., 2016). For instance, bolder individuals can choose concealed nest sites, where clutch survival is higher, despite the potential increase in predation risk for themselves – the reduced view of the surroundings implies fewer escape opportunities in such places (Seltmann et al., 2014). Accordingly, we found that innovations regarding nesting substrate choices may relate to intraspecific variation in neophobia, an important dimension of personality. Although both sexes may participate in nest site selection, we focused on females because they solely build the nest, incubate the eggs and brood the nestlings in this species (Ruiz et al., 2017). Thus, it is unlikely that females

would chose to nest in sites radically different from their own preferences, since they are the sex exposed to predation risk at the nest and pay the thermoregulatory costs associated with nest microhabitat.

Preferences on nest site selection can be vertically transmitted by both a heritable and a cognitive (imprinting) component (Slagsvold et al., 2013). Since animal personality is also heritable (Groothuis & Carere, 2005; van Oers et al., 2004), we might suppose a great potential for the vertical transmission of the use of buildings as nesting substrates. Nests in buildings provide multiple advantages in our study context, such as higher clutch survival and reduced nest attentiveness (Batisteli et al., 2021; A. F. Batisteli, personal observation). Thus, we strongly suspect that less neophobic females that nest in buildings are better candidates to establish urban lineages, in line with the adaptive flexibility hypothesis (Cohen et al., 2020), a topic worth of further studies.

Conclusions

We conclude that the use of anthropogenic nesting substrates in the pale-breasted thrush is associated with less neophobic females. This study is the first to relate neophobia and the use of buildings as nesting substrates by birds. Our results help to link access to anthropogenic resources to the predominance of certain personality traits in anthropogenic environments, contributing to shape animal behaviour in these habitats.

Data Availability

Data that support the findings of this study are available from the corresponding author upon reasonable request.

Author Contributions

Augusto F. Batisteli: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing; Marco A. Pizo: Conceptualization, Methodology, Writing – Original Draft, Writing – Review & Editing, Supervision; Hugo Sarmento: Conceptualization, Methodology, Writing – Original Draft, Writing – Review & Editing, Supervision.

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Conflict of Interest

None.

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