

Buildings promote higher incubation temperatures and reduce nest attentiveness in a Neotropical thrush

AUGUSTO F. BATISTELI,*¹  LEONARDO B. DE SOUZA,² ISADORA Z. SANTIEFF,³ GUILHERME GOMES,² TALITA P. SOARES,³ MARIANELA PINI,⁴ RHAINER GUILLERMO-FERREIRA,³  MARCO A. PIZO²  & HUGO SARMENTO³ 

¹Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, Rod. Washington Luiz km 235, São Carlos, SP, Brazil

²Instituto de Biociências, Universidade Estadual Paulista Júlio de Mesquita Filho, Av. 24A 1515, Rio Claro, SP, Brazil

³Departamento de Hidrobiologia, Universidade Federal de São Carlos, Rod. Washington Luiz km 235, São Carlos, SP, Brazil

⁴Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, Bahía Blanca, Buenos Aires, B8000, Argentina

Incubation is an energetically costly parental task of breeding birds. Incubating parents respond to environmental variation and nest-site features to adjust the balance between the time spent incubating (i.e. nest attentiveness) and foraging to supply their own needs. Non-natural nesting substrates such as human buildings impose new environmental contexts that may affect time allocation of incubating birds but this topic remains little studied. Here, we tested whether nesting substrate type (buildings vs. trees) affects the temperature inside the incubation chamber (hereafter ‘nest temperature’) in the Pale-breasted Thrush *Turdus leucomelas*, either during ‘day’ (with incubation recesses) or ‘night’ periods (representing uninterrupted female presence at the nest). We also tested whether nesting substrate type affects the incubation time budget using air temperature and the day of the incubation cycle as covariates. Nest temperature, when controlled for microhabitat temperature, was higher at night and in nests in buildings but did not differ between daytime and night for nests in buildings, indicating that buildings partially compensate for incubation recesses by females with regard to nest temperature stability. Females from nests placed in buildings exhibited lower nest attentiveness (the overall percentage of time spent incubating) and had longer bouts off the nest. Higher air temperatures were significantly correlated with shorter bouts on the nest and longer bouts off the nest, but without affecting nest attentiveness. We suggest that the longer bouts off the nest taken by females of nests in buildings is a consequence of higher nest temperatures promoted by man-made structures around these nests. Use of buildings as nesting substrate may therefore increase parental fitness due to a relaxed incubation budget, and potentially drive the evolution of incubation behaviour in certain urban bird populations.

Keywords: anthropogenic nesting sites, behavioural plasticity, nest microclimate, parental behaviour, urban birds.

Parental care in birds embraces a suite of energetically costly tasks, including nest construction, incubation, nestling provisioning and nest defence.

Corresponding author.
 Email: augustofb@gmail.com
 Twitter: @augustofb87

Although these activities may enhance offspring survival (Schmidt & Whelan 2005, Evans & Stutchbury 2012), there may be trade-offs of reduced body condition and life expectancy for parents (Fast *et al.* 2007, Santos & Nakagawa 2012). The evolution of parental care strategies

seeks to maximize the net fitness benefit (Ghalambor & Martin 2001). The optimal equilibrium point of this trade-off is influenced by variation in environmental contexts such as food availability and habitat structure, and can be actively altered by behavioural decisions of breeding birds, such as nest placement (Burhans & Thompson 2001, Eggers *et al.* 2008, Fan *et al.* 2017). Nest attentiveness (i.e. the percentage of time birds spend incubating) represents an important trade-off for passerine species with uniparental incubation, in which the incubating bird (usually the female) must balance nest attendance and self-maintenance activities. The presence of an incubating bird at the nest has multiple functions, such as warming the brood and defending the nest against opportunistic predators (Halupka & Greeney 2009). Thus, features of the nest-site that reduce brood exposure to predators and adverse weather conditions are expected to have a direct effect on incubation behaviour (Weidinger 2002, Hu *et al.* 2017).

Nest-site selection is a complex decision that involves inherited, cognitive and personality aspects (Chen *et al.* 2011, Breen *et al.* 2016) and has a direct influence on the parental care–survival trade-off by changing predation risk for breeding adults and their brood (Miller *et al.* 2007). Birds usually show intraspecific plasticity in nest-site preferences in response to nest predators and their local abundance (Forstmeier & Weiss 2004, Yeh *et al.* 2007). Nest-site features such as nest concealment are taken into account by birds in the selection of nest-sites as a proxy to minimize reproductive costs related to predation risk, nest attentiveness and the parental investment in nestling provisioning (Robertson 2009, Węgrzyn & Leniowski 2011, Latif *et al.* 2012). Nest concealment also has important effects on nest microclimate and therefore consequences for thermoregulatory costs to parents and offspring (Amat & Masero 2004, Robertson 2009).

The successful development of bird embryos requires eggs to be kept within a narrow, species-specific thermal range (Ricklefs & Brawn 2013, Robinson *et al.* 2014). Even small variations in mean incubation temperature influence the length of the incubation period, and the physiology and survival prospects of nestlings (Berntsen & Bech 2016, Griebel *et al.* 2018, Vedder *et al.* 2018). Parent birds are expected to cope with natural oscillations in environmental temperature mainly through the selection of a nesting site that

minimizes incubation costs (Robertson 2009, Bueno-Enciso *et al.* 2016, but see Lloyd & Martin 2004). Further, incubating birds modulate their incubation behaviour in response to air temperature. This topic has been extensively studied (reviewed by Conway & Martin 2000) and most studies report that higher air temperatures are related to shorter incubation sessions (hereafter ‘on-bouts’) and longer incubation recesses (‘off-bouts’). The effect of nest-site microclimate on incubation behaviour, however, has seldom been studied (e.g. Bryan & Bryant 1999, Ardia *et al.* 2009, Álvarez & Barba 2014, Bueno-Enciso *et al.* 2016, Mueller *et al.* 2019), especially among open-cup-nesting birds (Lloyd & Martin 2004, Londoño *et al.* 2008, Robertson 2009).

The colonization of novel habitats, such as urban areas, imposes new challenges in the adjustment of the trade-offs faced by breeding birds. Urban birds experience changes in the nest predator community (Rodewald & Kearns 2011) and opportunities to explore new resources, such as alternative foods and artificial nesting sites (Møller *et al.* 2015, Wang *et al.* 2015). The exploitation of those new resources shapes an urban behavioural profile, which include high levels of problem-solving skills, boldness and higher tolerance to human proximity in urban than in rural conspecifics (Evans & Stutchbury 2012, Audet *et al.* 2015, Møller *et al.* 2015). The use of anthropogenic nesting sites enhances occupation of urban areas where natural nesting substrates are limited or absent (Møller 2010, Tella *et al.* 2014, Reynolds *et al.* 2019).

Some studies have reported the costs and benefits of bird nesting in anthropogenic structures (reviewed by Mainwaring 2015, Reynolds *et al.* 2019) but the effect of buildings used as nesting substrate on nest temperature has not been studied. McCafferty *et al.* (2001) showed that the temperature in a building used as a roost site by Barn Owls *Tyto alba* was 1.4 °C higher than the external environment due to protection from rain and wind. Higher nest temperatures, in turn, are associated with reduced nest attentiveness during incubation in passerines with open-cup nests such as Northern Mockingbirds *Mimus polyglottos* (Londoño *et al.* 2008) and Dark-eyed Juncos *Junco hyemalis* (Robertson 2009). However, the effect of buildings on the thermal balance of bird nests and the likely behavioural adjustments of individuals using those nesting sites has not yet been studied.

Here we tested whether occupation of anthropogenic nesting structures affects the incubation behaviour of females of an open-cup-nesting Neotropical passerine, the Pale-breasted Thrush *Turdus leucomelas*. We tested whether (1) the temperature inside the incubation chamber (hereafter 'nest temperature') is affected by nesting substrate type (buildings vs. trees) and the presence of incubating females at the nest ('daytime', with possible incubation recesses, and 'night', when the female is uninterruptedly at the nest), and (2) the incubation budget (nest attentiveness, on- and off-bout durations) is affected by nesting substrate type, using as covariates air temperature and the day of the incubation cycle. We predicted that the use of buildings as nesting substrates permits the maintenance of higher nest temperatures, which may facilitate females to take longer off-bouts without harming embryonic development. We therefore predicted that female attentiveness should be lower for nests placed in buildings because of the thermal benefits provided by man-made structures. We also predicted that air temperature should be inversely associated with on-bout duration and positively associated with off-bout duration because of the narrow range of incubation temperature required for adequate embryo development, which imposes differences in thermoregulatory costs for incubating females.

METHODS

Study area

The study was conducted in two peri-urban areas in São Paulo State, southeastern Brazil: the campus of the Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP) in Rio Claro municipality (22°23'43"S, 47°32'46"W, 628 m asl), and the campus of the Universidade Federal de São Carlos (UFSCar) in São Carlos municipality (21°59'02"S, 47°52'58"W, 848 m asl). The study sites are 60 km distant from each other and are subject to similar climatic conditions. The regional climate is subtropical with dry winters and hot summers (Alvares *et al.* 2013). Mean annual rainfall is about 1344 mm in Rio Claro and 1435 mm in São Carlos, with rains concentrated between October and March in both sites. Monthly mean temperatures are 20.2 °C in Rio Claro (range: 16.5–23 °C) and 19.9 °C in São Carlos (range: 16.2–22.4 °C). The two sites held both urban greenspace and patches

of native vegetation (Brazilian savanna and riparian forests) (Potascheff *et al.* 2010, Lessi *et al.* 2016).

Temperature survey

During the 2012 breeding season (between August and December), Pale-breasted Thrush nests were found at UNESP by carefully inspecting buildings and trees, and by following adults carrying nesting material. Once located, we installed a pair of data loggers (iButtons/Maxim®) programmed to take temperature measurements every 2 min. Before installation, all data loggers were waterproofed by wrapping them in latex and camouflaged with mud to resemble nesting material. In each nest, we positioned one iButton in the bottom of the incubation chamber to register the temperature inside the nest (hereafter 'nest temperature'), and another outside the nest (~30 cm) to capture variations in microhabitat temperature. We used a nylon wire to attach the internal iButton to the nest structure and to the nest substrate to prevent females removing it. We installed loggers in nine active nests (four in trees and five in buildings). iButton installation took 5–10 min and no nest abandonment occurred after this procedure. We discarded temperature data before midnight following iButton installation to allow for female habituation after the intervention. Nest status was checked daily and we also discarded all temperature records after midnight on the day of hatching day or the day when the nest was depredated to ensure that data were only collected during incubation.

Incubation behaviour

From August to December 2017 and 2018, we searched for nests in UFSCar every other day in the same way as described above. Once located, nests were checked every 1–3 days using a pole with a mirror until the chicks hatched or the nest was depredated. Daily nest checking near the expected hatching date allowed us to infer the day of the incubation cycle in each of our behavioural observations during incubation (see below). We performed sessions of direct observation (1 h duration) of incubation behaviour following the focal animal method (Altmann 1974). Each nest was observed six times (twice each day, once between 07:00 and 09:00 h and once between 12:00 and 14:00 h, for 3 days), during the morning and

afternoon to record female behaviour under a wide range of air temperatures. To sample possible variation in female behaviour across the incubation cycle, each day of observation in the same nest was spaced 2–3 days from the next. All observations were carried out on days without rain, from places which had routine human pedestrian flow within 10 m of the nest. This was done to increase the probability that female thrushes were habituated to human activity near the nest so that the presence of a human observer would not affect their behaviour. Nevertheless, we waited for 5 min before starting data collection in each observation session to minimize any possible observer effect. Some nests were depredated early in the incubation phase or could not be repeatedly observed due to poor weather, leading to missing data. We included in the analysis only data from nests observed in at least four of the expected six observation sessions ($n = 15$ nests placed on trees and 21 nests placed on buildings).

During each observation session, we recorded the time when a female left the nest or resumed incubation. We estimated nest attentiveness as the percentage of time that females were incubating during each 1-h observation session. We assumed the first incubation day to be the day when the second egg was laid. For nests found after clutch completion, we inferred the incubation day at a given observation session by back-dating from the hatching day, considering that the incubation period of the Pale-breasted Thrush in the region lasts 14 days (A. F. Batisteli unpubl. data). Air temperatures were retrieved from the automatic meteorological station located at UFSCar to a resolution of 0.1 °C. Nesting substrate type was classified as 'buildings' (any man-made structure belonging to buildings, such as walls, concrete columns, windows and air conditioners) or 'trees'.

Statistical analyses

To assess the association between microhabitat temperature and nest temperature, we used a linear mixed-effects model with nest temperature as a continuous dependent variable. We defined 'daytime' as the period between 06:00 and 18:00 h and 'night' as the period between 19:00 and 05:00 h. Explanatory variables were nesting substrate type (tree/building), period of the day (daytime/night), microhabitat temperature (covariate) and the nesting substrate type \times period of the day

interaction term. Nest identity was set as a categorical, random effect. We tested for temporal autocorrelation in the data by adding an autoregressive correlation structure to the model, which improved it significantly. Given the temporal autocorrelation ($\Phi = 0.986$), degrees of freedom of the linear mixed-effects model were corrected based on the effective sample size according to Zuur *et al.* (2009). The residuals were graphically checked and supported model validation. The Tukey *post-hoc* test was used to address differences indicated by the statistical significance of the interaction term.

We used a Wilcoxon test to detect any temporal bias in female behavioural observations across the incubation phase, by comparing the day of incubation cycle for observations of nests in trees and in buildings.

Nest attentiveness and the duration of on- and off-bouts did not achieve a normal distribution even after statistical transformations. Accordingly, we used generalized estimating equations (GEEs) to assess whether the female attentiveness to the nest (a continuous variable with Gamma distribution), on-bout and off-bout durations were associated with nesting substrate type, incubation day, air temperature and all possible interactions between these terms. The conceptual model proposed by Conway and Martin (2000) suggests a complex, non-linear variation of incubation behaviour over a wide range of daytime environmental temperatures (from -8 to 45 °C). However, we tested a linear relationship between incubation behaviour and air temperature due to the absence of such extreme daytime temperatures in our study site (air temperature = 22.9 ± 4.5 °C, mean \pm sd, range 14.1–34.0 °C). Only complete on- and off-bouts were included in the analysis; events intercepted by the start or end of observation sessions were discarded. In all GEEs, nest identity was again set as a categorical, random effect. The best model was selected from a full factorial model employing a backward stepwise selection until all non-significant interactions or single terms had been removed (Zuur *et al.* 2009).

To assess whether any differences in incubation budget between nests in trees and in buildings were associated with egg survival, we used a generalized linear model (GLM) with binomial distribution to compare hatching success (number of hatchlings as the response variable; clutch size as the binomial denominator) between the two

nesting substrate types (Zuur *et al.* 2009). All analyses were conducted in the software R (R Development Core Team 2019) using the packages 'nlme' (linear mixed-effects model, Pinheiro *et al.* 2011) and 'geepack' (GEE, Højsgaard *et al.* 2014).

RESULTS

We obtained 43 915 nest temperature measurements over 63 nest-days (6.77 ± 4.17 (mean \pm sd) survey days for each nest). Nest temperature averaged 28.2 ± 4.3 °C (range: 15.1–37.5 °C) and was positively influenced by microhabitat temperature and period of the day (Table 1), being higher at night, when female presence on the nest is uninterrupted. Nest temperature was higher in buildings than in trees (buildings: 31.3 ± 3.7 °C, $n = 17\ 071$, trees: 25.5 ± 2.6 °C, $n = 19\ 644$; Table 1). Nest temperature in buildings was in general 6.0 °C higher than microhabitat temperature, whereas this difference was near zero (0.03 °C) for nests in trees. The interaction term (nesting substrate type \times period of the day) was significant (Table 1). The Tukey *post-hoc* test revealed that the nest temperature at a given microhabitat temperature did not differ between nests placed in trees at night (when the female was continuously at the nest) and in buildings during either daytime or night (Fig. 1).

We performed direct observation of female behaviour for 81 h in 15 nests placed in trees (5.40 ± 0.82 h for each nest) and for 108 h in 21 nests in buildings (5.14 ± 0.85 h for each nest). The day of incubation cycle did not differ between the two samples of nest observations (Wilcoxon test, $W = 4326$, $P = 0.898$). Nest attentiveness during observation sessions averaged $76.5 \pm 14.7\%$,

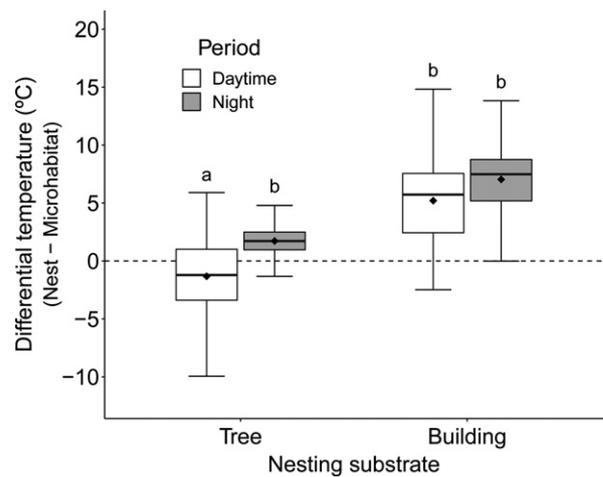


Figure 1. Differential temperature (the difference between the temperature inside the nest incubation chamber and microhabitat temperature) in relation to nesting substrate type and period of day in nests of Pale-breasted Thrush *Turdus leucomelas*. The dashed line represents equal nest and microhabitat temperature, boxplots show interquartile ranges, whiskers denote standard errors, diamonds represent means of differential temperatures, and lowercase letters indicate statistically significant differences after a Tukey *post-hoc* test.

ranging from 21.6% to 100%. Nest attentiveness was affected by nesting substrate type (Table 2), being lower for nests placed in buildings ($74.0 \pm 16.0\%$) than in trees ($80.0 \pm 12.0\%$) (Fig. 2a). There was a slight but significant decrease in nest attentiveness as incubation progressed but air temperature did not affect nest attentiveness (Table 2).

On-bouts lasted 1186 ± 653 s, ranging from 67 to 3121 s ($n = 135$ on-bouts in 101 h). On-bouts were shorter at higher air temperatures (Table 2, Fig. 3a) but their duration was not affected by nesting substrate type or incubation

Table 1. Results of the linear mixed-effects model on the temperature inside nests of the Pale-breasted Thrush *Turdus leucomelas* in relation to nest substrate type (buildings/trees), period of the day (daytime/night), the interaction nest substrate type \times period of the day, and microhabitat temperature.

	Estimate	se	df	t	P
Intercept	15.510	1.239	4008.457	12.523	<0.001*
Nest substrate	6.464	1.842	7	3.560	0.001*
Period of the day	0.901	0.120	4008.457	7.481	<0.001*
Nest substrate \times Period of the day	0.835	0.179	4008.457	4.667	<0.001*
Microhabitat temperature	0.640	0.030	4008.457	135.301	<0.001*

Degrees of freedom were calculated based on the effective sample size due to temporal autocorrelation in temperature, resulting in $n = 4020.457$ independent samples out of 36 715 temperature measurements (see details in Methods). *Statistical significance at $\alpha = 0.05$.

Table 2. Results of generalized estimating equations assessing the effect of nest substrate type (buildings/trees), air temperature and day of the incubation cycle ('incubation day') on nest attentiveness and the duration of on-bouts and off-bouts in the Pale-breasted Thrush *Turdus leucomelas*.

	Estimate	se	df	Wald	P
Nest attentiveness (%)					
Intercept	1.152	0.048	153	574.690	<0.001*
Nest substrate	0.109	0.050	33	4.680	0.031*
Air temperature				0.001	0.989
Incubation day	0.013	0.005	153	5.020	0.025*
On-bout duration					
Intercept	1.341	0.700	100	3.670	0.055
Nest substrate				2.390	0.122
Air temperature	0.079	0.035	100	5.100	0.024*
Incubation day				2.150	0.142
Off-bout duration					
Intercept	14.464	1.623	212	79.390	<0.001*
Nest substrate	-1.614	0.558	33	8.380	0.004*
Air temperature	-0.267	0.070	212	14.260	<0.001*
Incubation day				1.330	0.248

Estimates, standard error and degrees of freedom (df) are not shown for explanatory variables absent from final models.

*Statistical significance at $\alpha = 0.05$.

day (Table 2). We obtained the duration of 268 off-bouts (108 for nests in trees and 160 for nests in buildings), which averaged 268 ± 270 s (range: 19–1927 s). Off-bout duration differed between nesting substrate types (Table 2, Fig. 2b), being greater for nests in buildings. Off-bout duration was positively related to air temperature (Table 2, Fig. 3b) but not to incubation day (Table 2). Despite the differences in incubation budget, hatching success did not differ between nests in buildings and in trees (GLM, $df = 34$, $z = 0.286$, $P = 0.775$).

DISCUSSION

The use of buildings as a nesting substrate by the Pale-breasted Thrush promoted greater nest temperatures at a given microhabitat temperature and allowed a reduction in female nest attentiveness compared with nests in trees, thus corroborating our hypothesis. During daytime, even with incubation recesses, buildings kept nest temperature similar to those of nests placed in both trees and buildings with constant female presence (i.e. during the night). Therefore, the lower nest attentiveness that we observed in buildings was likely to have been enhanced by higher nest temperatures provided by man-made structures around the nests

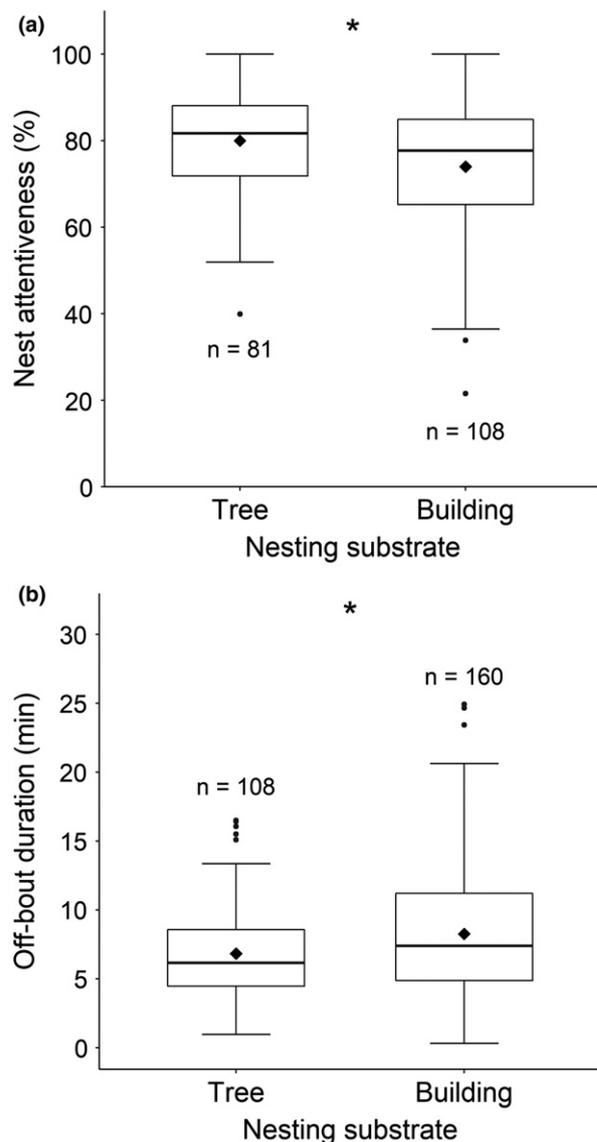


Figure 2. Nest attentiveness by Pale-breasted Thrush *Turdus leucomelas* females (a) and off-bout duration (b) in nests placed on trees and buildings. Sample sizes shown refer to hours of behavioral observation for 15 nests on trees and 21 nests on buildings. Boxplots show interquartile ranges, whiskers denote standard errors, diamonds represent means and dots indicate outliers. *Statistical significance at $\alpha = 0.05$.

which enabled longer off-bouts without affecting hatching success.

The energetic-bottleneck hypothesis states that the time that an incubating bird spends at the nest is energetically limited by its own demand for self-maintenance (Tov & Wright 1993). One prediction that stems from this hypothesis is that females in artificially heated nests should benefit from this

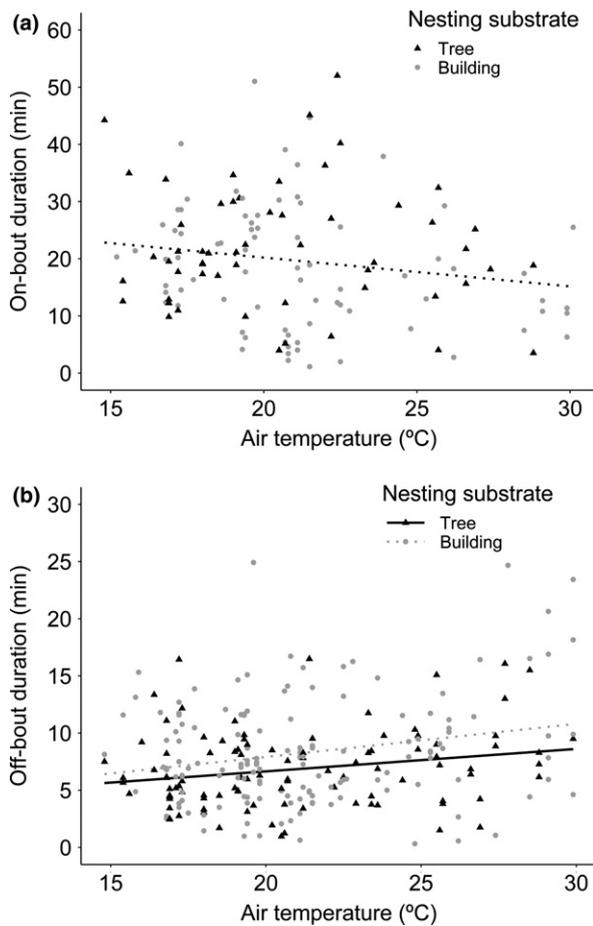


Figure 3. Duration of on-bouts (a) and off-bouts (b) of Pale-breasted Thrush *Turdus leucomelas* females incubating in nests placed in trees (triangles) and buildings (circles) in relation to air temperature. (a) Dashed line represents a general tendency of the linear relationship between the variables. (b) Dashed and continuous lines indicate linear relationships between the variables for nests in buildings and in trees, respectively.

extra energy and increase their nest attentiveness, as experimentally demonstrated for cavity nesters, such as Great Tits *Parus major* and Tree Swallows *Tachycineta bicolor*, and for the ground-nesting Pectoral Sandpiper *Calidris melanotos* in the Arctic (Bryan & Bryant 1999, Cresswell *et al.* 2004, Ardia *et al.* 2009). However, our data did not support such a prediction, as females took longer off-bouts from warmer nests (i.e. in buildings). Similarly, higher nest temperature is related to lower nest attentiveness in both cavity- and open-cup nesters (Londoño *et al.* 2008, Robertson 2009, Álvarez & Barba 2014, Amininasab *et al.* 2016, Bueno-Enciso *et al.* 2016). These differences indicate that nest

temperature may elicit adjustments in female incubation behaviour in species-specific ways (Mueller *et al.* 2019). Some species may direct any extra energy (either food or heat) to increase the time devoted to the current clutch (Ardia *et al.* 2009, Vafidis *et al.* 2018), whereas others may invest more in self-maintenance and consequently perhaps in future breeding attempts. One probable reason for these alternative strategies is related to specific life-history traits. Tropical species such as the Pale-breasted Thrush have lower adult mortality probability, and parents may prioritize future breeding attempts over additional investment in the current clutch (Ghalambor & Martin 2001, Martin *et al.* 2015).

Off-bout duration was greater for nests in buildings regardless of air temperature, probably as an effect of higher nest temperature in buildings. The physical barriers around nests in buildings provide better nest concealment and their lower exposure to wind sustains greater differences between nest and microhabitat temperatures (Hilton *et al.* 2004). It could be argued that buildings would be suboptimal nesting microhabitats where energy expenditure of incubating females is higher than in trees, which would in turn require longer foraging times to replace their energetic reserves, and result in longer off-bouts. If true, we should have observed shorter on-bouts for nests in buildings than in trees due to a more rapid depletion of female reserves (Yom-Tov & Wright 1993). However, on-bout duration did not differ between nesting substrate types. Longer off-bouts are therefore more likely to be a benefit than an obligation for females that nest in buildings, enabling greater foraging time. Females that nest in buildings spent 7.5% less time incubating, which corresponds to 0.9–1.01 h/day considering the duration of the photoperiod during the breeding season of the Pale-breasted Thrush in the region (12–13.5 h). The extra energetic resource acquired during this time may improve parental fitness either in the current or in future breeding attempts (Reid *et al.* 2000, Robertson 2009).

Lower nest attentiveness may be an ecological-time response to lower nest predation risk (Fontaine & Martin 2006). All nests at which female behaviour was studied were in the same area and were therefore experiencing the same predator community. So the specific features of each nesting substrate type may be responsible for the variation in nest attentiveness as a response to

perceived nest predation risk. Corvids are important predators in both study areas but they usually avoid buildings (Møller 2010). In our study populations, females frequently re-use successful nests within and between breeding seasons, as reported for the Common Blackbird *Turdus merula* (Wysocki 2004). The re-use of successful nesting sites may enable birds to accumulate experience of nest-site security and adjust behaviour to optimize the balance between self-maintenance and incubation. Thus, more than thermal benefits, thrush females that nest in buildings may take advantage of the visual protection of man-made structures around the nest to leave the clutch unattended for longer periods.

Air temperature affected both on-bout and off-bout duration, corroborating our hypothesis. Prolonged on-bouts under lower air temperatures suggest an effect of temperature on incubation efficiency (Capp *et al.* 2018). Even when an open-cup nesting bird is incubating, the external air is continuously penetrating the nest cup through nest walls in a convection flow (Deeming 2016). From this point of view, the warmer the external air, the higher the efficiency of the incubating female in keeping eggs at optimal temperatures (except in extremely hot environments, where air temperature exceeds that lethal for the embryos). Prolonged off-bouts under higher temperatures may be expected because air temperature provides an indirect assessment of egg cooling rates to incubating females, which respond by reducing their latency to return to the nest (Reneerkens *et al.* 2011, Forrester & Londoño 2016).

Incubation effort usually increases with incubation progress for tropical birds (Ruggera & Martin 2010, Martin *et al.* 2017), but our results showed an opposite pattern. However, the relationship between nest attentiveness and incubation progress is variable among species, with studies reporting increasing (Endo & Ueda 2016), decreasing (Cooper & Voss 2013, Forrester & Londoño 2016) or constant nest attentiveness across the incubation period (Biancucci & Martin 2008, Bueno-Enciso *et al.* 2016). This unclear relationship may also be affected by spatiotemporal fluctuations in food availability and nest predation risk (Vafidis *et al.* 2018). Incubating passerines continuously lose mass during the course of incubation (Suárez *et al.* 2005, Blem & Blem 2006, Redfern 2010). Thus, the need to manage body condition to permit adequate investment in nestling care after hatching

may explain the decreasing nest attentiveness across the course of incubation that we observed in our study population.

Three explanations other than the insulation and protection effects provided by man-made structures might apply to the differences in female behaviour between substrate types but are not supported by our data. First, lower nest attentiveness in nests in buildings might be a consequence of human proximity and frequent perturbation, eliciting escape behaviour of incubating females. If true, human movements should have induced repeated trips from and to the nest, resulting in shorter on-bout periods, because incubation would be prematurely interrupted (McGowan & Simons 2006). However, on-bout duration did not differ between nesting substrate types, thus refuting this argument. Additionally, birds that breed in disturbed sites such as our urban areas are usually habituated to human disturbance (Baudains & Lloyd 2007). Second, nests in buildings are generally surrounded by man-made structures, which implies a poor view of the surroundings and perhaps a higher predation risk to incubating females (Burhans & Thompson 2001, Gómez-Serrano & López-López 2014). If so, the need to leave incubation to monitor the nest vicinity for self-protection should have produced shorter on-bouts in nests in buildings, as discussed above, which was not the case. So, it is unlikely that poor view of nest surroundings was responsible for lower nest attentiveness of females nesting on buildings. Lastly, longer off-bouts of females nesting in buildings might be related to lower food availability in surrounding habitat, thus requiring longer foraging times. Accordingly, several experimental studies have reported that increased food availability enabled passerine females to spend more time on the nest (Londoño *et al.* 2008, Lothery *et al.* 2014, Vafidis *et al.* 2018), either prolonging on-bouts (Pearse *et al.* 2004) or shortening off-bouts (Chalfoun & Martin 2007, Amininasab *et al.* 2016). We were not able to test this hypothesis, but nests in both substrate types were uniformly distributed, and close enough to each other that strong differences in patch quality related to nesting substrate surroundings were unlikely.

We conclude that the use of buildings as nesting substrates enables a reduction in the energetic costs associated with nest attentiveness for incubating females of the Pale-breasted Thrush due to longer off-bouts, which are possible due to the

insulation provided by the building itself. Extended off-bouts allow greater foraging time for females, which may result in a higher energy intake. The use of anthropogenic nesting substrates may ultimately promote the settlement of birds in urbanized areas (Møller 2010, Reynolds *et al.* 2019). This advantage related to reduced breeding costs may contribute to increase parental fitness of the subset of individuals using human buildings as nesting sites, and potentially drive the evolution of the incubation behaviour in urban bird populations.

We are grateful to the editorial board of *Ibis*, to the Brazilian banding agency (CEMAVE – ICMBIO) for providing the metallic rings, and to Manoel M. Dias Filho, Odete Rocha and Victor S. Saito for their valuable comments on the first draft. A.F.B. thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a doctoral fellowship. M.A.P. received a research grant from the Brazilian Research Council (CNPq).

AUTHOR CONTRIBUTIONS

Augusto F. Batisteli: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Software (lead); Writing-original draft (equal); Writing-review & editing (lead). **Leonardo B. De Souza:** Conceptualization (equal); Data curation (equal); Methodology (equal); Writing-original draft (equal). **Isadora Z. Santieff:** Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal). **Guilherme Gomes:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal). **Talita P. Soares:** Data curation (equal); Methodology (equal). **Marianela Pini:** Data curation (equal); Methodology (equal). **Rhainer Guillermo-Ferreira:** Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal). **Marco A. Pizo:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal). **Hugo Sarmiento:** Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

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

REFERENCES

- Altmann, J.** 1974. Observational study of behavior: sampling methods. *Behaviour* **49**: 227–266.
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes, G., Leonardo, J. & Sparovek, G.** 2013. Köppen's climate classification map for Brazil. *Meteorol. Z.* **22**: 711–728.
- Álvarez, E. & Barba, E.** 2014. Behavioural responses of Great Tits to experimental manipulation of nest temperature during incubation. *Ornis Fenn.* **91**: 220–230.
- Amat, J.A. & Masero, J.A.** 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest-sites in a plover. *Anim. Behav.* **67**: 293–300.
- Amininasab, S.M., Kingma, S.A., Birker, M., Hildenbrandt, H. & Komdeur, J.** 2016. The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behav. Ecol. Sociobiol.* **70**: 1591–1600.
- Ardia, D.R., Pérez, J.H., Chad, E.K., Voss, M.A. & Clotfelter, E.D.** 2009. Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. *J. Anim. Ecol.* **78**: 4–13.
- Audet, J.N., Ducatez, S. & Lefebvre, L.** 2015. The town bird and the country bird: problem solving and immunocompetence vary with urbanization. *Behav. Ecol.* **27**: 637–644.
- Baudains, T.P. & Lloyd, P.** 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Anim. Conserv.* **10**: 400–407.
- Berntsen, H.H. & Bech, C.** 2016. Incubation temperature influences survival in a small passerine bird. *J. Avian Biol.* **47**: 141–145.
- Bianucci, L. & Martin, T.E.** 2008. First description of the breeding biology and natural history of the Ochre-breasted Brush Finch (*Atlapetes semirufus*) in Venezuela. *Wilson J. Ornithol.* **120**: 856–863.
- Blem, C.R. & Blem, L.B.** 2006. Variation in mass of female Prothonotary Warblers during nesting. *Wilson J. Ornithol.* **118**: 3–13.
- Breen, A., Guillette, L.M. & Healy, S.D.** 2016. What can nest-building birds teach us? *Comp. Cogn. Behav. Rev.* **11**: 83–102.
- Bryan, S.M. & Bryant, D.M.** 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in Great Tits, *Parus major*. *Proc. R. Soc. Lond. B* **266**: 157–162.
- Bueno-Enciso, J., Ferrer, E.S., Barrientos, R. & Sanz, J.J.** 2016. Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. *J. Ornithol.* **157**: 759–772.
- Burhans, D.E. & Thompson, F.R., III** 2001. Relationship of songbird nest concealment to nest fate and flushing behavior of adults. *Auk* **118**: 237–242.

- Capp, E., Liebl, A.L., Cones, A.G. & Russell, A.F. 2018. Advancing breeding phenology does not affect incubation schedules in Chestnut-crowned Babblers: opposing effects of temperature and wind. *Ecol. Evol.* **8**: 696–705.
- Chalfoun, A.D. & Martin, T.E. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Anim. Behav.* **73**: 579–585.
- Chen, J.N., Liu, N.F., Yan, C. & An, B. 2011. Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. *J. Ornithol.* **152**: 603–608.
- Conway, C.J. & Martin, T.E. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* **54**: 670–685.
- Cooper, C.B. & Voss, M.A. 2013. Avian incubation patterns reflect temporal changes in developing clutches. *PLoS One* **8**: e65521.
- Cresswell, W., Holt, S., Reid, J.M., Whitfield, D.P., Mellanby, R.J., Norton, D. & Waldron, S. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behav. Ecol.* **15**: 498–507.
- Deeming, D.C. 2016. How does the bird-nest incubation unit work? *Avian Biol. Res.* **9**: 103–113.
- Eggers, S., Griesser, M. & Ekman, J. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behav. Ecol.* **19**: 1056–1062.
- Endo, S. & Ueda, K. 2016. Factors affecting female incubation behavior in the Bull-headed Shrike. *Ornithol. Sci.* **15**: 151–161.
- Evans, M.L. & Stutchbury, B.J. 2012. Nest attendance and reproductive success in the Wood Thrush. *Condor* **114**: 401–406.
- Fan, L.Q., Chen, G.L., Da, X.W., Luo, J.J., Xian, L.L., Ren, Q.M., Xie, Y.Y. & Du, B. 2017. Seasonal variation in food availability influences the breeding strategy of White-collared Blackbirds *Turdus albocinctus* on the Tibetan Plateau. *Ibis* **159**: 873–882.
- Fast, P.L., Grant Gilchrist, H. & Clark, R.G. 2007. Experimental evaluation of nest shelter effects on weight loss in incubating Common Eiders *Somateria mollissima*. *J. Avian Biol.* **38**: 205–213.
- Fontaine, J.J. & Martin, T.E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**: 428–434.
- Forrester, T.R. & Londoño, G.A. 2016. Breeding biology and egg temperatures of Black-faced Brush-finches (*Atlapetes melanolaemus*), Neotropical montane songbirds. *J. Field Ornithol.* **87**: 260–272.
- Forstmeier, W. & Weiss, I. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* **104**: 487–499.
- Ghalambor, C.K. & Martin, T.E. 2001. Fecundity–survival trade-offs and parental risk-taking in birds. *Science* **292**: 494–497.
- Gómez-Serrano, M.Á. & 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.
- Griebel, I.A., Fairhurst, G.D., Marchant, T.A. & Clark, R.G. 2018. Effects of parental and nest-site characteristics on nestling quality in the Tree Swallow (*Tachycineta bicolor*). *Can. J. Zool.* **97**: 63–71.
- Halupka, K. & Greeney, H.F. 2009. The influence of parental behavior on vulnerability to nest predation in tropical thrushes of an Andean cloud forest. *J. Avian Biol.* **40**: 658–661.
- Hilton, G.M., Hansell, M.H., Ruxton, G.D., Reid, J.M. & Monaghan, P. 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. *Auk* **121**: 777–787.
- Højsgaard, S., Halekoh, U. & Yan, J. 2014. *geepack: Generalized estimating equation package. R package version 1–2*.
- Hu, Y.B., Zhao, Q.S., Lou, Y.Q., Chen, L.J., González, M.A. & 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.
- Latif, Q.S., Heath, S.K. & Rotenberry, J.T. 2012. How avian nest site selection responds to predation risk: testing an ‘adaptive peak hypothesis’. *J. Anim. Ecol.* **81**: 127–138.
- Lessi, B.F., Pires, J.S.R., Batisteli, A.F. & MacGregor-Fors, I. 2016. Vegetation, urbanization, and bird richness in a Brazilian periurban area. *Ornitol. Neotrop.* **27**: 203–210.
- Lloyd, J.D. & Martin, T.E. 2004. Nest-site preference and maternal effects on offspring growth. *Behav. Ecol.* **15**: 816–823.
- Londoño, G.A., Levey, D.J. & Robinson, S.K. 2008. Effects of temperature and food on incubation behaviour of the Northern Mockingbird, *Mimus polyglottos*. *Anim. Behav.* **76**: 669–677.
- Lothery, C.J., Thompson, C.F., Lawler, M.L. & Sakaluk, S.K. 2014. Food supplementation fails to reveal a trade-off between incubation and self-maintenance in female house wrens. *PLoS One* **9**: e106260.
- 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.
- Martin, T.E., Oteyza, J.C., Boyce, A.J., Lloyd, P. & Ton, R. 2015. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. *Am. Nat.* **186**: 223–236.
- Martin, T.E., Ton, R. & Oteyza, J.C. 2017. Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines. *Auk* **135**: 101–113.
- McCafferty, D.J., Moncrieff, J.B. & Taylor, I.R. 2001. How much energy do Barn Owls (*Tyto alba*) save by roosting? *J. Therm. Biol.* **26**: 193–203.
- McGowan, C.P. & Simons, T.R. 2006. Effects of human recreation on the incubation behavior of American Oystercatchers. *Wilson J. Ornithol.* **118**: 485–494.
- Miller, D.A., Grand, J.B., Fondell, T.F. & Anthony, R.M. 2007. Optimizing nest survival and female survival: consequences of nest site selection for Canada geese. *Condor* **109**: 769–780.
- 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., Tryjanowski, P., Díaz, M., Kwieciński, Z., Indykiewicz, P., Mitrus, C., Goławski, A. & Polakowski, M. 2015. Urban habitats and feeders both contribute to flight

- initiation distance reduction in birds. *Behav. Ecol.* **26**: 861–865.
- Mueller, A.J., Miller, K.D. & Bowers, E.K.** 2019. Nest microclimate during incubation affects posthatching development and parental care in wild birds. *Sci. Rep.* **9**: 5161.
- Pearse, A.T., Cavitt, J.F. & Cully, J.F.** 2004. Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *Wilson J. Ornithol.* **116**: 23–31.
- Pinheiro, J., Bates, D., Saikat, D., Sarkar, D., R Development Core Team** 2011. *Linear and nonlinear mixed-effects models (nlme)*. R package version 3.1-101. <http://CRAN.R-project.org/package=nlme>
- Potascheff, C.D.M., Lombardi, J.A. & Lorenzi, H.** 2010. Angiosperm trees and shrubs on the campus of the São Paulo State University Júlio de Mesquita, Rio Claro (SP), Brazil. *Bioikos* **24**: 21–30.
- R Development Core Team** 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.r-project.org/> (accessed 13 June 2019).
- Redfern, C.P.** 2010. Brood-patch development and female body mass in passerines. *Ring. Migr.* **25**: 33–41.
- Reid, J.M., Monaghan, P. & Ruxton, G.D.** 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proc. R. Soc. Lond. B* **267**: 37–41.
- Reneerkens, J., Grond, K., Schekkerman, H., Tulp, I. & Piersma, T.** 2011. Do uniparental Sanderlings *Calidris alba* increase egg heat input to compensate for low nest attentiveness? *PLoS One* **6**: e16834.
- Reynolds, S.J., Ibáñez-Álamo, J.D., Sumasgutner, P. & Mainwaring, M.C.** 2019. Urbanisation and nest building in birds: a review of threats and opportunities. *J. Ornithol.* **160**: 841–860.
- Ricklefs, R.E. & Brawn, J.** 2013. Nest attentiveness in several Neotropical suboscine passerine birds with long incubation periods. *J. Ornithol.* **154**: 145–154.
- Robertson, B.A.** 2009. Nest-site selection in a postfire landscape: do parents make tradeoffs between microclimate and predation risk? *Auk* **126**: 500–510.
- Robinson, W.D., Austin, S.H., Robinson, T.R. & Ricklefs, R.E.** 2014. Incubation temperature does not explain variation in the embryo development periods in a sample of Neotropical passerine birds. *J. Ornithol.* **155**: 45–51.
- Rodewald, A.D. & Kearns, L.J.** 2011. Shifts in dominant nest predators along a rural-to-urban landscape gradient. *Condor* **113**: 899–906.
- Ruggera, R.A. & Martin, T.E.** 2010. Breeding biology and natural history of the Slate-throated Whitestart in Venezuela. *Wilson J. Ornithol.* **122**: 447–454.
- Santos, E.S.A. & Nakagawa, S.** 2012. The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *J. Evol. Biol.* **25**: 1911–1917.
- Schmidt, K.A. & Whelan, C.J.** 2005. Quantifying male Wood Thrush nest-attendance and its relationship to nest success. *Condor* **107**: 138–144.
- Suarez, F., Traba, J. & Herranz, J.** 2005. Body mass changes in female Tawny Pipits *Anthus campestris* during the nesting stage. *J. Ornithol.* **146**: 372–376.
- Tella, J.L., Canale, A., Carrete, M., Petracci, P. & Zalba, S.M.** 2014. Anthropogenic nesting sites allow urban breeding in Burrowing Parrots *Cyanoliseus patagonus*. *Ardeola* **61**: 311–322.
- Tov, Y.Y. & Wright, J.** 1993. Effect of heating nest boxes on egg laying in the Blue Tit (*Parus caeruleus*). *Auk* **110**: 95–99.
- Vafidis, J.O., Facey, R.J., Leech, D. & Thomas, R.J.** 2018. Supplemental food alters nest defence and incubation behaviour of an open-nesting wetland songbird. *J. Avian Biol.* **49**: e01672.
- Vedder, O., Verhulst, S., Zuidersma, E. & Bouwhuis, S.** 2018. Embryonic growth rate affects telomere attrition: an experiment in a wild bird. *J. Exp. Biol.* **221**: jeb181586.
- Wang, Y., Huang, Q., Lan, S., Zhang, Q. & Chen, S.** 2015. Common blackbirds *Turdus merula* use anthropogenic structures as nesting sites in an urbanized landscape. *Curr. Zool.* **61**: 435–443.
- Węgrzyn, E. & Leniowski, K.** 2011. Nest site preference and nest success in Blackcaps *Sylvia atricapilla* in Poland. *Ardeola* **58**: 113–125.
- Weidinger, K.** 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *J. Anim. Ecol.* **71**: 424–437.
- Wysocki, D.** 2004. Nest re-use by Blackbirds—the way for safe breeding? *Acta Ornithol.* **39**: 164–168.
- Yeh, P.J., Hauber, M.E. & Price, T.D.** 2007. Alternative nesting behaviours following colonisation of a novel environment by a passerine bird. *Oikos* **116**: 1473–1480.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M.** 2009. *Mixed effects models and extensions in ecology with R*. New York: Springer Science & Business Media.

Received 23 October 2019;

revision accepted 31 May 2020.

Associate Editor: Jose Antonio Sanchez-Zapata.