Air movement affects insulatory values of nests constructed by Old World Warblers

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A B S T R A C T

Avian nests provide a location for incubation, and in many cases rearing of nestlings. These energetically demanding activities have meant that nest insulation has been the subject of many studies but few to date have dealt with how variation among species in nest construction materials could affect nest insulation. This study investigated the insulation of nests constructed by three species of Old Word warblers (Sylviidae), which vary in size and composition. Insulatory values, *i.e.* difference in cooling rate of temperature loggers placed inside and outside a nest, and internal cooling rates within the nest cup were determined using temperature loggers under still-air and moving-air conditions. Insulatory values determined in still-air conditions of a laboratory were significantly different among nests of the different species but not when the values were determined within the smaller volume of a wind tunnel. Moving-air increased insulatory values by an order of magnitude but also increased internal cooling rates in all species. Insulatory values were positively correlated with the nest base thickness. Moving-air increased the cooling rate of the external temperature logger much more than the internal logger, which inflated the insulatory value of a nest wall in moving-air. Reasons for these results may reflect the thermal properties of the materials individually or in combination. Future testing of nest insulation should be under standard conditions that limit air movement but the role of the nest location *in situ* should be investigated in future research.

1. Introduction

Avian nests are complex bio-engineered structures that are the location for incubation, provide protection from prevailing weather conditions and, in many cases, provide the site for chick rearing (Sidis et al., 1994; Hansell, 2000; Heenan et al., 2015). Nests may also play a variety of roles in reproduction of different species, including: structural support for the incubating bird, eggs and chicks (Biddle et al., 2015, 2017, 2018b), sexual selection during pair formation (Moreno, 2012; Mainwaring et al., 2014b), and providing protection from parasites (Suárez-Rodríquez et al., 2013; Mainwaring et al., 2014b). The structure and composition of a nest are, therefore, likely to reflect a compromise among these different roles but it can be argued that a primary role is to create a suitable environment for the eggs (and nestlings) that is crucial for successful reproduction (Deeming, 2011, 2016).

The type and quantity of material used to construct nests vary widely between even closely-related species (Hansell, 2000; Biddle et al., 2018a). This variability seems to reflect the need for structural support in larger species (Deeming, 2018) and, it is often assumed, the need for good thermal insulation in smaller species (Deeming, 2016). The potential adverse effects of heat loss during incubation on the energetics of the incubating bird (Nord and Williams, 2015) have meant that thermal insulation of nests has been an area of research interest for many years, albeit sporadically (Palmgren and Palmgren, 1939; Whittow and Berger, 1977; Walsberg and King, 1978a, 1978b; Skowron and Kern, 1980; Kern and Van Riper, 1984; Kern, 1984; Rodgers et al., 1988; Heenan and Seymour, 2011, 2012). Thermal insulation is typically tested for whole nests (see review by Deeming and Mainwaring (2015)) but the effects of inter-specific variation in the nest materials has only rarely being considered. Hilton et al. (2004) showed that feathers and wool (animal-derived materials) offered better insulation than moss and grass (plant-derived materials). However, whilst many small birds incorporate animal-derived materials in their nests (Biddle et al., 2018a; Dickinson, 2018), nests of the Common Blackbird (*Turdus merula*) and European Robin (*Erithacus rubecula*) have few animal-derived materials in their nests. These species seem to rely on dry grasses to line the cup, the amounts of which significantly correlate with the insulatory properties of the nest (Mainwaring et al., 2014a; Taberner Cerezo and Deeming, 2016).

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The architecture of nests appears to vary in response to different environmental conditions. Cool temperatures during nest construction in Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*) were associated with heavier nests with heavier cup linings and with higher insulatory values (Deeming et al., 2012; Mainwaring et al., 2012). With increasing spring temperatures, the insulatory properties of Common Blackbird nests decreased due to a reduction in nest wall thickness and a decrease in the mass of dry grass present within the nests (Mainwaring et al., 2014a). Yellow Warbler (*Setophaga* [*Dendroica*] *petechia*) nests found in the colder climate of Churchill, Manitoba were less porous and retained heat better than nests built in the warmer climate of Elgin, Ontario (Rohwer and Law, 2010). Although the thermal properties of the nests were not determined, Crossman et al. (2011) showed that birds nesting in the colder climate of Northern Manitoba built nests with thicker walls and nests of the Yellow Warblers and Common Redpolls (*Carduelis flammea*) had more soft plant fibres and feathers, possibly allowing the nest to retain heat better. Common Amakihi (*Hemignathus virens virens*) nests constructed at cooler, high altitudes had denser walls and so were better insulated than those nests constructed at warmer, lower altitudes (Kern and Van Riper, 1984). Mountain White-Crowned Sparrows (*Zonotrichia leucophrys oriantha*) nesting off the ground in bushes had larger nests with thicker walls and less porous floors, and so therefore lost heat at a significantly slower rate than nests constructed on the ground (Kern, 1984).

Thermal properties of nests can be influenced by not only the prevailing temperature but also by air movement and precipitation; such factors can create sub-optimal conditions within nests that have detrimental effects on offspring fitness (reviewed by DuRant et al. (2013)). Therefore, whilst the design of a nest can be expected to create suitable incubation conditions, placement in the environment may play an important role in the degree of thermal insulation a nest provides. Although nests constructed in colder climates were better insulated (Rohwer and Law, 2010; Crossman et al., 2011; Mainwaring et al., 2012, 2014a), windy conditions can increase the rate of heat loss from a nest and increase the thermal conductance of the walls (Heenan and Seymour, 2012). Gray and Deeming (2017) showed that moving-air increases convective heat loss from temperature loggers placed inside and outside an inverted nest but the effect of air movement is very much greater for the external logger. Hence, the insulatory value (*i.e.* the cooling rate of a temperature logger inside the nest minus the cooling rate of a logger outside the nest; McGowan et al., 2004) was increased in moving-air compared with still-air. Moreover, compared to dry conditions, wet nest materials had lower insulatory values (Hilton et al., 2004) and wet nests had lower insulatory values and increased internal cooling rates (Deeming and Campion, 2018). However, these studies have dealt with nests from relatively few species of finches (Fringillidae), wagtails and pipits (Motacillidae) that have around 20–30% animal derived materials by mass (Biddle et al., 2018a; Dickinson, 2018). Given that those Old World Warblers (Sylviidae) studied to date construct nests with limited amounts of animal-derived materials (< 10% of nest mass; Dickinson, 2018) it is interesting to determine whether thermal insulation is affected by this plasticity in nest construction, both within and among species (Deeming and Mainwaring, 2015).

In this investigation, we hypothesised that the different types and amounts of materials used in nests of three species of Old World Warblers (Sylviidae) would affect thermal insulation in both still air and moving air. Experiments used nests of the Willow Warbler (*Phylloscopus trochilus*), the Eurasian Reed Warbler (*Acrocephalus scirpaceus*), and the Eurasian Blackcap (*Sylvia atricapilla*), which had used quite different materials in nest construction (Dickinson, 2018; Fig. 1).

2. Methods

Nests used in this study were constructed by the Willow Warbler (N = 23), the Eurasian Reed Warbler (N = 21), and the Eurasian Blackcap (N = 10). Nests were collected by volunteers of the British Trust for Ornithology from various locations within the UK. All nests had been monitored during breeding and collected at the end of the breeding season during 2014, 2015, and 2016. Upon arrival at the University of Lincoln, all nests were frozen for 72 h at −20 °C to kill parasites and pathogens present in the nests (Britt and Deeming, 2011). All nests were subsequently stored dry in plastic bags within cardboard boxes and kept at room temperature. Each nest had its linear dimensions, *i.e.* nest diameter, nest height, wall thickness, cup diameter and depth, measured as described by Biddle et al. (2018a). Base thickness was calculated by subtracting the cup depth from the nest height.

Two bespoke plinths (*i.e.* a made-to measure block specific to each nest) were cut from a long 25 × 25 mm square piece of polystyrene that were the depth of the cup minus the depth of a temperature logger (*i*Button®). Once the inverted nest was placed on top of one plinth (Fig. 2), the logger would be in contact with the material present at the bottom of the cup (Deeming and Gray, 2016; Biddle, 2018). For data collection, two temperature loggers were then heated to a temperature of approximately 80 °C in a water bath. One was then placed on the top of a 'plinth' under the inverted nest, and the other temperature logger, the control, was placed on the second plinth, which was approximately 3 cm away from the outside of the nest (Fig. 2). Both temperature loggers were left to cool for 30 min at room temperature (24 °C) and humidity (51%), automatically recording temperature every minute. A third temperature logger was used to measure the temperature of the laboratory or the inside of the wind tunnel throughout the experiment. Each nest was tested three times following this procedure for every condition.

Cooling rates of the temperature loggers inside and outside the nest cup were used to calculate nest insulatory values using the method described by McGowan et al. (2004) and Mainwaring et al. (2012). The cooling rate ($°C\,min^{-1}$) of each logger was determined by fitting the temperature data to a logistic model:

$$\text{Temperature of temperature logger}(°C) = \text{ambient temperature}(°C)$$
$$+ [B \exp^{(-C \times \text{time(mins)})}]$$

where B is the initial temperature gradient between the temperature logger and the ambient and C is the cooling rate of the temperature logger per minute. This method converted a curvilinear line to a linear relationship. To allow for comparison with previous studies (*e.g.* McGowan et al., 2004; Mainwaring et al., 2012, 2014a) the difference in the rates of cooling ($°C\,min^{-1}$) of the temperature logger within the nest and of the control were divided by three to produce an insulatory value ($°C\,20\,s^{-1}$). Larger values indicated a bigger difference between the inside and outside of the nests which reflected better insulation by the nest wall.

To determine the effect of moving-air, nests were studied inside a custom-built wind tunnel described by Gray and Deeming (2017). Briefly, the tunnel (1.5 × 0.5 × 0.5 m, length × width × depth) was composed of three sections: a fan section, a test section, and an end section from which air left the tunnel, divided by wooden plates with uniformly punched holes (15-mm diameter) to reduce turbulence. An air-tight lid allowed access to the test section. To create the moving-air, an AC axial 230 V fan (150 mm diameter × 55 mm depth, ebm-papst W2S130) was used at a set maximum speed of $1.5\,m\,s^{-1}$ (Gray and Deeming, 2017). Nests were placed in the centre of the test section on a wooden plinth (19 cm high, 25 cm square), which was covered by a 3 mm sheet of polystyrene. The nests were central in the test section if their mid-point was ± 5 cm of the central point of the wind tunnel height. During testing nests were inverted and oriented such that the long axis of the cup was parallel with the flow of air. Thermal properties of the nests were tested under three conditions: 1) on a bench in the still-air in a laboratory measuring 5 × 5 × 3 m [length × breadth × height] in size; 2) within the wind tunnel with no air movement; and 3)

Fig. 1. Images of typical nests, as viewed from above, for (left to right) Eurasian Blackcap (*Sylvia atricapilla*), Eurasian Reed Warbler (*Acrocephalus scirpaceus*), and Willow Warbler (*Phylloscopus trochilus*).
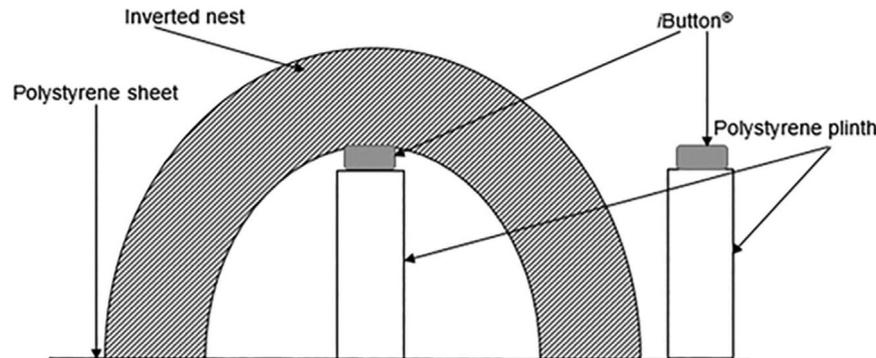

Fig. 2. Experimental design used to measure the temperature data for thermal measures of passerines nests, adapted from Biddle (2018).

within the wind tunnel with air moving at $1.5 \, \text{m s}^{-1}$.

All statistical analyses were conducted with Minitab (version 17). Preliminary Anderson-Darling tests in Minitab showed that all of the data for a species were normally distributed. Pearson's correlation tests were used to investigate the relationships among nest mass, wall thickness and base thickness with insulatory values and internal cooling rates measured under still-air conditions in the laboratory and the wind tunnel.

General linear mixed modelling (GLMM) was used to investigate whether differences in insulatory values and internal cooling rate were significantly affected by species and testing environment (lab versus wind tunnel) for still-air measurements. GLMM was also used to determine the effects of species and air movement (still air versus moving air, both in the wind tunnel). Full models were run initially but if there was a non-significant interaction term, it was removed and the model run again. Interaction terms were sequentially removed according to p-value and model reduction continued until only significant interactions remained. Nest ID was included in each model as a random factor to control for the two values collected from the same nest under the two different conditions. Species differences for each treatment were explored further using one-way analysis of variance, with a post hoc Tukey test to make pairwise comparisons. A critical value for α of 0.05 was used in all tests.

3. Results

Willow Warbler nests were the heaviest nests and those of the Eurasian Reed Warbler were the lightest (mean ± SD in g: 19.0 ± 3.7 g and 7.5 ± 2.9 g, respectively with Eurasian Blackcap nests weighing 11.2 ± 3.0 g). All nest dimensions for all species exhibited highly significant correlations (P < 0.001) with mass. For Eurasian Blackcap nests there was no significant correlation between nest mass and the individual dimensions with either insulatory value or cooling rate with two exceptions. Base thickness was negatively correlated with insulatory value measured in the still-air within the wind

tunnel (r = −0.665, df = 8, P = 0.036), and cup depth was positively correlated with insulatory value measured in the still-air within the wind tunnel (r = 0.733, df = 8, P = 0.016). Willow Warbler nests tested in still-air in the wind tunnel showed significant positive correlations between insulatory value and base thickness (r = 0.506, df = 21, P = 0.014), and nest mass (r = 0.503, df = 21, P = 0.014). No other relationships for any species showed any significant correlations (all P > 0.25).

There was no significant effect of test location (*i.e.* tunnel versus laboratory) on the insulatory values measured in still-air (Table 1). Species was a highly significant factor determining insulatory value (Table 1) and one-way ANOVA and post hoc tests showed that Eurasian Blackcap nests consistently had significantly higher insulatory values than nests of the other two species in the still-air conditions of the laboratory (effect of species: $F_{2,51} = 9.3$, P < 0.001). There was, however, no effect of species when recorded in still-air in the wind tunnel (one-way ANOVA: effect of species: $F_{2,51} = 1.2$, P = 0.323; Fig. 3).

Insulatory values measured in the moving-air treatment were an order of magnitude greater than for still-air in the wind tunnel (Table 2). Although Willow Warbler nests had the highest values, and, compared to still-air conditions, showed the largest proportional

Table 1
Effect of species of Warbler and treatment (still-air: laboratory conditions and wind tunnel) on thermal measures. Shown are F-values (p-values), with the coefficient of determination (R^2) for the model, for species and treatment assigned as fixed factors. Initially the full model* was used but non-significant interactions were dropped from the model, which was re-run.

Factor (df)	Insulatory value (°C 20 s⁻¹)	Internal cooling rate (°C min⁻¹)
Species (2,53)	5.9 (0.005)	25.1 (< 0.001)
Treatment (1,53)	01.0 (0.326)	35.4 (< 0.001)
R²	0.507	0.694

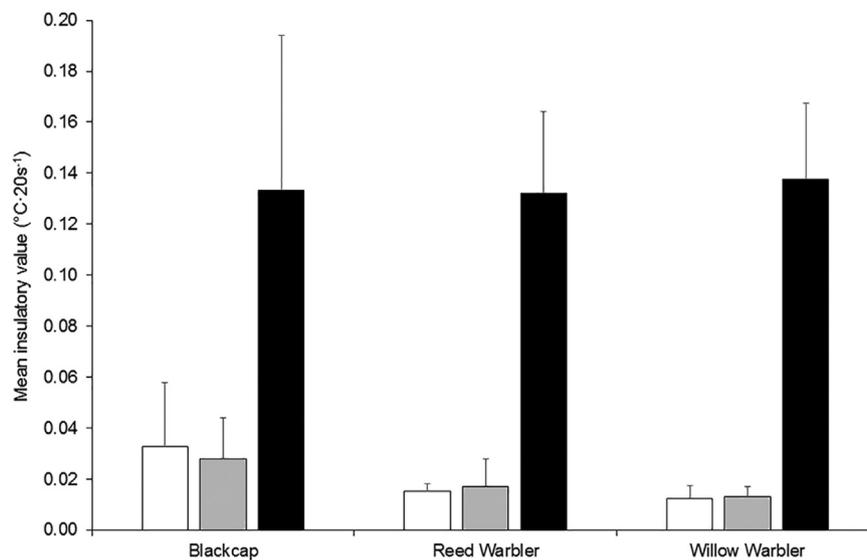*Model controlled for repeated measures from individual nests by including nest ID as a random factor.

Fig. 3. Mean ($+$SD) insulatory values (°C 20 s^{-1}) of Warbler nests in: 1) still-air in the laboratory (white columns); 2) still-air in the wind tunnel (gray columns), and 3) moving-air (black columns).

Table 2
Effect of species of Warbler and treatment (wind tunnel: still-air versus moving-air) on thermal measures. Shown are F-values (p-values), with the coefficient of determination (R^2) for the model, for species and treatment assigned as fixed factors. Initially the full model[*] was used but non-significant interactions were dropped from the model (indicated by -), which was re-run.

Factor (df Insulatory value/ Cooling rate)	Insulatory value (°C s^{-1})	Internal cooling rate (°C min^{-1})
Species (2,53)/(2,51)	0.2 (0.828)	26.7 (< 0.001)
Treatment (1,53)/(1,51)	395.9 (< 0.001)	264.7 (< 0.001)
Species[*]Treatment (2,51)	-	9.6 (< 0.001)
R^2	0.895	0.887

[*] Model controlled for repeated measures from individual nests by including nest ID as a random factor.

increase in insulatory value among treatments (Fig. 3), there was no significant effect of species on the insulatory values recorded during moving-air (one-way ANOVA: effect of species: $F_{2,51} = 0.3$, $P = 0.780$).

Mean internal cooling rates were consistently lower in still-air conditions in the laboratory and highest under moving-air conditions with Reed Warblers consistently having the lowest values (Table 1; Fig. 4). Eurasian Blackcap nests had significantly higher values for both testing conditions than the other two species (one-way ANOVA: effect of species: still-air in lab - $F_{2,51} = 15.4$ $P < 0.001$; still-air in wind tunnel - $F_{2,51} = 12.2$ $P < 0.001$; Fig. 4) but there were no significant differences in internal cooling rates for nests produced by Eurasian Reed Warblers and Willow Warblers.

Comparison of moving-air and still-air treatments in the wind tunnel showed highly significant effects of species, treatment and there was a highly significant interaction (Table 2). The interaction seemed to be associated by a disproportionately greater increase by Eurasian Blackcap nests measured in moving air wind tunnel (one-way ANOVA: effect of species: moving air in wind tunnel - $F_{2,51} = 20.1$, $P < 0.001$; Fig. 4).

4. Discussion

4.1. Effects of nest wall characteristics

Thermal insulation of the nest was generally not significantly correlated with nest mass or dimensions for any species. The larger Willow Warbler nests did show a positive relationship with mass but for base

thickness, which is immediately above the temperature logger, no consistent pattern was observed among species. The positive relationship between base thickness and insulatory value for Willow Warbler nests may reflect their larger size and the negative relationship for Eurasian Blackcap nests may reflect a more open nest structure. Akresh et al. (2017) reported a negative effect of nest mass on internal cooling rates of Prairie Warbler (*Setophaga discolor*) nests, which suggested that heavier nests were better insulated. Gray and Deeming (2017) found a significant, positive effect of nest mass on the insulatory values of nests from several species of the Motacillidae and Fringillidae. The lack of consistent pattern among species suggests that there is a need to explore further the relationships among measures of thermal insulation and intra-specific variability in nest size.

Across species, nests with comparable masses produce similar insulatory values. For example, Gray and Deeming (2017) reported Common Linnet (*Linaria cannabina*) nest mass at 18.3 g, which is similar to an average nest mass of 19.0 g for the Willow Warbler and the insulatory values in still and moving-air were remarkably similar: Common Linnet nest insulatory values averaged 0.018 and 0.134 °C·20 s^{-1} in still-air and moving-air, respectively. Equivalent values for Willow Warbler nests were 0.019 and 0.138 °C 20 s^{-1}. Similarly, average nest mass and thermal measures were very similar in the Meadow Pipit (*Anthus pratensis*) reported by Gray and Deeming (2017) and for Eurasian Reed Warblers reported here. Similarities among species are of interest given that these species use different materials in varying combinations and amounts to construct their nests (Dickinson et al., unpublished data). To date the effects of varying nest wall composition on thermal insulation remains poorly reported but studies have investigated the insulatory role of feathers. McGowan et al. (2004) and Pinowski et al. (2006) showed that the insulatory properties of Long-tailed Bushtit (*Aegithalos caudatus*) and Eurasian Tree Sparrow (*Passer montanus*) nests, respectively, were positively correlated with the mass of feathers within the nests. Experimental removal of feathers resulted in a reduction in insulation of Tree Swallow (*Tachycineta bicolor*) nests resulting in negative effects on fledgling success (Lombardo et al., 1995; Windsor et al., 2013). However, more recently experimental heating of Tree Swallow nestboxes did not affect the numbers of feathers incorporated in the nests, which is contrary to a role in insulation (Holland and Shutler, 2018). A better understanding of the role of particular construction materials, either individually or in combination with others, may help explain varying results for the relationship between nest mass and thermal insulation. How different nest materials
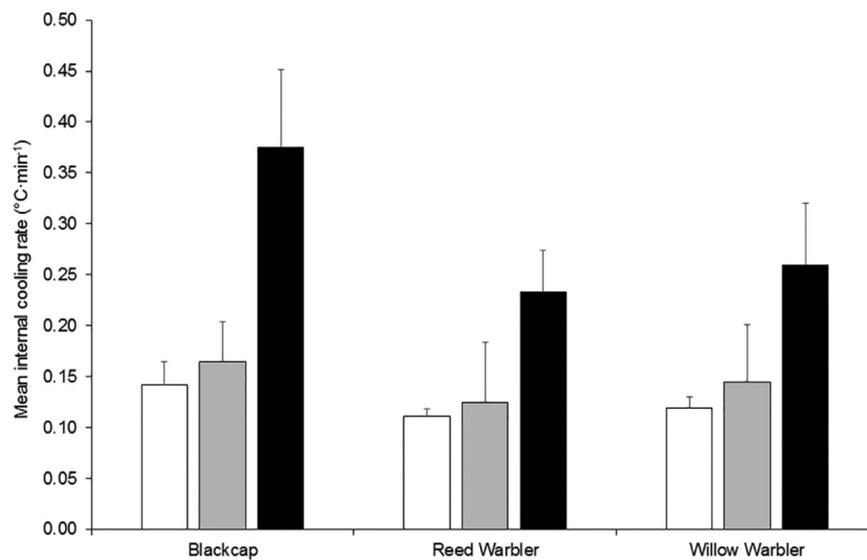
Fig. 4. Mean (+SD) 'internal cooling rate' (°C·min^{-1}) of temperature loggers placed inside the nest cup during three experimental treatments: 1) still-air in the laboratory (white columns); 2) still-air in the wind tunnel (gray columns), and 3) moving-air (black columns).

contribute to the thermal insulation of the nest wall in a range of species is an important topic for further investigation.

Previous studies have shown nest wall thickness can influence nest thermal properties (Heenan and Seymour, 2012; Akresh et al., 2017), but wall thickness was not associated with the thermal properties of Warbler nests in this study. The lack of an effect of wall thickness on the thermal properties of the nests, within each species, may have been because of our specific experimental set-up. During these experiments the temperature logger within the nest was only in contact with the base of the cup, which meant that it was the thickness of the base, rather than the side walls that influenced the insulatory values and internal cooling rates. A thicker nest base may allow for improved insulation because it is a greater physical barrier to heat loss from the temperature logger in the cup. By contrast, base thickness was not a significant factor influencing thermal properties in Fringillidae and Motacillidae nests (Gray and Deeming, 2017). However, species from this latter study with similar base thickness to the Warbler nests studied here produced similar thermal values.

The physical properties of nest walls can be characterised in ways other than dimensions. Porosity of the nest wall to light positively correlated with heat loss from nests of the White Crowned Sparrow (*Zonotrichia leucophrys*; Kern, 1984). In addition, nest thermal conductance and light porosity positively correlated (Skowron and Kern, 1980). Differences in nest wall porosity or density were not measured in the present study but Willow Warbler nests had the thickest walls and produced the slowest internal cooling rates during still-air trials inside the wind tunnel. By contrast, Eurasian Reed Warbler nests, which were tightly woven, dense cups with no visible gaps had the lowest internal cooling rates during episodes of air movement. Eurasian Blackcap nests had loosely constructed nest walls and base with visible gaps in the material. Unsurprisingly these nests experienced the greatest rate of heat loss in all test conditions, presumably due to heat energy escaping through these gaps in a similar way to that seen in the loosely woven stick nests of Eurasian Bullfinches (*Pyrrhula pyrrhula*; Biddle et al., 2018c). However, air gaps within a nest wall do confer some insulation to the nest in some species (Deeming and Biddle, 2015). Therefore, increased nest wall thickness, or the presence of a lining, may serve to trap more air, which may be important in determining nest insulation under still-air conditions. By contrast, in moving-air a tightly woven nest wall may prove to be a better physical barrier to air movement and so provide better insulation in moving air. Further investigation into the role of nest wall structure and the role air-gaps in a wider range of

passerine nests will help improve our understanding of the effects of wall properties on nest insulation.

The thermal properties of the materials may also be crucial in determining the thermal properties of a nest wall because Hilton et al. (2004) showed that animal and plant materials had different insulative properties. This may reflect differences in thermal conductivity of the materials. The thermal conductivity values of keratin, which forms the bulk of hair and feather, and cellulose, which is the bulk of plant materials, are relatively similar (0.192 and 0.230 W m^{-1} K^{-1}, respectively; Fuller, 2015; Anon, no date) but feathers have a much lower thermal conductivity of 0.034 W m^{-1} K^{-1} (Anon, no date) and so offer better insulation (Hilton et al., 2004). The differences observed among internal cooling rates for the Warbler species may reflect the different thermal conductivities of the materials in direct contact with the temperature logger. Unfortunately, thermal conductivity of most materials used to construct nests have yet to be reported but this may prove to be an interesting avenue of research. Moreover, similarities in thermal properties among species may reflect comparable types of materials used in the nest walls. Perhaps the low incidence of feathers in Common Linnet nest cups (0.8% of nest mass; Biddle et al., 2018a), and the absence of feathers in Willow Warbler nest cups, help to explain similarities in thermal values?

4.2. Effect of air movement

Despite the fact that nests constructed in the open will be naturally exposed to air movement (Sidis et al., 1994; Rohwer and Law, 2010) few studies have investigated the effect moving-air has on the thermal properties of nests. Previous studies (Heenan and Seymour, 2012; Gray and Deeming, 2017) have used a wind tunnel to investigate the thermal properties of nests in moving-air. As shown previously the insulatory values observed here were an order of magnitude higher in moving-air compared to still-air (Gray and Deeming, 2017). However, the increase in the insulatory value was not unexpected because the value is determined by the difference in the cooling rates between the temperature loggers inside and outside of the nest (McGowan et al., 2004; Mainwaring et al., 2012, 2014a; Deeming and Biddle, 2015; Gray and Deeming, 2017). A temperature logger in moving-air has a much higher cooling rate than a logger in a nest so the insulatory value only increased relative to the external conditions (Gray and Deeming, 2017). Thus, we concur with Gray and Deeming (2017) in concluding that using the cooling rate of the temperature logger within the nest better

reflects the effect of moving-air on the nest's insulative properties.

Our results confirm those of Gray and Deeming (2017) that insulatory values measured in still-air conditions were significantly higher, and the internal cooling rates significantly lower, when carried out under laboratory conditions rather than in the wind tunnel. Willow Warbler and Eurasian Reed Warbler nests had higher insulatory values when tested within the wind tunnel than when tested within the laboratory. By contrast, the insulatory values of Eurasian Blackcap nests were not different between the two testing locations. Gray and Deeming (2017) found that insulatory values of nests were lower when tests were carried out in the still-air of the wind tunnel for Common Linnets, Common Chaffinch (*Fringilla coelebs*), European Goldfinch (*Carduelis carduelis*) and Pied Wagtail (*Motacilla alba*) nests. In the still-air of the wind tunnel insulatory values for Common Linnet, Common Chaffinch, and European Goldfinch nests tested under laboratory conditions (Biddle, 2018) differed little from values reported by Gray and Deeming (2017). It is likely that air movement was more variable within the laboratory because of the air currents generated by human activity. This in turn may lead to a more rapid cooling of the external temperature logger compared to those within the still-air of the wind tunnel chamber. As per Deeming and Campion (2018), it is recommended by that future studies to determine the insulation of bird nests should be carried out in a fixed, closed volume of air, *e.g.* in a wind tunnel, to minimise effects of air movement on measures of insulation.

Our study supports that of Gray and Deeming (2017) that reported an increase in internal cooling rate for nests when exposed to moving-air. In our study, Warbler nests produced similar percentage increase in rate of heat loss to those reported for other passerines in the literature (Palmgren and Palmgren, 1939; Heenan and Seymour, 2012; Gray and Deeming, 2017). Palmgren and Palmgren (1939) measured cooling rates of a flask of warm water placed inside the nest and during windy conditions recorded an increase of 144% for cooling rates of Common Rosefinch (*Carpodacus erythinus*) nests and 191% for Common Chaffinch nests, compared to still-air conditions. Under laboratory conditions, thermal conductance of the nest wall increased by 170% when passerine nests were tested at maximum air speed of $0.88\,\mathrm{m\,s^{-1}}$ compared with still air conditions (Heenan and Seymour, 2012). The maximum speed of air movement used in our study, and Gray and Deeming (2017), was almost double that of Heenan and Seymour (2012) and the range of average percentage increase in our study was higher (70–225%). Percentage increase in internal cooling rate was greater overall for Warbler nests than for nests reported by Gray and Deeming (2017), an average of 156% higher rates of cooling for Motacillidae and Fringillidae nests combined, compared to 190% reported here for Warbler nests. More research is needed to assess the effects of air movement on nest insulation in additional species with different patterns of nest composition but also nesting location.

4.3. Effect of nest location

This study, in common with most other studies, investigated nest wall insulation in a laboratory environment. However, birds have to build their nests in a natural environment that can be affected by insolation, precipitation and air movement. Therefore the location of the nest may influence nest construction and hence, thermal properties. Willow Warblers are ground-nesting species, whereas Eurasian Reed warblers build elevated nests in reedbeds so they may be more relatively exposed to more air movement (Cramp, 1992). Typically, ground nests are subjected to better vegetative cover and are exposed to lower velocities of air movement than elevated nests (Kern, 1984; With and Webb, 1993). The combination of lower wind velocity and being under vegetative cover decreases the convective heat loss from the nest (With and Webb, 1993). Therefore, perhaps closely woven Eurasian Reed Warbler nests are be better adapted at mitigating the effect of moving-air on the internal microclimate of the nest than the bulky nests of Willow Warblers?

Eurasian Blackcap nests are also built above the ground in shrubs and bushes that provide vegetative cover (Cramp, 1992), but they have a high rate of cooling, which may reflect their loosely built nests. Where previous *in situ* studies have found egg temperatures to be lower and less stable in elevated nests than in ground nests, *ex situ* studies have found that elevated nests are typically better insulated than ground nests under laboratory conditions (Zerba and Morton, 1983; Kern, 1984). Although Eurasian Blackcap nests have the poorest insulation during *ex situ* studies, their walls still acted as a buffer from air movement. However, we have very little understanding of the extent to which the site of nest construction offers protection to the clutch in addition to that provided by the nest wall. A better understanding of the environmental conditions that surround nests *in situ* may help in explaining the variability in nest construction among species.

5. Conclusions

This study showed that the thermal properties of nests can vary within and among species but values for nest insulation do not appear to differ as much as the differences in nest construction would suggest. As we develop a better understanding of how nests serve to insulate the incubation environment (Deeming, 2016) there will be an increasing need to develop methods to assess nests *in situ*. Practical difficulties have perhaps limited the development of such techniques but it is likely that the localised environment of a nest site will affect construction behaviour and nest functionality. The approach used here and elsewhere where nest wall insulation is measured by a single temperature logger may need to be replaced by more sophisticated techniques, such as infrared thermography or multiple thermistors (Biddle et al., 2018c).

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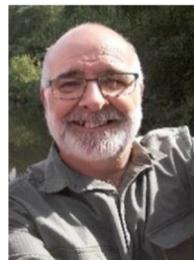
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