



Effect of air movement on the thermal insulation of avian nests

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Review

1 **Effect of air movement on the thermal insulation of avian nests**

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5

6 **ABSTRACT**

7 **Capsule:** Air movement over a nest increases the rate of cooling within the nest cup but the walls provide good
8 thermal insulation.

9 **Aims:** This study compared nests of six bird species of the families Fringillidae and Motacillidae to investigate
10 the insulative properties in still and moving air treatments. It was hypothesised that differences in nest size and
11 moving air would mean that species would have a significant effect on insulatory values of the nests.

12 **Methods:** Nest dimensions were measured for a total of 35 nests from six species. Thermal properties of the nests
13 were recorded using temperature loggers within nests placed in a wind tunnel under still and moving air
14 conditions.

15 **Results:** Insulatory values and internal nest cooling rates were significantly increased by moving air. Species had
16 no significant effect on thermal properties of the nests but nest mass correlated with greater insulatory values and
17 lower rate of cooling within the nest cup. Wall thickness had no significant effects on the thermal characteristics
18 of the nests.

19 **Conclusion:** The presence of a nest mitigated the effects of air movement but the differences between species
20 reflected difference in nest mass rather than wall thickness.

21

22 **Short title:** Thermal characteristics of nests.

23 **Keywords:** Air movement, Fringillidae, insulatory values, Motacillidae, nest dimensions, thermal properties

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25 Construction behaviour and the building of physical structures such as nests is widespread in nature, and assists
26 individuals in controlling environmental conditions beyond the capabilities of their body (Hansell 1984, 2000).
27 For birds, a key function of nests is as a receptacle for eggs and chicks (see review by Deeming & Mainwaring
28 2015) but there may be other roles, such as sexual signalling or predator avoidance (Moreno 2012, Mainwaring *et*
29 *al.* 2014, Mainwaring 2017). However, there is an increasing interest in understanding of how nests function as a
30 whole and in particular the nest has to function in a way to allow successful incubation (Deeming 2016).
31 Fundamental to this role is presumably the need to minimise energy loss by the adult birds whilst eggs are being
32 incubated and so thermal properties of nests have been of interest for a long time (see review by Deeming &
33 Mainwaring 2015).

34 Avian reproduction centres on contact incubation by parents who must regulate the thermal environment
35 within the nest. Egg incubation has long been considered as being energetically costly (Visser & Lessells 2001)
36 and Nord & Williams (2015) identified several species where the field metabolic rate during incubation is 3.4
37 times greater than basal metabolic rate. Any factor that mitigates the energy lost during incubation should be
38 advantageous to the parents so, for instance, selection of microclimates around nest sites, and the design of nests
39 that account for environmental conditions, are consequently expected to be a response to such energetic pressures
40 (Collias & Collias 1984, Deeming 2016). Studies support the view that nest location or physical characteristics

41 have thermal benefits. For instance, Reid *et al.* (2002) showed that greater scrape depth and increased scrape-
42 lining depth in Pectoral Sandpiper *Calidris melanotos* nests significantly reduced convective cooling and heat loss
43 to the ground. In the Orange-tufted Sunbird *Nectarinia osea*, thermal characteristics of nest-site selection indicate
44 the importance of orientating nests away from solar radiation and wind (Sidis *et al.* 1994). Sunbird nests
45 orientated towards the wind saw an increase in egg cooling rate by 30%, and nest wall thermal conductance
46 increased by 20%. Providing artificial shelters around Common Eider *Somateria mollissima* nests reduced wind
47 speed in the nest, increased nest temperature and reduced female mass loss during incubation (D'Alba *et al.*
48 2009). The presence of a Common Blackbird *Turdus merula* nest reduced the rate of cooling of a heated steel ball
49 compared with cooling in the open (Ar & Sidis 2002). The effect of air movement on the thermal dynamics and
50 insulatory properties of nests is, however, still relatively unknown. To date only Heenan & Seymour (2012) have
51 demonstrated a significant increase in the thermal conductance of nests of two species of passerine when exposed
52 to moving air. No other studies of the effects of moving air on the thermal characteristics of nests are known.

53 This study investigated the effects of moving air on insulatory values (see Deeming & Mainwaring 2015
54 for a review of published data) and internal cooling rates of nests of three species of the Motacillidae and three
55 species of the Fringillidae. These species were chosen partly on the basis of availability of sufficient examples but
56 the species were of interest because the nests vary in size between the species and are built in generally open
57 environments where they would be exposed to air movements. Insulatory properties were studied in still and
58 moving air treatments using temperature loggers to test the hypothesis that the physical properties of the nest
59 would influence its thermal properties. From this we predict that: nest dimensions and nest thermal measures
60 would show positive correlations, moving air would adversely affect the insulative properties of the nests, and
61 because of structural and compositional differences of the nests there would be species differences in their thermal
62 properties.

63

64 **Methods**

65 Nests from Meadow Pipits *Anthus pratensis*, Pied Wagtails *Motacilla alba*, and Grey Wagtails *Motacilla cinerea*
66 of the Motacillidae, and Common Linnets *Linaria cannabina*, Common Chaffinches *Fringilla coelebs*, and
67 European Goldfinches *Carduelis carduelis* of the Fringillidae. Volunteers who monitor nests for the British Trust
68 for Ornithology collected the nests at the end of breeding season during 2014, 2015 and 2016 at a variety of
69 locations across Great Britain. The dry nests were sent to the University of Lincoln where they were frozen at -
70 20°C for 72 hours to kill biting invertebrate ectoparasites present in the nest material (Britt & Deeming 2011)
71 before being stored dry in plastic bags within cardboard boxes at room temperature until testing commenced
72 (Deeming & Gray 2016a). We have no evidence to suggest that this procedure adversely affected the structure of
73 the nests. A total of 35 nests were collected, six were investigated for each species except Grey Wagtails for
74 which only five nests were available.

75 Nest mass was measured to the nearest 0.1g using an electric balance (A&D Company Limited, model
76 FX-3000i). The following linear dimensions were measured using Mitutoyo digital callipers with an accuracy \pm
77 0.02 mm (Biddle *et al.* 2016): diameter of the cup (mm) (long and short axes were averaged), cup volume (cm³),
78 diameter of total nest (mm) (long and short axes were averaged), width of long axis and short axis walls
79 (averaged, mm), cup depth (mm), and total nest depth (mm).

80 A custom-built wind tunnel, largely based on the design by Heenan & Seymour (2012), enabled wind
81 speed to be controlled, measured, and set for treatment conditions. The tunnel consisted of a long wooden box
82 (150 x 50 x 50 cm, length x width x depth) divided into three sections: the fan section, the test section (where the
83 nest was placed) and the end settling chamber through which air would leave the tunnel (Figure 1). Uniformly
84 punched holes (15 mm diameter) in wooden plates formed the dividers of the tunnel chambers and functioned to
85 straighten the air flow and reduce turbulence. A removable, air-tight lid in the top panel provided access to the test
86 chamber. A perspex sheet screwed on to the front of the wind tunnel allowed for viewing of the nests under test
87 conditions. An AC axial 230V fan mounted in the end panel of the fan section (150 mm diameter x 55 mm depth,
88 ebm-papst W2S130 series) blew air into the tunnel. The speed settings of the fan could be altered with a variable
89 fan speed controller (model A72229, United Automation Ltd) that varied the voltage from 0 to 230V to give 10
90 variable speeds.

91 Preliminary studies used a vane anemometer (Benetech GM8902; Air velocity measuring error: $\pm 3\%$) in
92 the test section of the wind tunnel to measure the wind speed at set distances along the length, and through the
93 centre of the chamber at all ten fan speed settings. Wind speed was determined to be consistent across all
94 measured points in the test chamber during preliminary trials, and mean wind speeds over five minutes at each
95 variable setting were calculated to indicate this. The maximum achievable wind speed was $1.5 \text{ m}\cdot\text{s}^{-1}$ at the highest
96 setting and this was used in all subsequent tests to ensure uniformity between different nest recordings. This is 5.4
97 $\text{km}\cdot\text{h}^{-1}$, which is a relatively light wind, but it is around 25% faster than the maximum speed used by Hilton *et al.*
98 (2004) and Heenan & Seymour (2012).

99 The central test section was between the two dividers, and contained an elevated wooden plinth (20 x 20
100 x 19.5 cm, l x w x h) that was positioned in the centre point of the base, and also so that the nest sat centrally
101 within the height of the box. The plinth had a thin wooden frame consisting of a base (20 x 20 cm) and top (20 x
102 20 cm) that were supported by four wooden legs that were approximately 0.5 x 0.5 cm. This was designed to
103 allow air flow through the structure so as to minimise turbulent air flow. The top of the plinth was covered with a
104 33 mm thick layer of non-conductive sheet polystyrene that could be layered to adjust the centrality of the nest
105 within the height of the tunnel. Nest height measurements indicated the extent to which the nest needed to be
106 raised or lowered and the centre point of the wind tunnel height measured 23 cm; the nests were 'central' in the
107 box if their midpoint was ± 5 cm of this value.

108 An iButton® temperature logger (Maxim.com; see Smith *et al.* 2015) was heated to 80°C in a water bath
109 (Mainwaring *et al.* 2012, Smith *et al.* 2015, Deeming & Gray 2016a) and placed on a small polystyrene block
110 such that with the temperature logger mounted on it and the nest inverted on it, would equal the depth of the nest
111 cup so that the temperature logger would contact the inner cup surface. The nests were inverted and placed cup-
112 downwards over the temperature logger and orientated with the long axis of the cup lying parallel to the direction
113 of the air movement. The height of the polystyrene block within the nest cup was measured to ensure that the nest
114 wall made contact with the polystyrene base of the wooden plinth. A second (control) temperature logger was also
115 heated to 80 °C in a water bath at the same time as the first, and this was placed on the plinth within 10 cm of the
116 nest on a polystyrene block of equal height to that of the nest. A third temperature logger (not heated) was
117 mounted on an inside wall of the test chamber of the wind tunnel and recorded the ambient temperature. The
118 temperature loggers were programmed to record temperature (°C) every minute for 20 minutes beneath the
119 inverted nests. All 35 nests were tested three times in the wind tunnel under two treatments: still air (fan turned

120 off) and moving air ($1.5 \text{ m}\cdot\text{s}^{-1}$) with a 20 min cooling interval between each repeat to allow the nest to cool to
121 room temperature, and the temperature loggers to reheat in the water bath (Deeming & Gray 2016a).

122 Cooling rates for individual nests were determined via fitting the temperature data to logistic models as
123 described by McGowan *et al.* (2004), Mainwaring *et al.* (2012), and Deeming & Gray (2016a). Differences in the
124 rates of cooling ($^{\circ}\text{C}\cdot 20\text{s}^{-1}$) of the nest and the control temperature loggers indicated the insulatory value of the
125 nest. Large positive differences indicate a high level of nest insulation (Mainwaring *et al.* 2012, Taberner Cezero
126 & Deeming 2015). The effects of moving air were also investigated by comparing the rates of cooling of the
127 temperature logger within the nest in still and moving air conditions.

128 Data were tested for normality prior to analysis with Log_{10} -transformation being used to stabilise any
129 data that did not have a normal distribution. We determined repeatability for the trials based on the method
130 described by Lessels & Boag (1987) using the ICC package in R (R Core Team, 2014). One-way analysis of
131 variance (ANOVA) was used to determine the effect of species on nest dimensions, and to test the effect of
132 species on some thermal measures. Significant differences between species were determined by post-hoc Tukey
133 test pairwise comparisons. Spearman signed-rank correlation was used to investigate associations between nest
134 dimensions and thermal measures. Analysis of covariance (ANCOVA) tested the effect of species and nest mass
135 on the insulatory value of the nest in the wind treatment. All statistical analyses were carried out using Minitab
136 version 17.

137

138 Results

139 Species differences were observed for nest mass, wall thickness, cup diameter and nest diameter but not base
140 thickness, cup depth or nest depth (Table 1). These differences were attributable to the nests constructed by Pied
141 Wagtails and Grey Wagtails, which were significantly heavier and larger than the nests of the other species. That
142 cup and nest diameter were both significant is reflected in the significant effect of species on wall thickness.
143 Hence, subsequent analysis concentrated on the effects of nest mass and wall thickness on the thermal properties
144 of the nests.

145 For all species, the mean insulatory value ($^{\circ}\text{C}\cdot 20\text{s}^{-1}$) was an order of magnitude higher in the moving air
146 treatment than in still air (Table 2). Repeatability values were higher for still air trials (mean 0.49, range 0.25–
147 0.80) than for moving air trials (mean 0.29, range -0.17–0.66). Although Pied Wagtail nests showed the greatest
148 increase in insulatory value this difference between still and moving air was not significantly affected by species
149 (ANOVA: $F_{5,29} = 2.37$, $P = 0.064$). The cooling rate of the temperature logger within the nest ($^{\circ}\text{C}\cdot\text{min}^{-1}$) was
150 higher in moving air than still air but the difference between the two values was unaffected by species (ANOVA
151 on Log_{10} -transformed data: $F_{5,29} = 1.56$, $P = 0.202$). The percentage increase in cooling rate was greatest for
152 Meadow Pipit nests and smallest for Pied Wagtail nests but again variation in values were unaffected by species
153 (ANOVA on Log_{10} -transformed data: $F_{5,29} = 2.40$, $P = 0.062$).

154 Spearman rank correlations showed that differences in insulatory value showed a significant positive
155 correlation with nest mass (Table 3); the differences in insulatory values of light nests between still and moving
156 air were smaller than for heavier nests (Fig. 2). By contrast, there were significant negative relationships between
157 nest mass and difference in cooling rate within the nest (Fig. 3), and the percentage increase in this cooling rate
158 (Table 3). Heavier nests seem to reduce the effects of moving air on internal rates of cooling. By contrast, there
159 were no significant correlations between wall thickness and any of the thermal parameters (Table 3).

160 Investigation of the effect of species whilst controlling for nest mass showed no significant effects on
161 insulatory values (Table 4). By contrast, for both the difference in cooling rate, and the percentage increase in
162 cooling rate, nest mass was a significant covariate but there was no effect of species (Table 4).

163

164 Discussion

165 Exposing nests to moving air at a relatively slow rate dramatically increased their insulatory value relative to still
166 air but internal cooling rates were also significantly increased. Only these latter values were significantly
167 correlated with nest mass and there were no observable effects of species, or any other nest dimension, on the
168 thermal properties of the nests.

169 Insulatory values recorded here were lower than values reported previously (Deeming & Mainwaring
170 2015, Deeming & Gray 2016b). In particular, the values for Linnet nests reported by Deeming & Gray were
171 around 70% greater than reported here (0.031 vs 0.018 $^{\circ}\text{C}\cdot 20\text{s}^{-1}$). Values for Common Chaffinch, European
172 Goldfinch and Pied Wagtail nests were also higher in the report by Deeming & Gray (2016). The reason for this
173 may lie with methodology – Deeming & Gray (2016b) recorded insulatory values of nests in an open laboratory
174 environment, which may have been subjected to more air flow than the enclosed air of the wind tunnel.

175 The increase in insulatory value of the nest observed in this study could be anticipated because this
176 measurement of nest insulation is determined by the difference in cooling rate of temperature loggers inside and
177 outside of a nest (McGowan *et al.* 2004, Mainwaring *et al.* 2012, 2015). Whilst increased air movement increases
178 the rate of cooling of the temperature logger inside the nest, the rate of cooling of the temperature logger outside
179 of the nest was massively increased, as was also shown by Heenan & Seymour (2012). As a result the insulatory
180 value (i.e. the difference in cooling rates) is much higher in moving air than still air. The nest buffers the effects of
181 the air movement but the observed ten-fold increase in insulatory value is potentially misleading. The nest did not
182 become better insulated in moving air but the properties of the wall did reduce its effects. The nests only increased
183 their insulatory values relative to the external conditions. These results mean that future studies should consider
184 insulatory values only in the context of any particular study and comparative studies need to ensure that
185 methodologies are comparable before making any overarching conclusions.

186 The rate of cooling of the temperature logger inside the nest cup increased significantly so the increased
187 air flow was affecting the internal microclimate. This may seem counter-initiative to an increased insulatory value
188 in moving air but it does better reflect the effect of the experimental treatment on the nest. Whether the increased
189 rate of cooling reflects an increased loss of heat conducted from the hot temperature logger to the outside surface
190 of the nest is unclear and requires further investigation. It is possible that air is moving through the nest wall and
191 cooling the temperature logger directly. Air movement had similar significant effects on nest thermal conductance
192 in the study by Heenan & Seymour (2012). The maximum air speed achieved by Heenan & Seymour (2012) was
193 0.88 $\text{m}\cdot\text{s}^{-1}$, which increased thermal conductance by around 170%. In this study a wind speed almost twice this
194 value only increased internal cooling rates by an average of 156%, which implies that the nests in this study were
195 better insulated than those studied by Heenan & Seymour (2012). No difference between the nests of the two
196 species studied by Heenan & Seymour (2012) despite the significantly different wall thicknesses and composition.
197 In this study species was also not a significant factor affecting changes in cooling rate but there was a significant
198 effect of nest mass. The lighter nests showed the greatest variation in increase in cooling rates, which were
199 considerably higher than those of heavier nests. Palmgren and Palmgren (1939) found that heat loss increased by

200 44% for the Common Rosefinch *Carpodacus erythrinus*, and 91% in the Chaffinch *Fringilla coelebs* in windy
201 conditions. Rates of heat lost from nests of the Yellow Warbler *Dendroica petechia* nests were higher for nests
202 collected in Elgin, Ontario than for the nests from the more northerly and windier Churchill, Manitoba (Rohwer &
203 Law 2010). The use of artificial nests has also indicated the impact of wind on convective heat loss, with cooling
204 coefficients being 3x greater in winds of $1.2 \text{ m}\cdot\text{s}^{-1}$ than still air (Hilton *et al.* 2004) but it is unclear to what extent
205 the artificial nests were representative of real nests. Whilst air movement increases rates of cooling within nests
206 the presence of the nest does have a beneficial effect by reducing the rate of heat loss relative to the external air.
207 Ar & Sidis (2002) also showed that the presence of a nest reduced rates of cooling of steel balls placed within the
208 cup.

209 Nest mass and wall thickness have been shown to be factors influencing nest thermal characteristics in a
210 variety of species (Heenan and Seymour, 2012; Heenan, 2013; Windsor *et al.*, 2013). Results presented here for
211 the effect of nest mass on thermal measures support such findings but previous evidence suggesting an effect of
212 wall thickness on thermal properties was not supported in this study. Thicker walls are of course associated with a
213 heavier nest and it may be difficult to disentangle the relative effects of each, particularly when different materials
214 are used in nest construction. In this study wall thickness did not necessarily correlate with nest mass across
215 species. In Penduline Tit *Remiz pendulinus* nests cooling rates of dummy eggs inversely correlated with wall
216 thickness but not with other measures of nest size (Szentirmai *et al.* 2005). Kern (1984) also found correlation
217 between wall thickness and thermal measures in White-Crowned Sparrows *Zonotrichia leucophrys leucophrys*. In
218 addition, the presence of air-gaps within the nest wall have an insulative role in some species (Deeming & Biddle
219 2015) but how this applies to the species investigated here is unclear. Further research is needed to tease out the
220 relationships between nest mass, wall thickness and construction and the insulative properties of the nest as a
221 whole.

222 Few studies have attempted to correlate the materials used in a nest with its insulative properties. Hilton
223 *et al.* (2004) showed that cooling rates within nests were significantly affected by nesting material with respect to
224 wind. Grass had lower insulative values than animal-derived fur or feathers, but these materials were studied in
225 isolation rather than in the context of a complete nest where the materials are combined. Studies that have
226 investigated the effect of environmental temperature on nest composition perhaps indirectly reflect difference in
227 insulative properties. For instance, wall thickness and composition of passerine nests varied between different
228 latitudes in Canada (Crossman *et al.* 2011). Yellow Warbler nests from Elgin, Ontario, which allowed faster rates
229 of cooling, had thinner walls, composed mainly of bark and grasses, compared with the grasses, feathers and plant
230 fibres found in thicker better insulated nests from Churchill, Manitoba (Rohwer & Law 2010). Whether this
231 relates to colder, windier conditions found at Churchill, or rates of heat loss from the nests, is unclear. Temperature
232 at different latitudes also affects insulatory values in Common Blackbirds (Mainwaring *et al.* 2015) and Blue Tits
233 *Cyanistes caeruleus* and Great Tits *Parus major* (Mainwaring *et al.* 2012). Mainwaring *et al.* (2015) showed that
234 insulatory values strongly correlated with the amounts of grass in the cups of Common Blackbirds nests.
235 Similarly, altitude significantly affected Common Amakihi *Hemignathus virens virens* nest construction, whereby
236 nests from higher and cooler altitudes had denser and thicker walls and better thermal insulation than nests at
237 lower altitudes (Kern & van Riper 1984). More research is required to better understand the relationships that
238 exist between nest composition and insulative properties. The present study did not investigate the effect of nest

239 composition on the thermal properties but these data will form part of an on-going study into the relationship
240 between insulatory value and nest composition.

241 This study, in common with most other studies on nest thermal characteristics, was carried out with nests
242 *ex situ*. However, nest location is a key element of avian reproductive biology and the chances are that the
243 microclimate around nests will impact upon their function. However, few studies have recorded actual wind
244 speeds at nests. Reid *et al.* (2002) recorded wind speeds of $3.2 \text{ m}\cdot\text{s}^{-1}$ at relatively exposed nests of Pectoral
245 Sandpipers *Calidris melanotos*. We presume that the more sheltered passerine nests reported here will experience
246 lower wind speeds than this. Indeed Sidis *et al.* (1994) showed that nest site location reduced the wind speeds
247 experienced by Palestine Sunbird *Nectarinia osea* nests by around 50% to $0.25 \text{ m}\cdot\text{s}^{-1}$. There is certainly scope for
248 more detailed studies of the environmental conditions experienced by nests *in situ*.

249 Despite being comparable in mass to most of the species in this study (species means ranged from 16-20
250 g; Cramp 1988, Cramp & Perrins 1994), the Pied and Grey Wagtails had the heaviest and largest nests. This may
251 reflect differences in composition or nest site. For instance, wagtails tend to nest in sheltered cavities whereas
252 Meadow Pipits nest on the ground (Simms 1992). By contrast, the smallest species represented in this study,
253 finches tend to nest in bushes (Cramp & Perrins 1994) and may be more exposed to increased wind speeds and
254 fluctuations in wind speed and direction. Ground-nests in general experience lower wind velocity, greater
255 vegetative cover, and therefore decreased convective heat loss (With & Webb 1993). Indeed in three species of
256 ground-nesting passerines wind speeds recorded inside nests were a small fraction of the wind speeds outside the
257 nest. Gaul (1975) demonstrated that at nests of the Mountain Plover *Charadrius montanus* wind speed readings
258 taken at just 7 cm above ground level were 3.5-fold higher than the average wind velocity at ground level.
259 Investigating the relationship between species, nest placement and nest thermal properties, Kern (1984) found that
260 nest dimensions and location both contributed to the thermal properties of White-Crowned Sparrows. Elevated
261 nests of the Mountain White-crowned Sparrows *Z. leucophrys oriantha* race are larger, with thicker and less
262 porous bases, losing heat through the base at a slower rate, than ground nests of the Eastern White-crowned
263 Sparrow *Z. leucophrys leucophrys*. These nests were shown to be better insulated than ground nests, and it was
264 suggested that their increased insulation offset or mediated convective cooling to which they were more exposed.
265 Reid *et al.* (2002) showed that depth of scrape on/within the ground correlated with the cooling coefficient in
266 under windy conditions ($3.2 \text{ m}\cdot\text{s}^{-1}$). The cooling coefficient increased significantly with wind speed in shallow
267 scrapes, such that shallower, more elevated nests were less insulated. It is entirely possible, as concluded by Reid
268 *et al.* (2002), that the differing nest dimensions and placements of the nests of species studied here are maximising
269 insulatory optima in their nests, in so far as they are also subject to other competing abiotic factors such as rainfall
270 and solar radiation (Sidis *et al.* 1994, Ar & Sidis 2002). Our understanding of nest function is relatively poor
271 (Deeming & Mainwaring 2015) but as it improves there will be a need for *ex situ* investigations of nest thermal
272 characteristics. The challenge is to develop techniques that will allow for investigations *in situ*, which allow nest
273 function to be studied in the nest site chosen by the birds.

274 To conclude, this study has shown that thermal inertia of nests is a function of their mass rather than
275 being a function of the species' nest construction behaviour. Whether this is true for other species that show a
276 difference in body mass remains to be seen. Nests certainly offer protection from air movement and so reduce heat
277 loss but other studies should aim to expand on these findings, including other species and families from varied
278 geographical, latitudinal, and nest site locations.

279

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286

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360

For Peer Review

361 **Figure 1.** Illustrations of the wind tunnel used in this study in 3D (top) and from the lateral perspective (bottom).
362 Arrow indicates wind direction. 1 – fan section; 2 – test section; 3 – end settling chamber; 4 – wind-tight tunnel
363 lid; 5 – one of three diffusing divider panels. Images produced by Image Displays UK Ltd..

364

365 **Figure 2.** Relationship between nest mass and the difference in insulatory value between still and moving air for
366 all species combined. Values for individual nests are identified by the symbols indicated.

367

368 **Figure 3.** Relationship between nest mass and the difference in cooling rate of the temperature logger within the
369 nest between still and moving air for all species combined. Values for individual nests are identified by the
370 symbols indicated.

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1 **Table 1.** Descriptive statistics of mean (with \pm SD values) nest dimensions. Sample size was 6 for all species except the Grey Wagtail, where five nests were studied.
 2 ANOVA (F -value with P -value in parentheses) results at the base of each column indicate the effect of species on nest dimensions.

3

Species	Nest mass (g)	Wall thickness (mm)	Base thickness (mm)	Cup diameter (mm)	Nest diameter (mm)	Cup depth (mm)	Nest depth (mm)
Meadow Pipit	12.44 ^A \pm 3.35	24.40 ^A \pm 8.78	18.75 \pm 10.23	59.66 ^A \pm 12.02	103.36 ^A \pm 11.76	29.53 \pm 5.67	48.28 \pm 11.62
Pied Wagtail	45.02 ^B \pm 18.0	36.03 ^{A,B} \pm 7.13	30.37 \pm 20.21	75.33 ^{A,B} \pm 7.22	135.07 ^B \pm 8.07	32.89 \pm 5.06	63.27 \pm 22.7
Grey Wagtail	36.63 ^{B,C} \pm 16.70	46.88 ^B \pm 18.77	16.68 \pm 13.61	60.03 ^A \pm 10.63	131.40 ^{B,C} \pm 22.39	38.94 \pm 13.40	55.62 \pm 15.95
Linnet	18.32 ^{A,C} \pm 4.17	21.09 ^A \pm 6.19	24.10 \pm 4.60	62.99 ^A \pm 4.06	100.22 ^A \pm 10.74	34.32 \pm 8.14	58.42 \pm 10.49
Chaffinch	11.13 ^A \pm 1.40	20.37 ^A \pm 2.82	12.34 \pm 9.07	54.78 ^{A,C} \pm 6.57	94.15 ^{A,C} \pm 6.55	38.65 \pm 5.40	50.99 \pm 6.87
Goldfinch	14.01 ^A \pm 9.47	20.17 ^A \pm 12.65	14.48 \pm 4.53	55.64 ^{A,C} \pm 15.63	95.06 ^{A,C} \pm 13.99	28.25 \pm 6.89	42.74 \pm 10.7
$F_{(5,29)}$	10.98 (<0.001)	4.62 (0.003)	1.98 (0.112)	3.28 (0.018)	11.77 (<0.001)	1.93 (0.120)	1.28 (0.140)

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5 Within columns superscript letters indicate significant species differences (where $P \leq 0.05$) as determined by Post-hoc Tukey test pairwise comparisons.

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1 **Table 2.** Descriptive statistics of mean (with \pm SD) nest thermal measures in still and moving air conditions: insulatory value, cooling rate, and % increase in cooling rate.

Species	Insulatory Value ($^{\circ}\text{C}\cdot 20\text{s}^{-1}$)			Cooling rate ($^{\circ}\text{C}\cdot\text{min}^{-1}$)			% Increase in cooling rate
	Still air	Moving air	Difference	Still air	Moving air	Difference	
Meadow Pipit	0.017 ± 0.002	0.134 ± 0.032	0.117 ± 0.031	0.123 ± 0.003	0.232 ± 0.057	0.109 ± 0.054	188.3 ± 43.24
Pied Wagtail	0.016 ± 0.002	0.160 ± 0.015	0.143 ± 0.014	0.124 ± 0.004	0.162 ± 0.026	0.038 ± 0.026	130.8 ± 21.34
Grey Wagtail	0.018 ± 0.012	0.137 ± 0.024	0.119 ± 0.022	0.132 ± 0.008	0.202 ± 0.056	0.070 ± 0.058	153.4 ± 43.97
Linnet	0.018 ± 0.002	0.134 ± 0.016	0.116 ± 0.016	0.122 ± 0.004	0.178 ± 0.029	0.055 ± 0.027	144.5 ± 21.07
Chaffinch	0.020 ± 0.002	0.139 ± 0.011	0.119 ± 0.012	0.125 ± 0.006	0.183 ± 0.018	0.058 ± 0.016	146.9 ± 13.0
Goldfinch	0.015 ± 0.005	0.120 ± 0.024	0.105 ± 0.020	0.153 ± 0.035	0.221 ± 0.083	0.068 ± 0.050	177.1 ± 22.08

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- 1 **Table 3.** Spearman signed-rank correlation of the association between thermal properties of nests (insulatory
 2 value, °C/20s; cooling rate °C·min⁻¹) and the mass and thickness values of nests of all species combined. Values
 3 are *rho* with *P*-value in parentheses and degrees of freedom of 33 for all variables.

Thermal measures	Nest Dimensions	
	Nest mass (g)	Wall thickness (mm)
Insulatory value: still air	0.036 (0.837)	-0.284 (0.099)
Insulatory value: moving air	0.460 (0.005)	0.161 (0.356)
Difference in insulatory value	0.407 (0.015)	0.150 (0.389)
Cooling rate: still air	0.245 (0.156)	-0.042 (0.810)
Cooling rate: moving air	0.536 (0.001)	0.055 (0.755)
Difference in cooling rate	-0.503 (0.002)	0.033 (0.850)
% increase in cooling rate	-0.442 (0.008)	-0.028 (0.873)

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Table 4. Results of analysis of covariance to test the effect of species as a fixed factor whilst controlling for Log₁₀ nest mass as a covariate, on differences in insulatory value, cooling rate of the iButton within the nest between still and moving air, and the percentage increase in cooling rate. Values are *F*-ratios with *P*-value in parentheses.

Factor (Degrees of freedom)	Difference in insulatory value	Difference in cooling rate	Percentage increase in cooling rate
Log ₁₀ Nest mass (1,28)	2.27 (0.143)	8.57 (0.007)	6.20 (0.019)
Species (5,28)	1.06 (0.402)	1.20 (0.333)	2.29 (0.073)

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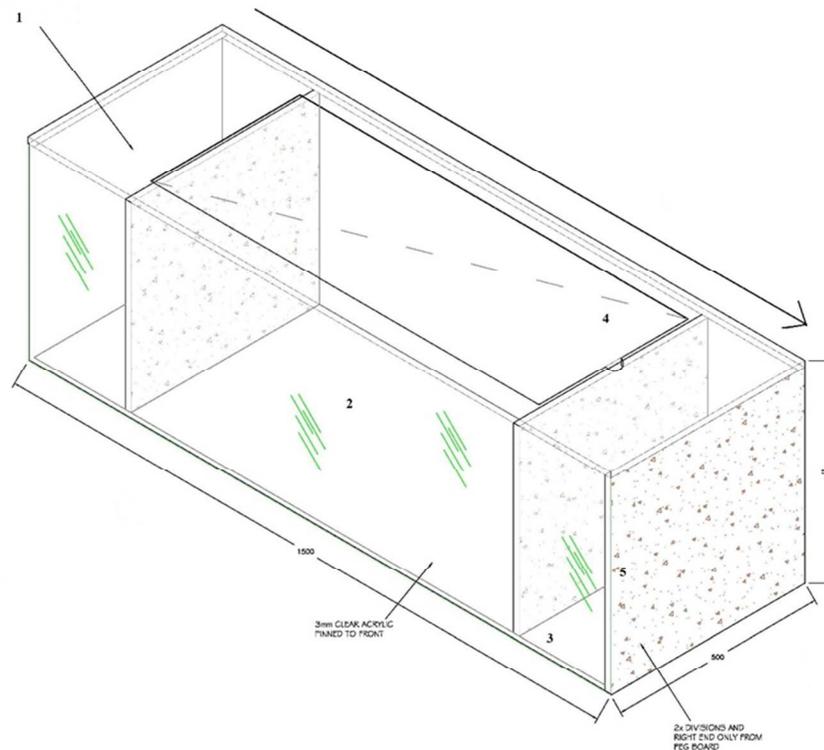


Figure 1. Illustrations of the wind tunnel used in this study in 3D (top) and from the lateral perspective (bottom). Arrow indicates wind direction. 1 – fan section; 2 – test section; 3 – end settling chamber; 4 – wind-tight tunnel lid; 5 – one of three diffusing divider panels. Images produced by Image Displays UK Ltd..

160x128mm (149 x 149 DPI)

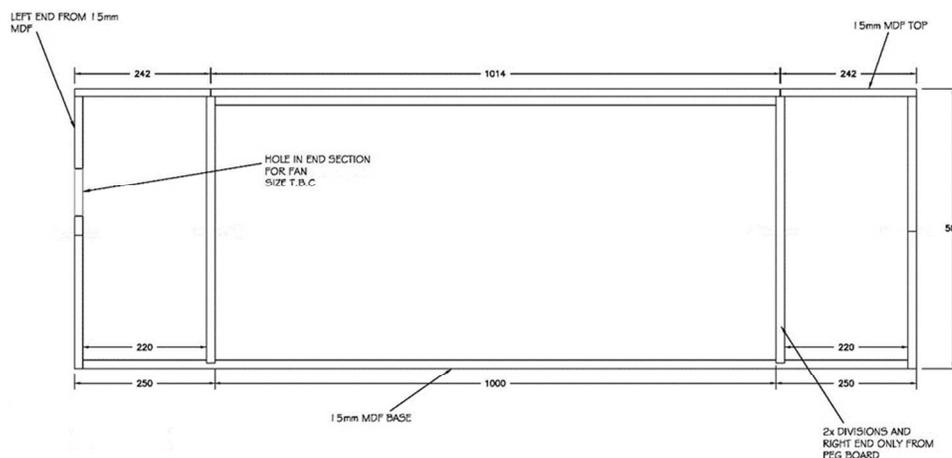


Figure 1. Illustrations of the wind tunnel used in this study in 3D (top) and from the lateral perspective (bottom). Arrow indicates wind direction. 1 – fan section; 2 – test section; 3 – end settling chamber; 4 – wind-tight tunnel lid; 5 – one of three diffusing divider panels. Images produced by Image Displays UK Ltd..

179x85mm (149 x 149 DPI)

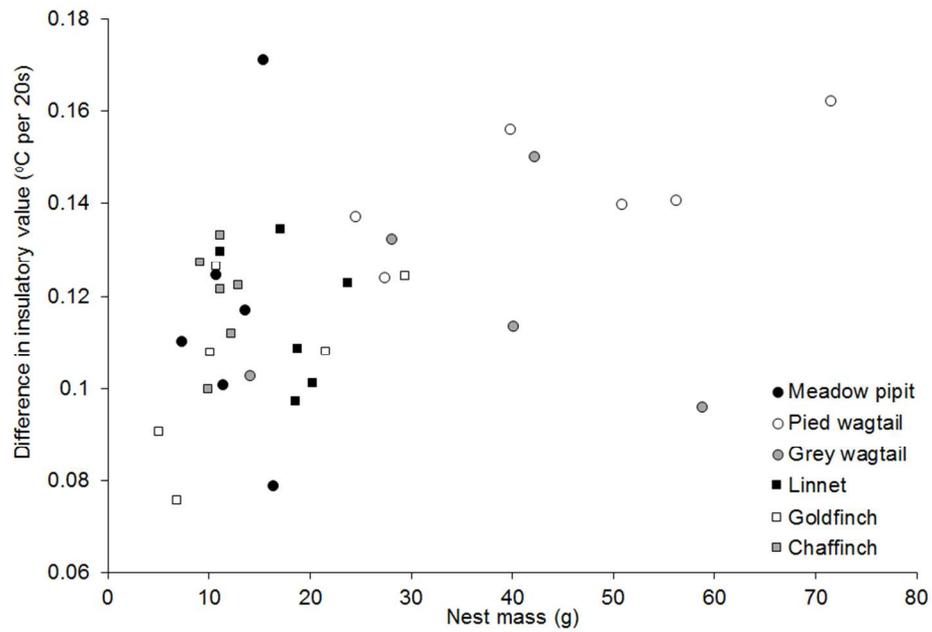


Figure 2. Relationship between nest mass and the difference in insulatory value between still and moving air for all species combined. Values for individual nests are identified by the symbols indicated.

262x170mm (96 x 96 DPI)

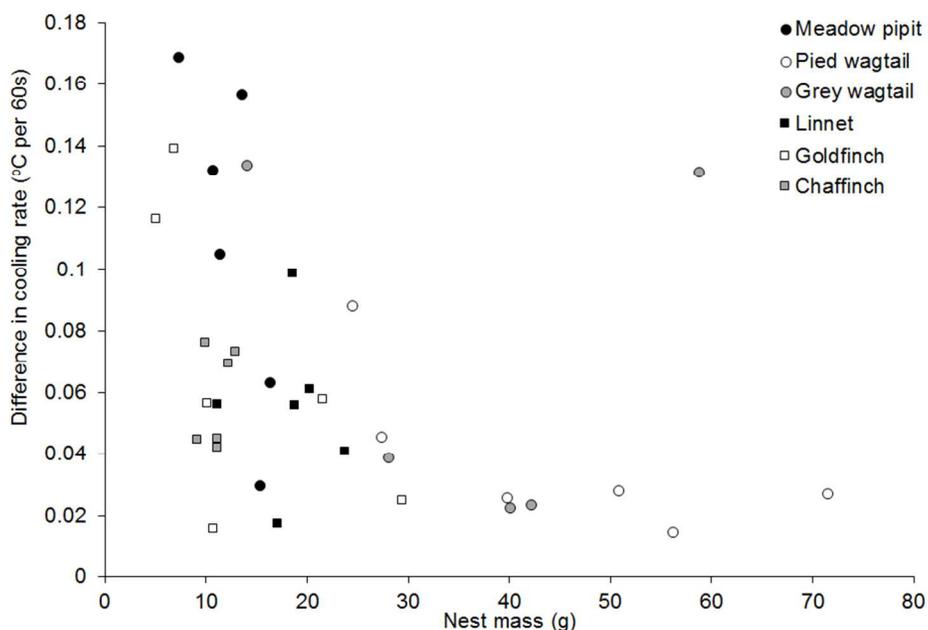


Figure 3. Relationship between nest mass and the difference in cooling rate of the temperature logger within the nest between still and moving air for all species combined. Values for individual nests are identified by the symbols indicated.

262x170mm (96 x 96 DPI)

Review