Material type and position determines the insulative properties of simulated nest walls

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Keywords – feathers; hair; insulation; nest materials; plant materials; thermal conductivity
Reading header – Thermal properties of artificial nest walls
Word count – 4117
Type of article – Short Communication
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Author contributions – DCD and LEB devised the study; LEB collected data; All authors analysed and interpreted data and contributed to writing the manuscript.

Summary

Incubation in birds takes place within a nest that is often assumed to confer a degree of thermal insulation. The range, amounts and organisation of materials used to construct nest walls hampers our understanding of the degree to which they provide insulation during incubation. This experimental study used temperature loggers in a model system to test the insulative properties of materials extracted from bird nests to determine: 1) whether differences existed in terms of insulation, and, 2) if the position of a material mattered when two materials were tested in combination. Animal-derived materials had better insulation than plant-derived materials, whether tested singly or in combination. Halving the mass of each material did not affect insulation conferred by the material proximal to the temperature logger. Differing thermal conductivities of the materials in contact with the temperature logger may explain these results. If a bird strategically places an animal-derived material only into a nest cup lining then it may be sufficient to provide good insulation for the whole nest. More research is needed to generate thermal conductivity data for commonly used nest materials to test this idea more rigorously in finite element heat transfer models.

Bird nests can be considered an extended phenotype that can affect fitness (i.e., overall lifetime reproductive success) because, among other things, the nest wall confers thermal insulation to the adult and incubating eggs (Deeming, 2016). Nest building is an energetically expensive process (Smith et al., 2012) and so the choice and placement of nest building material may be important in minimising the energetics of nest construction and maintenance. Contact incubation in birds is also an energetically expensive behaviour and factors that minimise energy loss from the eggs will help reduce the energetic impact on the incubating adult (Nord & Williams, 2015). Nest insulation increases with nest mass and wall thickness (also in mammals, e.g. Redman et al., 1999), and is affected by nest composition (Rohwer & Law, 2010; Mainwaring et al., 2014a; Gray & Deeming, 2017; Dickinson et al., 2019). Within a species, environmental temperatures during nest construction, due to latitude or altitude, negatively correlate with nest wall thickness and composition in birds (Kern, 1984; Rohwer & Law, 2010; Crossman et al., 2011; Mainwaring et al., 2012, 2014a; Altamirano et al., 2019) and mammals (Altamirano et al., 2019).

Our understanding of the roles different materials play in determining nest wall insulation is hampered by inter-species variation in constructing a nest that is typically a composite structure with a variety of materials (Deeming & Mainwaring, 2015; Biddle et al., 2018a). It is further complicated by intra-specific plasticity in nest construction as influenced by, for instance, environmental temperature (Mainwaring et al., 2014a). This high level of variation is making it difficult to tease apart those factors that are important in determining nest construction behaviour. Nests constructed using very different materials often have very similar insulative properties (Crossman et al., 2011; Biddle, 2018; Dickinson et al., 2019). Materials commonly used in nests have differing insulative properties, with animal-derived materials, e.g. feathers, being better insulators than plant-derived materials, e.g. dry grass (Hilton et al., 2004). Nest construction in small passerine species is not a random process because animal-derived materials are more often found in the cup lining, rather than the outer wall (Møller, 1984; Hansell & Ruxton, 2002; Biddle et al., 2018a; Dickinson, 2018). However, it is unclear to what extent this spatial distribution of materials has upon the insulation of the nest wall as a whole, and thus its adaptive nature. We do not know how nest wall insulation is affected, if at all, by the relative position of materials in the nest; if all other things are equal, is there an additive effect on nest insulation such that it doesn't matter if, for instance, feathers line the cup or the outer nest surface?

The physical complexity of the materials used in the nest is not the only issue in better understanding nest insulation. During incubation (or experimental testing) the flow of heat in nest materials could occur by a variety of mechanisms including conduction, convective heat transfer from the cup, direct radiation, and evaporation-condensation in the presence of moisture (Heenan & Seymour 2012). In an attempt to disentangle the role of various materials, and the different mechanisms of heat movement, in determining nest insulation, this study sought to simplify the nest by creating standardised artificial nest walls comprising of either one or two materials. This experimental manipulation sought to focus on assessing heat flux by conduction through direct contact with dry nest materials.

This study used materials previously collected from deconstructed passerine nests to determine the individual thermal characteristics of each material in a standardised, simulated nest wall. Thereafter, to investigate whether stratification of materials in a nest wall has any functional role in insulation, two different nest materials were tested in equal masses to determine whether the position of the material relative to a temperature measuring device was important in determining thermal properties of the whole structure. We predicted that the experiment would confirm that animal-derived materials are better insulators than plant-derived materials. Given that bird nests are layered structures, we also predicted that the proximity of a material to the temperature logger would be important.

Several previously deconstructed nests, of a variety of passerine species (e.g. thrushes [Turdidae], and finches [Fringillidae]), yielded feathers, hair, moss, grass, leaves, lichen and roots, which are the most common components of nests of small passerines (Deeming & Mainwaring, 2015; Biddle et al., 2018a; Dickinson, 2018). These materials were derived from numerous (at least 5 and up to 10-15 nests for some materials, such as feathers) nests, and were stored dry, irrespective of species, in paper bags at room temperature. To create a simulated nest wall, 5 g of material was loosely placed so that it completely filled a cardboard tube (102 mm long and 46 mm diameter) with an open plastic mesh attached to the bottom end to prevent the material from being lost.

Twelve, 5 mm deep, 16 mm diameter circular wells, each accommodating an iButton® temperature logger (with an accuracy of ± 0.5ºC), were drilled spaced 55 mm apart in a sheet of 10 mm thick expanded polystyrene (Figure 1), measuring 345 by 255 mm. Temperature loggers were set to record the temperature (°C) every minute prior to being heated to 80°C in a water bath and then dried with a paper towel before being placed in the wells. A cardboard tube filled with nest material was placed centrally on top of each of 11 temperature loggers and the twelfth was left open to the air. The cardboard tubes were weighed down using a 1 Kg metal grid and the experimental set up was left for 20 minutes for the temperature loggers to cool down. This procedure was repeated three times for each tube of material and there were 10 tubes per material type or combination of two materials.

The procedure took place within the closed test chamber of a custom-built wind-tunnel (Gray & Deeming, 2017) so as to minimise the effects of air movement on the cooling rate of the isolated temperature logger (Deeming & Campion, 2018). There was a temperature logger placed on the sidewall of the chamber to record the air temperature during the experiment.

Cooling rates were recorded in a similar way to that reported by previous authors (McGowan et al., 2004; Mainwaring et al., 2012, 2014a). Cooling rates ($^oC \cdot min^{-1}$) of the pre-heated temperature loggers were determined by fitting the temperature data to a logistic model (McGowan et al., 2004; Mainwaring et al., 2012). The difference in cooling rate (ΔCR) of each artificial nest was the difference in the rates of cooling ($^oC \cdot min^{-1}$) of the temperature logger under the material filled tube and of the exposed control temperature logger (*sensu* McGowan et al., 2004; Mainwaring et al., 2012, 2014a), with larger values indicating better insulation.

The first experiment used 5 g of an individual material in the tube placed over the temperature logger. Each material was tested in 10 separate tubes with three repetitions per tube. Each test run involved 11 tubes containing materials, and an exposed logger, which was always in the centre position of the experimental set-up. In order to minimise trial effects, the materials in the tubes used in each test run were randomly chosen. Thus, any one run had a mixture of materials being tested at the same time.

The second experiment paired four combinations of materials based on the results of the first experiment. Feathers were paired with grass, and with roots, and hair was tested with lichen, because these materials exhibited significant differences in ΔCR. Hair and moss were also tested because they did not show significant differences in mean ΔCR. For each pair of materials, 2.5 g of the one material was placed in the lower half of the tube proximal to the temperature logger and 2.5 g of the second material was used to fill up the rest of the tube. After three replicates to determine ΔCR, the materials were carefully removed, their order reversed and the experiment was re-run.

The three repeat measurements for each tube were averaged and analysis was carried out on the 10 mean values for ΔCR for each material type or combination. Anderson-Darling tests showed that the datasets were normally distributed, so the effect of material on ΔCR was investigated using one-way analysis of variance (ANOVA), with Tukey *post hoc* pairwise comparisons run in Minitab (ver. 17; www.minitab.com). For combinations of materials, the data were combined with the values for the 5 g samples of the relevant materials prior to one-way ANOVA tests.

Animal-derived materials had the highest ΔCR values (Figure 2), which were significantly greater than all plant-derived materials ($F_{6,63} = 11.34$, $P < 0.001$, $R^2 = 51.9\%$; Figure 2), except for the differences between hair, moss and grass which were non-significant. The degree of insulation offered by roots was approximately half that offered by feathers (Figure 2).

For combinations of materials, if the animal-derived material was proximal to the temperature logger then the ΔCR was always significantly higher than when the plant-derived material was proximal to the logger (Figure 3). Differences in cooling rates for the 2.5 g of the material proximal to the temperature logger were not significantly different from the values for 5 g of the same material.

Therefore, the combination of material significantly affected differences in cooling rates for feathers and grass (Figure 3A; $F_{3,36} = 17.9$, $P < 0.001$, $R^2 = 59.9\%$), although whether there was 2.5 or 5 g of feathers proximal to the temperature logger had no effect on ΔCR. This same pattern was observed for combinations of lichen and hair (Figure 3B $F_{3,36} = 9.8$, $P < 0.001$, $R^2 = 44.9\%$) and feathers and roots (Figure 3C, $F_{3,36} = 44.0$, $P < 0.001$, $R^2 = 78.45\%$). Differences in cooling rates for 5 g of either hair or moss were not significantly different (Figure 2), and the effect of switching these materials was much less than for other materials. However, having hair proximal to the temperature logger did produce a significantly greater ΔCR than having moss proximal to the logger when the materials were used in combination (Figure 3D; $F_{3,36} = 4.0$, $P = 0.015$, $R^2 = 24.8\%$).

Nests are composite structures consisting of differing amounts of animal-derived and plant-derived materials, depending on species (Hansell, 2000; Biddle et al., 2018a). Thermal insulation varied between different materials used in avian nests with, as expected, animal-derived materials having higher ΔCRs than plant-derived materials. We showed that halving the amounts of materials adjacent to the temperature logger had no effect on insulation compared with 5 g of the same material, although values were higher if the animal-derived material was proximal to the logger. Therefore, the contribution of each material in a combination does not seem to be additive and, even in a relatively simple combination, the effect on insulation is non-linear.

Differences in cooling rates for the different materials were lower than previously recorded values for actual nest walls from which the materials were derived (Gray & Deeming, 2017; Dickinson et al., 2019), which may reflect the fact that nests are much heavier than the 5 g of material used. The material in the simulated nest walls was loosely packed and this low density does not directly relate to how nest walls are constructed. Whilst differences in the insulative properties of materials used in nests have been reported previously (Hilton et al., 2004), our study demonstrated that the positioning of animal-derived materials relative to the heat source, i.e. the incubating bird sitting in the nest cup, may be important in determining the insulation value of the nest wall. More importantly, the mass of the material adjacent to the heat source was not a determinant of the degree of insulation. In whole nests, there seems to be variation in the significance of the intraspecific relationships between nest mass and insulation, with some bird species exhibiting no relationship (Deeming & Campion, 2018), whereas other species show significant positive relationships (Dickinson et al., 2019). Measures of insulation also seem to correlate with base thickness but not with wall thickness (Gray & Deeming, 2017; Dickinson et al., 2019) but other studies do report significant relationships with wall thickness (Heenan & Seymour, 2012; Akresh et al., 2017). Mass of *Microtis* vole nests also did not correlate with insulation but their wall thickness did (Redman et al., 1999). These differences, may reflect differences in the thermal inertia of the materials used in nests, or the mass range of the nests produced by a single species, but further research is required to better understand how nest mass and dimensions contribute to thermal insulation.

We know that birds place materials of differing structural characteristics in different parts of the nest according to their role (Biddle et al., 2017, 2018b). Eurasian bullfinches (*Pyrrhula pyrrhula*) position stronger woody stems in the base of their nest to help to support the nest built at the end of thin branches, while the hawfinch (*Coccothraustes coccothraustes*) builds its nest on top of a thick branch so the stronger woody materials are in the side walls (Biddle et al., 2018b). Other species have a predominance of animal-derived nest materials in their cup lining (Møller, 1984; Hansell & Ruxton, 2002); in the common chaffinch (*Fringilla coelebs*) nest the cup lining has large amounts of feathers and hair present (68% of cup lining by mass; Biddle et al., 2011a), whereas the nest of the common linnet (*Linaria cannabina*) is lined with a lot of hair (39% of cup lining by mass; Biddle et al., 2011a). Such differences in the distribution of materials may reflect the bird positioning particular materials within the cup that then may determine the insulative properties of the whole nest wall. Simply lining a nest cup with feathers may provide sufficient insulation for the incubating bird. Whilst feathers are assumed to be plentiful in the environment (Møller, 1984), limiting such animal-derived materials to the nest cup may have a positive impact on the energetic demands of nest construction. Further research should investigate the minimum amount of a well-insulating material before insulation is compromised in a model system, and then test whether this value reflects what is found in real nests.

Nest materials confer a physical structure to the nest wall that can trap air, which can serve as an insulator. Vacuum-packing whole bird nests reduces the insulation of the nest wall by 20-25% despite a 90% reduction in volume (Deeming & Biddle, 2015). During incubation and particularly nestling rearing the nest materials get compressed which may impact on the amount of insulation provided by air gaps in the structure. Although materials density was controlled in this study, the materials were relatively loosely packed and we can assume that the level of insulation provided by air gaps was similar for all materials. Future research could explore the effects of reducing the density and, hence the amount of air, on the insulation conferred by the materials.

We acknowledge that the material was dry and ‘used’, having been derived from nests, but this did apply to all materials studied. It would be interesting to repeat this study with fresh materials from nests under-going construction because some plant-derived materials, e.g. moss, leaves and grass, will have a higher water content that could affect thermal conductivity. However, other materials, e.g. feathers, hair, twigs, have little water content and so would not exhibit big differences to our results. Not unsurprisingly, if nest materials are wet (Hilton et al., 2004), or a whole nest is wet after being rained upon (Deeming & Campion, 2018), insulation is decreased compared to dry conditions. The effects of air humidity on the insulative properties of dry materials can be assumed to change but to date these effects have not been quantified.

Given the standardised experimental design that minimised convection and cooling associated with evaporative-condensation (materials were dry), we have interpreted our results as primarily reflecting the differences in the thermal conductivity of the various materials tested. Those materials with low thermal conductivity, e.g. feathers (0.034 $W \cdot m^{-1} \cdot K^{-1}$; Fuller, 2015), will confer better insulation than those with higher values, e.g. dry leaves (0.27–0.50 $W \cdot m^{-1} \cdot K^{-1}$; Jayalakshmy & Philip, 2010). Unfortunately, there is a general lack of data for thermal conductivity of the materials used in this study but the patterns of insulation shown here suggest that, when measured, thermal conductivity of plant roots will be higher than that of moss. Knowledge of the thermal properties of nest materials will allow finite element heat transfer models to be developed to predict the rate of heat loss through the nest wall. Such models can then be compared to empirical data to help us to understand the impact of nest composition on insulating properties of the nest wall.

Further studies will allow a better understanding of the factors that have affected the evolution of nest construction and function within passerines and non-passerines alike. It is unlikely that nest construction is solely based on thermal considerations but will include the effects of other environmental factors, such as precipitation (Biddle et al., 2019) and air movement (Gray & Deeming, 2017; Dickinson et al., 2019). There are likely to be other factors, such as minimising predation, and possible signalling roles (Mainwaring et al., 2014b), that will impact upon nest construction and thereafter individual reproductive performance and fitness.

Acknowledgements.

We thank Greg Sutton, Roger Jovani and anonymous reviewers for commenting on previous drafts.

Conflict of interest

The authors declare that they have no conflict of interest.

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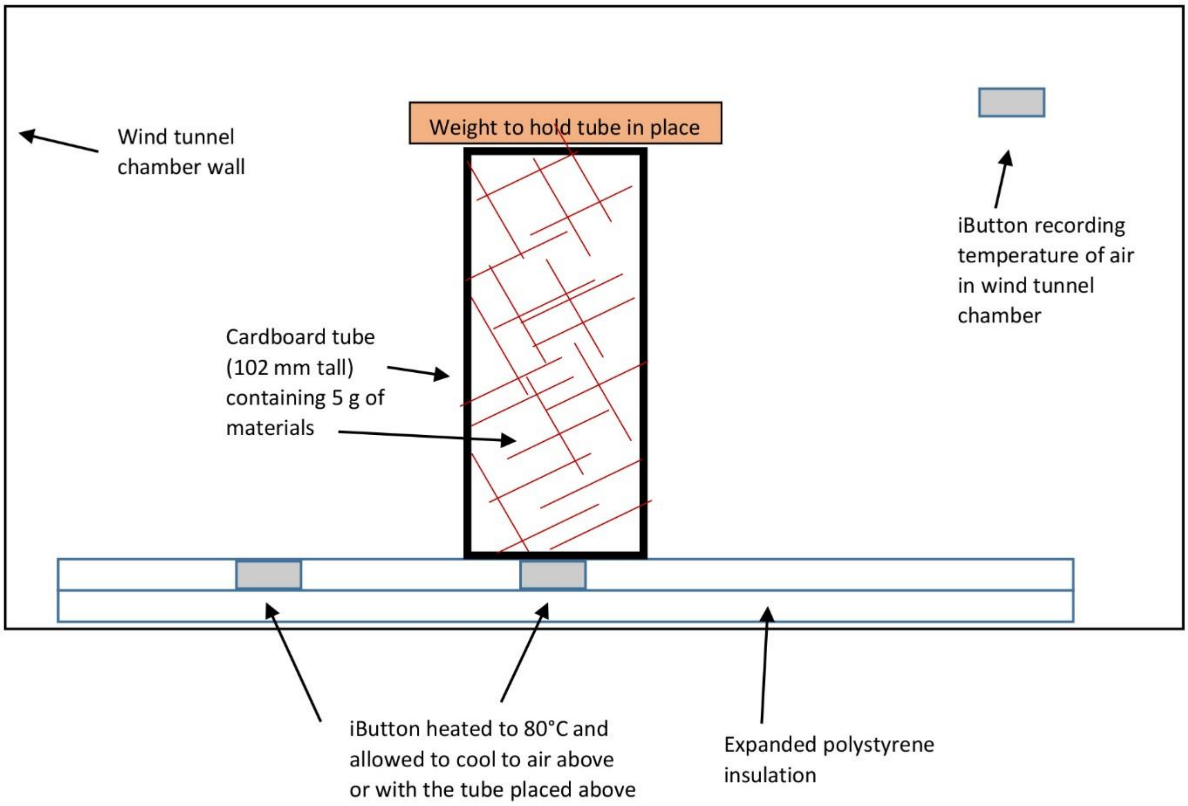

Figure 1. Diagrammatic illustration of the experimental set to indicate the positioning of the cardboard tube over the temperature logger. Each run of the experiment involved 11 tubes, containing a variety of different materials tested simultaneously in a closed wind tunnel (no air flowing) to minimise effects of extraneous air-flow.

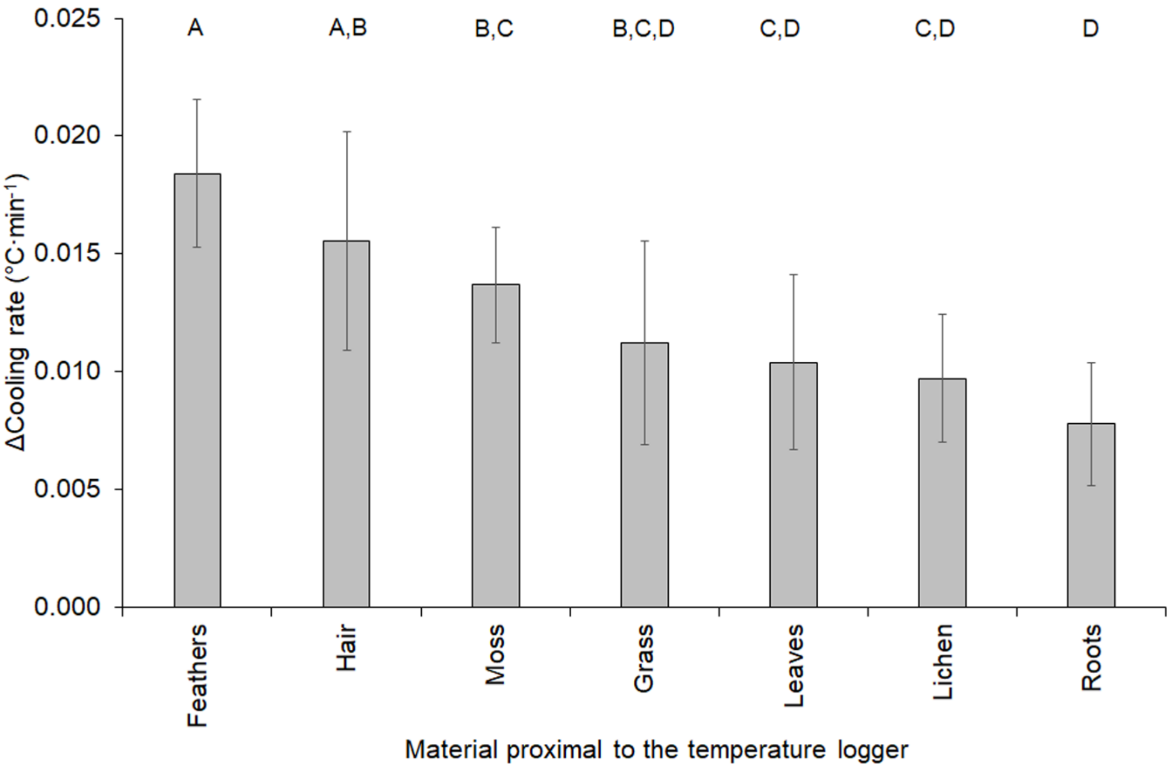

Figure 2. Mean (± SD) values for differences in cooling rate between an isolated temperature logger and a temperature logger covered with a cardboard tube filled with 5 g of the material shown. Columns that do not share a common letter are significantly different at α = 0.05.

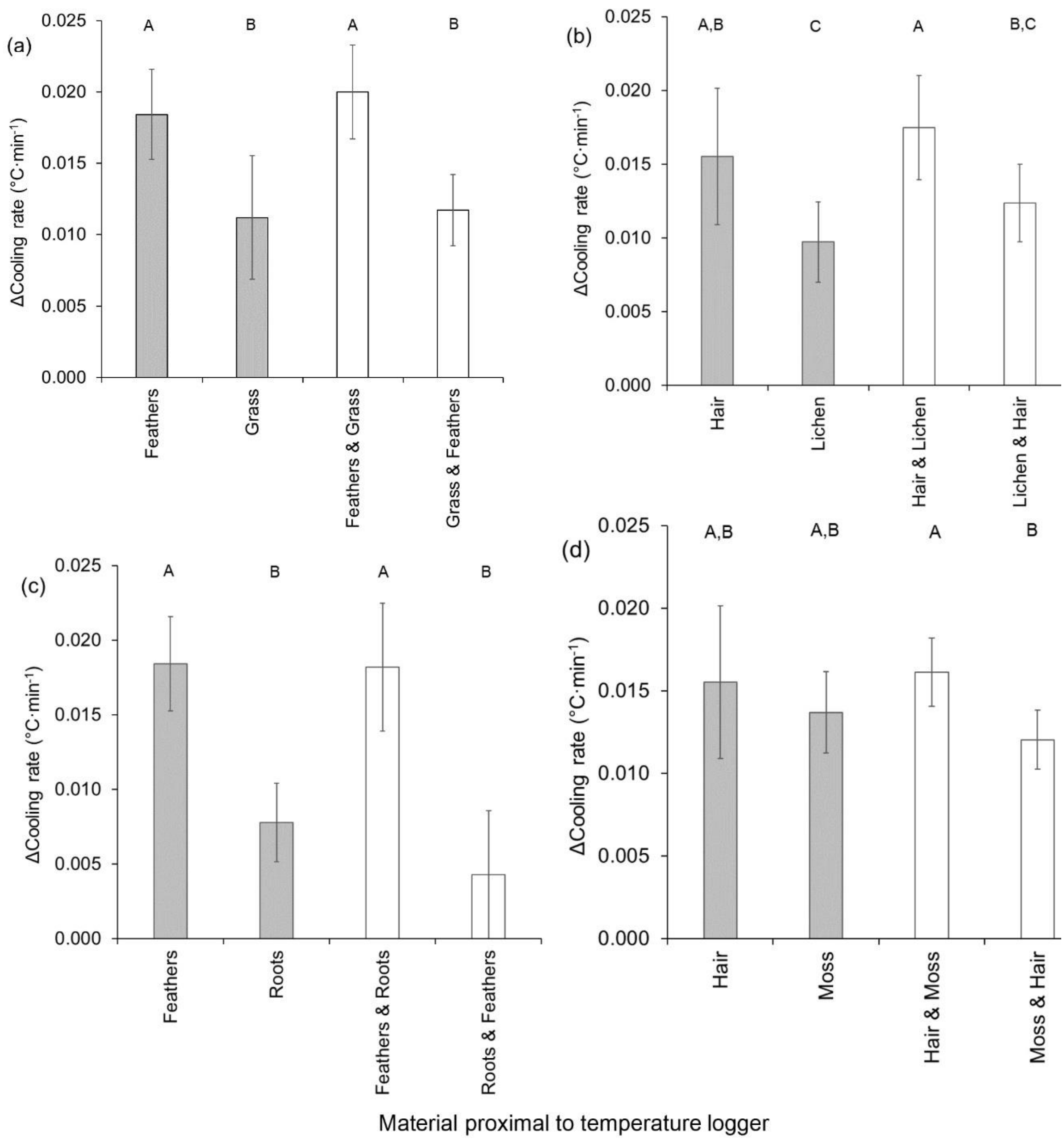

Figure 3. Mean (± SD) values for differences in cooling rate between an isolated temperature logger and a temperature logger covered with a cardboard tube filled with the material(s) shown. The first mentioned material was proximal to the logger. Grey columns indicate values from Figure 2. Columns that do not share a common letter are significantly different at $\alpha = 0.05$.