

Domed nests do not offer additional environmental protection in some songbirds

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Abstract Nest architecture in birds is highly variable ranging from simple scrapes through to elaborate woven constructions. In species that nest in open situations the nest can have a cup open to the elements or the nest has a dome positioned over the cup. The functional properties of domed nests have yet to be explored and this study compared the thermal insulation and rainproofing properties of nests built by four species of European songbird, two of which build domed nests whereas the others build open cup nests. Insulatory values were recorded using temperature loggers. Nests were exposed to a simulated rain event and the amount of water absorbed and the minutes for the nest to dry were determined. The nests were then deconstructed into their component parts. Materials used to build the nests differed among the species. Differences in thermal insulation were associated with the species and the size of the nest. The amount of water absorbed by a nest during a simulated rainfall event was negatively associated with the size of the nest. Feathers and moss had significant positive effects on thermal insulation and rainproofing, respectively. There was no significant difference between domed and open nests in terms of thermal insulation or rainproofing, except for the time taken for a nest to dry, which showed a significant interaction between nest mass and type of nest. Insulatory values and degree of rainproofing were like data from previous reports for songbird nests of comparable size. That no differences observed between domed and open cup nests in the species studied may reflect similarity among species, although it may be due to a paucity of data from a wider range of species building domed nests.

Keywords: cup nest, domed nest, insulatory value, Long-tailed Tit, Northern Wheatear, rainproofing, Reed Bunting, Wood Warbler

Összefoglalás A madárfészkek formája és szerkezete igen változatos, az egyszerű kaparékoktól a bonyolultan szövött szerkezetekig terjed. A nyílt helyen fészkelő fajoknál a fészkek lehet az időjárásnak jobban kitett nyitott csésze vagy a csésze fölött kupola helyezkedhet el. A kupolás fészkek funkcionális tulajdonságainak feltáráshoz még további vizsgálatok szükségesek. Ez a tanulmány négy európai énekesmadárfaj fészkeinek hőszigetelő és esőszigetelő tulajdonságait hasonlította össze, amelyek közül két faj kupolás fészket, míg a másik kettő nyitott fészket épít. A szigetelési értékeket hőmérséklet-nyilvántartó készülékekkel rögzítettük. A fészkeket szimulált esőzésnek tettük ki, és meghatároztuk a felszívódó víz mennyiségét, valamint a fészkek száradásához szükséges időt. Ezután a fészkeket alkotóelemeikre bontottuk. A fészkek építéséhez használt anyagok a fajok között különböztek. A hőszigetelésben mutatkozó különbségek a fajhoz és a fészkek méretéhez kapcsolódtak. A fészkek által egy szimulált esőzés során elnyelt vízmennyiség negatívan függött a fészkek méretétől. A tollak és a moha jelentős pozitív hatást gyakoroltak a hőszigetelésre, illetve az esőszigetelésre. Sem a hőszigetelés, sem az esőszigetelés tekintetében nem volt szignifikáns különbség a kupolás és a nyitott fészkek között, kivéve a fészkek száradási idejét, amely szignifikáns kölcsönhatást mutatott a fészkek tömege és a fészkek típusa között. A szigetelési értékek és az esőszigetelés mértéke megegyezett a hasonló méretű énekesmadár fészkekben mért adatokkal. Az, hogy a vizsgált fajoknál nem észleltünk különbséget a kupolás és a nyitott fészkek között, a fajok közötti hasonlóságot tükrözheti, bár lehet, hogy ez a kupolás fészket építő fajok szélesebb köréből származó adatok hiányának tulajdonítható.

Kulcsszavak: csésze-alakú fészkek, esőszigetelés, hantmadár, kupolás fészkek, nádi sármány, őszapó, sisegő füzi-ke, szigetelési érték

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Introduction

Nest construction is a critical aspect of successful reproduction in birds because it is the location for incubation (Deeming 2016) and, in many cases, rearing of chicks through to fledging (Deeming 2023). Whether reproduction is successful will depend on, *inter alia*, the nest minimising energy loss, providing protection from adverse environmental conditions and from possible predation, and remaining physically secure during incubation and rearing (Hansell 2000, Deeming 2023). Over recent years there have been many studies that have explored the key role of the materials used to construct songbird nests in terms of maintaining structural integrity (Biddle *et al.* 2017, 2018b), providing thermal insulation (Crossman *et al.* 2011, Mainwaring *et al.* 2012, 2014, Deeming *et al.* 2020a), maintaining an appropriate nest humidity (Deeming *et al.* 2020b), and providing adequate protection from rainfall (Biddle *et al.* 2019). Despite these studies, our understanding of functional properties of nests remains limited to relatively few species of songbirds despite the observed diversity in nest architecture (Hansell 2000, Deeming 2023).

For thermal insulation, studies have mainly focussed on European species that build cup nests in open environments or, in a few cases, in cavities (see Deeming *et al.* 2020). However, many passerine species build domed nests, which may have been the primitive condition for nest architecture (Price & Griffith 2017). Several macroecological studies have suggested that a domed nest confers an advantage to the species that this is linked to reduced predation and increased environmental protection (Hall *et al.* 2015, Medina *et al.* 2022, Vanadzina *et al.* 2024). A nest cup with a domed roof could potentially offer increased protection against heat loss, increase waterproofing of the cup, or hide the incubating bird, its eggs and/or chicks from predators approaching the nest from above. For instance, Duursma *et al.* (2018) found that in Australia domed nests were more prevalent in hotter, drier regions and likely provided shade to the nest contents where there were sparse plant canopies. Indeed, Zebra Finches (*Taeniopygia guttata*) appear to modify their nest architecture to ameliorate the effects of high environmental temperatures (Griffith *et al.* 2016). Moreover, the pendent nests of some weaverbird (Ploceidae) and icterid (Icteridae) species may offer structural and environmental protection to the eggs and chicks (Street *et al.* 2022). Comparing temperate and tropical locations, Martin *et al.* (2016) concluded that enclosed nests offered important thermal benefits compared with open nests, but this conclusion was only based on indirect evidence associated with factors such as nest size and presumed cooling rates of eggs. All these things could confer an advantage to the parent or its offspring during incubation or chick rearing, although Humphries *et al.* (2007) found that a domed nest seemed to offer no advantage with respect to protection from predation of flooding to clutches of Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*). The studies above all offer only indirect evidence that domed nests confer an advantage to the birds that build them and to date there has been no study that has tested the thermal properties of domed nests in the same way as

for open-nesting species (Deeming *et al.* 2020a). Developing a better appreciation of the functional properties of domed nests could improve our understanding of variation in nest architecture is being exploited by birds when reproducing.

This study describes the detailed composition of domed nests from two species of European passerine in comparison with two species of European passerine that build open cup nests. Data are available for insulatory values for all species except the Northern Wheatear (*Oenanthe oenanthe*) although methodologies vary among studies (Deeming *et al.* 202a). Limited data are available for composition of the Long-tailed Tit (*Aegithalos caudatus*) nest (Hansell 2000, McGowan *et al.* 2004) but this falls short of other more detailed studies of nest composition (e.g. Biddle *et al.* 2018a, Briggs & Deeming 2016, 2012, 2022, Dickinson *et al.* 2022). There are no compositional data for the other species in this study, which determined values for thermal insulation as an insulatory value (McGowan *et al.* 2004, Deeming *et al.* 2020a), and measures of the degree of rainproofing, i.e. water absorbed and minutes to dry (Biddle *et al.* 2019), were also determined for all nests. The effect of species was explored in the analysis but the main hypotheses were that: (1) the roof of the domed nests would offer more physical protection and so provide better thermal insulation and rainproofing than open nests; and (2), as has been demonstrated in other nests of songbirds, amount of materials, such as feathers, would contribute to thermal insulation, whereas amounts of moss would be associated with the degree of rainproofing during a simulated rain event. Data on detailed nest composition could also help improve our understanding of factors that affect the degree of inter- and intra-specific plasticity in nest construction.

Methods

Data were collected for nests from four species of passerine bird: two species that build domed nests, i.e., the Long-tailed Tit (*Aegithalos caudatus*, Aegithalidae; body mass = 8.6 g; n = 17 nests) and the Wood Warbler (*Phylloscopus sibilatrix*, Phylloscopidae; body mass = 9.2 g; n = 5), and two species that build open cup nests, i.e. the Northern Wheatear (*Oenanthe oenanthe*, Muscicapidae; body mass = 24.0 g; n = 7) and the Reed Bunting (*Emberiza schoeniclus*, Emberizidae; body mass = 17.2 g; n = 8). The Long-tailed Tit nests were all collected in Sheffield, South Yorkshire, Great Britain, during 2021 but the other nests were supplied from various locations within Great Britain between 2013 and 2021. Prior to being tested, all nests were stored dry in plastic bags kept in cardboard boxes held at room temperature and humidity.

Thermal insulation of the nests was determined using temperature loggers (McGowan *et al.* 2004, Mainwaring *et al.* 2012, 2014, Deeming & Gray 2016, Deeming & Campion 2018, Deeming *et al.* 2020a). Briefly, for open nests, a temperature logger heated in a water bath to a temperature of 80 °C (iButtons, Maximintegrated.com, accuracy ± 1 °C from -30 °C to $+70$ °C in 0.5 increments) was placed on a small polystyrene plinth and the nest was placed upside down over the logger so that it contacted the base of the nest. A second logger heated at the same time was placed on a similar plinth next to the nest. Data collection took place within a closed box (which contained a third, unheated logger that recorded the temperature

in the box during the experiment) that controlled for air movements as the loggers cooled (Gray & Deeming 2017). For the domed nests, the heated logger was pushed through the entrance hole into the depths of the nest and a block of polystyrene was pushed into the nest cavity to hold the logger next to the nest wall. Otherwise, the domed nests were treated in the same way as the open cup nests. The difference in cooling rates of the two loggers (i.e. the one under or in the nest and the one adjacent to the nest) was the insulatory value (IV in $^{\circ}\text{C}\cdot\text{min}^{-1}$) (McGowan *et al.* 2004). For each nest, data were collected three times and the mean IV calculated, with larger values indicating better insulation.

Each nest was weighed (in g) using an electronic balance (Sartorius) prior to being exposed to simulated rainfall using the method described by Biddle *et al.* (2019). Briefly, for nests of the Reed Bunting and Common Wheatear, a nest was placed in a metal household sieve placed over a bowl. To stimulate a rainfall event, 250 ml of water was poured into a plastic cup with holes in its bottom, which was held and rotated about 30 cm above the nest. Water fell as droplets on to the nest for about three minutes and percolated through the nest wall to drain into the bowl. A sheet of 3 mm thick polystyrene was cut to the shape of the nest cup and placed over the cup to exclude water during the simulated rain. After draining at room temperature ($\sim 22^{\circ}\text{C}$) and humidity ($\sim 50\%$ RH) for 10 minutes from the start of the 'rainfall', nests were weighed. Thereafter, nests were kept at room temperature and humidity and weighed 1, 2, 4, and 6 hours after the rain event. The only difference for domed nests was that they were placed in the sieve with the opening to the interior of the nest facing downwards thereby preventing water from directly entering the nest cavity and pooling in the nest cup. The amount of water absorbed (WA) was determined by subtracting the original dry mass of the nest from its mass after 10 minutes. The WA value was also expressed as a percentage of the dry nest mass (%WA). The time in minutes taken for nests to dry out (MTD) was determined by using an exponential equation from Biddle *et al.* (2019) to predict when the nest returned to its original dry mass.

After thermal and rainproofing testing the nests were deconstructed into their component materials, which were allocated to either the outer nest wall or the cup lining (Biddle *et al.* 2018a). Nests were deconstructed by systematically pulling the nest wall apart with forceps and separating the various materials (Britt and Deeming 2011, Biddle *et al.* 2018a, Dickinson *et al.* 2022). Materials, such as droppings or bones of dead neonates, were considered as being added to the nest after initial construction so dry nest mass (in g) was determined after deconstruction by summing all the materials deemed to be part of the original nest. There were three categories for animal-derived materials: feathers, hair, and invertebrate silk. Plant-derived materials were separated into: grass (including reed leaves), moss, leaves, lichen, bark, roots, and plant stems (woody and more flexible stems combined). Any mineral material was classified as mud.

Prior to analysis, to ensure that values of zero (for example, many nests lacked certain nest materials) could be analysed, all data values had 1 added before being $\log_{10}$ -transformed. Linear modelling performed in R version 2.4.3 (R Core Development Team 2023) tested for effect of species on the variables of interest, including nest materials, IV, WA, etc. Analysis of covariance tested for the effects of species as a fixed factor and total nest mass as a covariate using linear models in R. Where there was a significant effect of species pairwise

comparisons were conducted (with Bonferroni correction) to identify where significant difference lay. A linear model was also used to determine the effects of the different nest materials on IV or measures of rainproofing; the model included all material types and was applied to data for all nests irrespective of species.

Linear mixed effects regression analysis was carried out in R using the R packages *lme4* (Bates *et al.* 2015) and *lmerTest* (Kuznetsova *et al.* 2017) to test for the effect of total nest mass as a covariate and type of nest (i.e., domed versus open) as a fixed factor, on insulatory value and measures of rainproofing. Species was included as a random factor in the model.

Results

On average, the masses of the nests were similar for the four species. Although Long-tailed Tits built the heaviest nest (*Figure 1*), the differences between species were significant ($F_{3,33} = 2.92$, $P = 0.048$; $R^2 = 0.21$) and none of the pairwise comparisons were statistically significant (*Figure 1*). The outer nest formed the bulk (65–77%) of the total nest mass but was significantly affected by species ($F_{3,33} = 6.68$, $P = 0.001$; $R^2 = 0.38$). This effect was due to data for the Northern Wheatear nests where the outer wall was only ~50% of the total mass, which was significantly lower than values for the Long-tailed Tit and Wood Warbler (*Figure 1*). Similarly, cup lining mass was significantly affected by species ($F_{3,33} = 6.58$, $P = 0.001$; $R^2 = 0.37$) with the cup lining of Reed Bunting nests being significantly lighter in mass from that of the Long-tailed Tit and Northern Wheatear (*Figure 1*).

Not all materials were found in nests, nor in the outer nest, nor in the cup lining, of all species (*Figure 2*). Reed Bunting nests were dominated by grass in the outer nest and the cup lining (*Figure 2*). Northern Wheatear nests were characterised by a large amount of hair found in the cup lining with a range of plant materials in the outer nest (*Figure 2*). Long-tailed Tit nests had a lot of moss and lichen (especially *Parmelia sulcata*, *Parmelia subaurifera*, and *Xanthoria parietina*) held together by silk in the outer nest but the cup lining was almost all feathers, which were largely absent in the other species' nests (*Figure 2*). It was interesting to note that simulated rainfall hydrated the moss and lichen on outside of Long-tailed Tit nests changing the colour to a dull grey-green to a more vibrant green within only a few seconds (DCD *per. obs.*). Wood Warblers built nests that had a wide range of plant materials but had no animal-derived materials present (*Figure 2*). This distribution of materials meant that linear models used to make among-species comparisons showed that mass of all the material categories was significantly affected by species (*Table 1*).

Insulatory value was higher for Long-tailed Tit nests compared with the other species and there was a significant effect of species ($F_{3,33} = 9.64$, $P < 0.001$; $R^2 = 0.47$) with significant pairwise differences between the Long-tailed Tits and the Reed Bunting and Northern Wheatear nests, but not Wood Warbler nests (*Figure 3*). Linear models to test for the effect of species did not show any significant effect of species on WA, %WA, or MTD ($F_{3,33} = 2.09$, $P = 0.12$; $R^2 = 0.16$; $F_{3,33} = 0.48$, $P = 0.700$; $R^2 = 0.04$; and $F_{3,33} = 1.58$, $P = 0.213$; $R^2 = 0.13$, respectively).

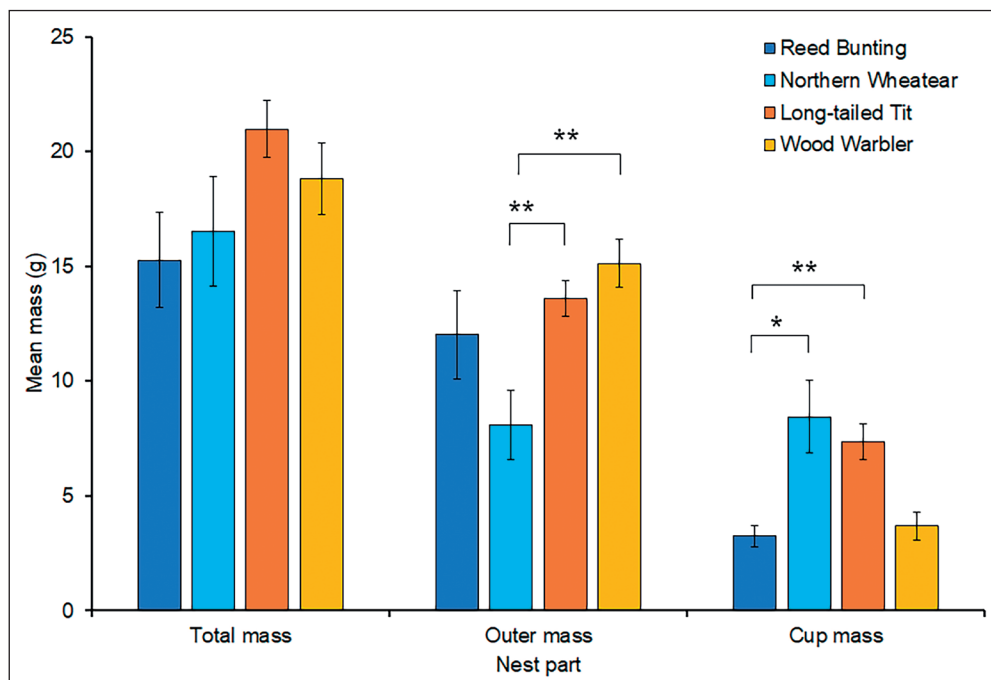


Figure 1. Mean ($\pm$ SE) values for total nest mass, outer nest mass and mass of the cup lining for the species studied. Blue columns indicate species that have open nests with orange/yellow columns indicating species with domed nests. Significant ($P < 0.05$) differences between species are indicated by brackets and * above the relevant columns. Other comparisons between columns were not significant

1. ábra A fészkek teljes tömegének, a fészkek külső tömegének és a csésze bélése tömegének átlagértékei ($\pm$ sztenderd hiba) a vizsgált fajoknál. A kék oszlopok a nyitott fészkek fajokat, a narancssárga/sárga oszlopok a kupolás fészkek fajokat jelölik. A fajok közötti szignifikáns ($P < 0,05$) különbségeket zárójel és * jelzi a vonatkozó oszlopok felett. Az oszlopok közötti egyéb összehasonlítások nem voltak szignifikánsak

Given this result, further linear models were run to test for the effect of total nest mass, species, and any interaction. For IV, there was a significant effect of species and total nest mass plus there was a significant interaction between these two terms (Table 2). By contrast, both WA and %WA were significantly affected by total nest mass but not species and there was no significant interaction (Table 2). Values for MTD were unaffected by nest mass or species and there was no significant interaction (Table 2).

To test for the type of nest on IV or WA, linear mixed effect modelling showed that there was no effect of total nest mass or nest type with no significant interaction (Table 2). By contrast, the total nest mass exhibited a significant negative relationship with %WA (Figure 4) but there was no significant interaction with nest type (Table 2). For MTD, type of nest was significant as was the interaction with total nest mass (Table 2); domed nests had higher values for MTD as nest mass increased but for open cup nests this relationship was negative (Figure 5).

Linear models showed that different nest materials contributed to IV and the various measures of rainproofing. For IV, the mass of feathers was the most significant covariate but

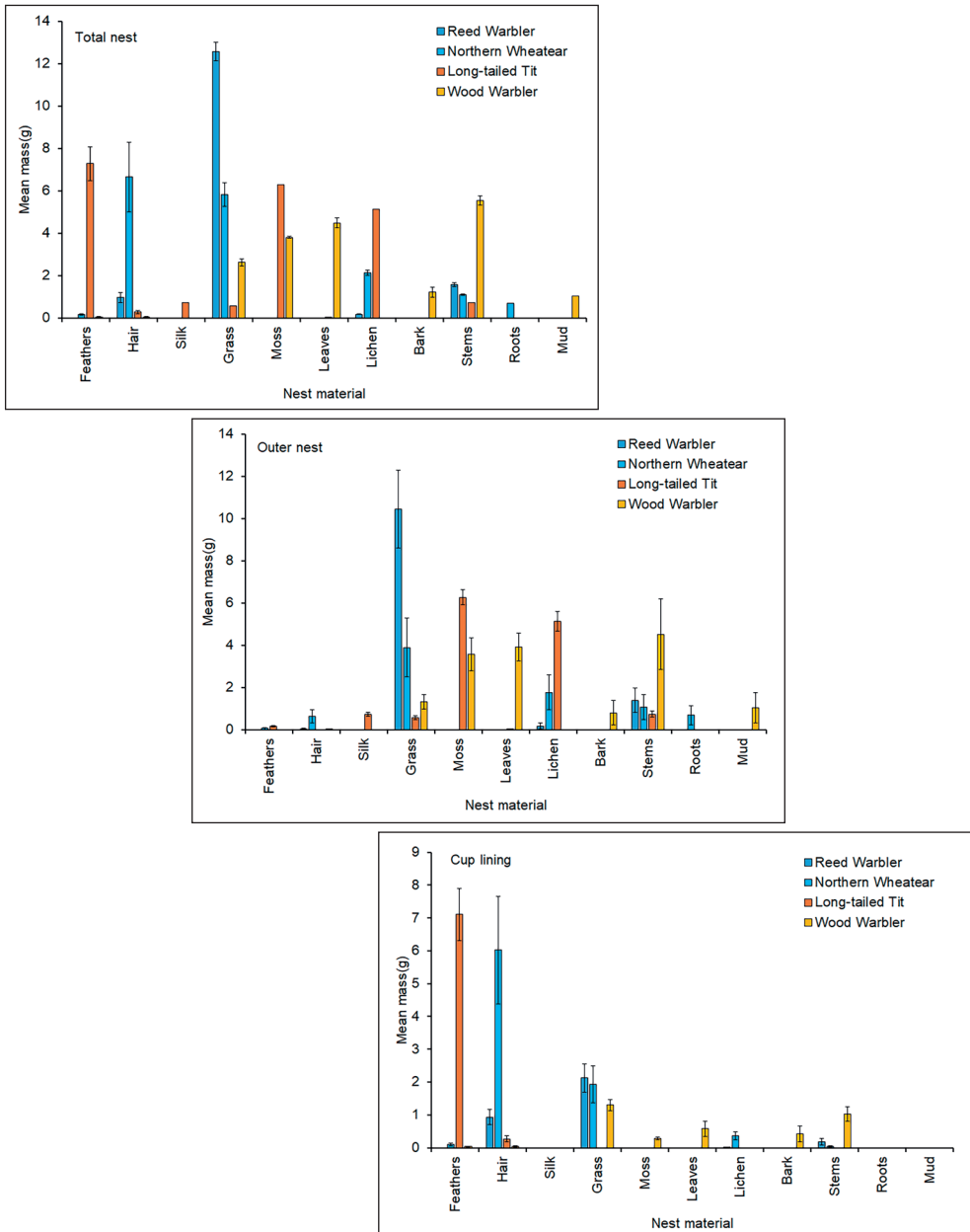


Figure 2. Mean ($\pm$ SE) values for the eleven categories of materials found in the total nest (top panel), the outer nest (middle panel) and the cup lining (bottom panel) for four species of songbird. Blue columns indicate species that have open nests with orange/yellow columns indicating species with domed nests

2. ábra A teljes fészkekben (felső panel), a fészkek külsejében (középső panel) és a csésze bélésében (alsó panel) található tizenegy anyagkategória átlagos ($\pm$ szterderd hiba) értékei négy énekesmadárfaj esetében. A kék oszlopok a nyitott fészű fajokat, a narancssárga/sárga oszlopok a kupolás fészű fajokat jelölik

Table 1. Results of analysis of variance to test the significance of species as a categorical factor on log₁₀-transformed data for the various nest materials found in the total nest, the outer nest wall, and the cup lining. R² = coefficient of determination

1. táblázat A faj mint kategorikus tényező hatásának vizsgálatára szolgáló varianciaanalízis eredményei a teljes fészket, a külső részt és a csésze bélését felépítő különböző anyagok log-transzformált adatainak felhasználásával. R² = determinációs együttható

Nest material	Total nest		Outer nest		Cup lining	
	F _{3,33} (P-value)	R ²	F _{3,33} (P-value)	R ²	F _{3,33} (P-value)	R ²
Feathers	207.15 (< 0.001)	0.95	9.57 (< 0.001)	0.47	198.01 (<0.001)	0.95
Hair	55.19 (< 0.001)	0.83	10.54 (< 0.001)	0.49	36.31 (< 0.001)	0.77
Silk [#]	51.00 (< 0.001)	0.82	51.00 (< 0.001)	0.82	-	-
Grass	51.08 (<0.001)	0.82	41.31 (< 0.001)	0.79	24.39 (< 0.001)	0.69
Moss	296.63 (< 0.001)	0.96	271.88 (< 0.001)	0.96	115.71 (< 0.001)	0.91
Leaves	323.59 (< 0.001)	0.97	271.95 (< 0.001)	0.96	22.28 (< 0.001)	0.67
Lichen	47.87 (< 0.001)	0.81	49.44 (< 0.001)	0.82	18.43 (< 0.001)	0.63
Bark	10.99 (< 0.001)	0.50	6.34 (0.002)	0.37	8.71 (< 0.001)	0.44
Stems	7.29 (0.001)	0.40	5.11 (0.005)	0.32	32.19 (< 0.001)	0.75
Roots [#]	3.50 (0.026)	0.24	3.50 (0.026)	0.24	-	-
Mud [#]	8.68 (< 0.001)	0.31	8.68 (< 0.001)	0.44	-	-

#dash (-) indicates no analysis because the component was absent in the cup lining.

amounts of hair, stems, roots, and mud also had significant effects (Table 3). By contrast, WA values were only significantly affected by the significant positive relationship with the mass of moss in nest (Table 3). None of the nest materials had any significant effect on %WA or MTD (Table 3).

Discussion

The materials used to build the nests of the four species were very different from each other. Differences in thermal insulation were associated with the species and the size of the nest whereas the amount of water absorbed by a nest during a simulated rainfall event had a negative relationship with the size of the nest. Contrary to expectations there was little effect of nest type, i.e. domed versus open cup, on thermal insulation or rainproofing and a range of materials significantly contributed to IV and WA but not for other measures of rainproofing. As predicted materials, especially feathers and moss, used in the nests had significant effects on thermal insulation and rainproofing.

Nest composition is a species-specific characteristic (Deeming 2023). Data for a range of passerine species show that whilst some closely related species, e.g., thrushes (Turdidae), can have similar nest compositions, other species that are closely related, e.g. finches (Fringillidae), can differ greatly in nest composition and architecture (Biddle *et al.* 2018a, Dickinson *et al.* 2020). Nest architecture for any species is broadly comparable among individuals, which means that a range of field guides for nests can be produced (e.g. Beruldsen

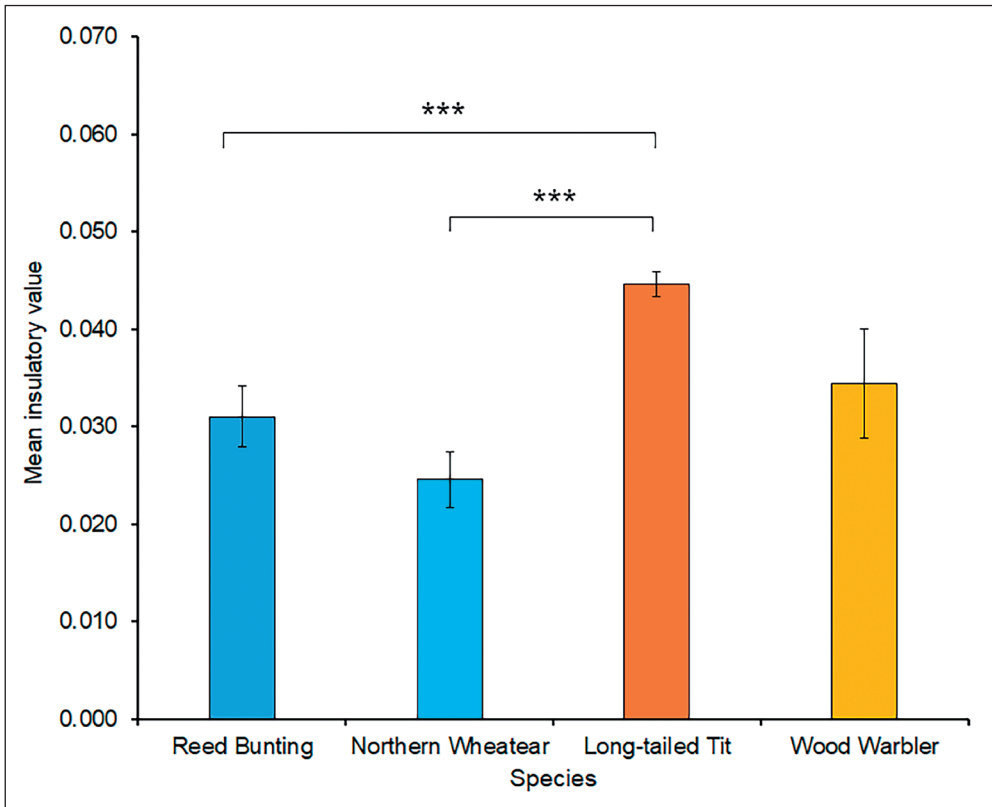


Figure 3. Mean ($\pm$ SE) values for insulatory value in four species of songbird. Blue columns indicate species that have open nests with orange/yellow columns indicating species with domed nests. Significant ($P < 0.001$) differences between species are indicated by brackets and *** above the relevant columns. Other comparisons between columns were not significant

3. ábra A szigetelési értékek átlagos ($\pm$ sztenderd hiba) értékei négy énekesmadárfajnál. A kék oszlopok a nyitott fészekű fajokat, a narancssárga/sárga oszlopok a kupolás fészekű fajokat jelölik. A fajok közötti szignifikáns ($P < 0,001$) különbségeket a zárójelek és a *** jelzi a vonatkozó oszlopok felett. Az oszlopok közötti egyéb összehasonlítások nem voltak szignifikánsak

2003, Ferguson-Lees *et al.* 2011, McFarland *et al.* 2021). However, choice of nesting material appears to be very plastic. For instance, intra-specific variation in nest composition can be affected by geographical location across several hundred kilometres (e.g. Crossman *et al.* 2011, Briggs & Deeming 2016), or locally across less than 10 km (e.g. Briggs & Deeming 2021, 2022). Indeed, when building a nest birds will take advantage of material types found nearby close at hand (Briggs & Deeming 2016, 2022) or use materials that resemble materials used previously, such as Pied Flycatchers (*Ficedula hypoleuca*) using plastic string instead of mammal hair (Briggs *et al.* 2023). For the Long-tailed Tit, nest composition described here was comparable to previous reports in terms of the birds using feathers to line the nest cavity (Hansell 2000, McGowan *et al.* 2004). However, the nest built almost entirely out of artificial insulation materials reported by Broughton and Parry (2020) rather than lichen, moss, and feathers, further highlights the plasticity of nest construction behaviour in birds. Nest

Table 2. Mean ($\pm$ SE) values for insulatory value, water absorbed 10 minutes after simulated rain, the amount of water absorbed expressed as percentage of nest mass, and the time in minutes that the nest was predicted to dry back to its original dry condition. At the base of each column there the results of (1) linear models to test for the effect of total nest mass as covariate, species as a fixed factor plus the interaction; and (2) linear mixed effects regression analysis using Satterthwaite's method that tested for the effect of total nest mass as a covariate, type of nest (domed versus open cup) as a fixed factor, and the interaction whilst controlling for species as a random factor. Significant values are highlighted in bold. For the linear model the F-value and R^2 = coefficient of determination for the model is included

2. táblázat A szigetelési érték, a szimulált eső után 10 perccel elnyelt víz, a fészek tömegének százalékában kifejezett elnyelt vízmennyiség és a száradási idő (percben kifejezve) átlagértékei ($\pm$ sztenderd hiba). Az egyes oszlopok alján (1) a fészek teljes tömege mint kovariáns, a faj mint fix tényező és a kettő kölcsönhatását vizsgáló lineáris modellek eredményei; és (2) a Satterthwaite-féle módszert alkalmazó lineáris kevert regressziós elemzés, amely a fészek teljes tömege mint kovariáns, a fészek típusa (kupolás vagy nyitott) mint fix tényező és ezek kölcsönhatását vizsgálta, miközben a faj mint véletlen tényező szerepelt a modellben. A szignifikáns értékek félkövérrel szedettek. A lineáris modell esetében az F-érték és az R^2 , vagyis a modell determinációs együtthatója szerepel

	Insulatory value (°C·min ⁻¹)	Water absorbed (g)	%Water absorbed	Minutes to dry
Open				
Reed Bunting	0.031 (0.003)	14.85 (1.50)	105.17 (12.39)	3036.3 (637.3)
Northern Wheatear	0.025 (0.003)	17.21 (2.72)	111.86 (10.07)	1705.8 (252.8)
Domed				
Long-tailed Tit	0.045 (0.001)	19.31 (1.47)	95.48 (7.76)	2206.7 (517.0)
Wood Warbler	0.034 (0.006)	21.97 (2.18)	110.22 (9.34)	2204.6 (449.44)
Linear model				
Total nest mass	20.15 (< 0.001)	14.71 (0.001)	9.79 (0.004)	0.11 (0.745)
Species	12.30 (< 0.001)	0.64 (0.595)	0.64 (0.594)	1.61 (0.208)
Total nest mass * Species	3.68 (0.023)	0.32 (0.813)	0.32 (0.813)	1.64 (0.203)
F _{7,29} (P-value) for model	9.66 (< 0.001)	2.51 (0.038)	1.81 (0.123)	1.41 (0.240)
R ²	0.70	0.38	0.30	0.25
Linear mixed effects model				
Total nest mass	3.37 (0.076)	6.06 (0.019)	10.56 (0.003)	1.56 (0.221)
Type	0.06 (0.814)	0.62 (0.435)	0.62 (0.435)	5.62 (0.024)
Total nest mass * Type	0.29 (0.594)	0.49 (0.491)	0.49 (0.491)	5.33 (0.028)

composition for the Reed Bunting, Northern Wheatear, and Wood Warbler were generally like nest composition reported for closely related species (Biddle *et al.* 2018a, Deeming *et al.* 2020a, Dickinson *et al.* 2022). For instance, like the Reed Bunting, Yellowhammer (*Emberiza citrinella*) nests were mainly built from grass (Deeming *et al.* 2020a), and Northern Wheatear

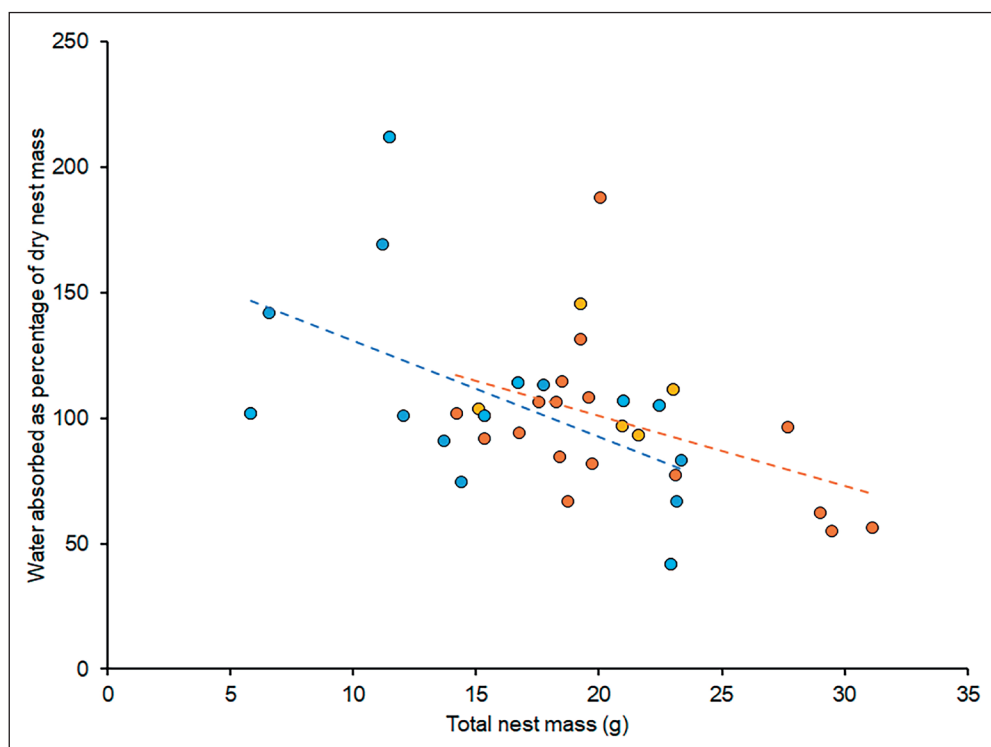


Figure 4. Relationships between total nest mass and water absorbed during simulated rainfall, expressed as a percentage of dry nest mass, for open cup nests (blue symbols) and domed nests (orange symbols). Dashed lines represent least squares linear regression relationships calculated by Excel to illustrate the pattern for the two nest types

4. ábra A fészkek teljes tömege és a szimulált esőzés során elnyelt vízmennyiség közötti összefüggés, a fészkek száraz tömegének százalékában kifejezve, a nyitott fészkek (kék szimbólumok) és a kupolás fészkek (narancssárga szimbólumok) esetében. A szaggatott vonalak az Excel programmal kiszámított legkisebb négyzetek lineáris regressziós összefüggéseit jelölik, amelyek a két fészektípusra vonatkozó mintázatot külön szemléltetik

nests were similar in composition to those of Stonechats (*Saxicola torquatus*) (Biddle *et al.* 2018a). Like Wood Warblers, Willow Warblers (*Phylloscopus trochilus*) built nests with a mix of grass, moss but with more feathers and hair (Dickinson *et al.* 2022). It would be interesting to systematically compare dissimilarity in nest composition across a range of passerine species to determine whether closely related species are building nests that more similar than we perhaps expect.

The mean insulatory value for Long-tailed Tit nests reported here was about a third lower than values reported by McGowan *et al.* (2004). This may reflect differences in methodology because McGowan *et al.* (2004) used thermistors attached to the surface of heated clay ‘eggs’ left in the nest cup rather than self-recording data loggers. Moreover, in the present study the nest was upside-down, which suggests that the IV value should have been greater because convection from the temperature logger would be minimal compared to a dummy egg placed in the base of the nest (see also Boulton & Cassey 2012). In any case, the IV

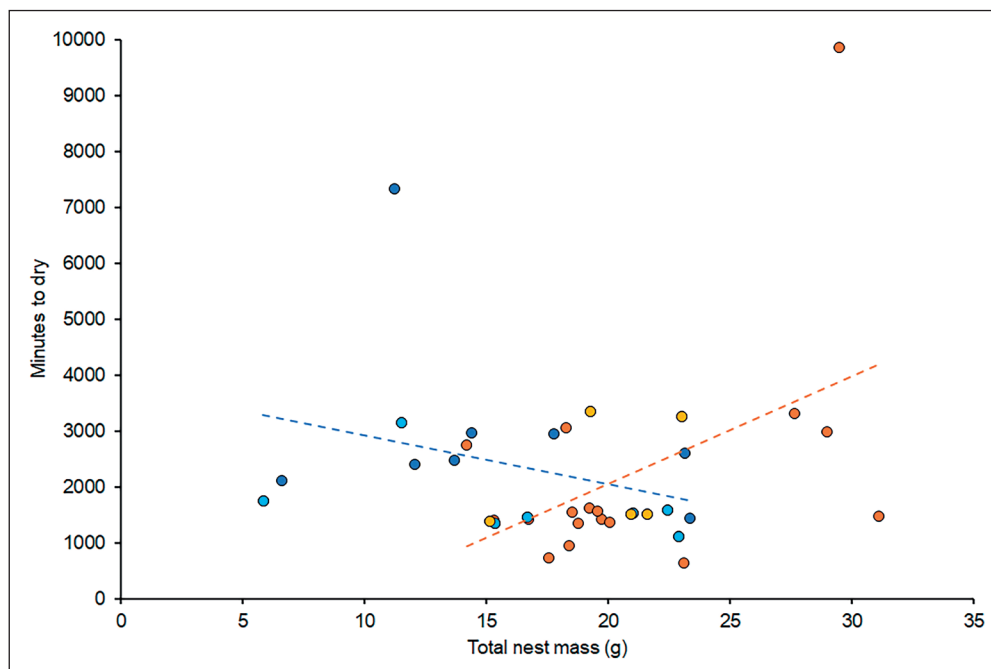


Figure 5. Relationships between total nest mass and time in minutes for a nest to dry after simulated rainfall for open cup nests (blue symbols) and domed nests (orange symbols). Dashed lines represent least squares linear regression relationships calculated by Excel to illustrate the pattern for the two nest types

5. ábra A fészkek teljes tömege és a fészkek kiszáradásához szükséges idő (percben kifejezve) közötti összefüggés a szimulált esőzés után a nyitott fészkek (kék szimbólumok) és a kupolás fészkek (narancssárga szimbólumok) esetében. A szaggatott vonalak az Excel programmal kiszámított legkisebb négyzetek lineáris regressziós összefüggéseit jelölik, amelyek a két fészektípusra vonatkozó mintázatot külön szemléltetik

values for species studied here were comparable to species means reported for a range of similar-sized songbirds, i.e. $0.03\text{--}0.08\text{ }^{\circ}\text{C}\cdot\text{min}^{-1}$ (Deeming *et al.* 2020a). Exceptionally, IV for the Wood Warbler nests were much lower than a previous report, i.e. 0.034 vs $0.120\text{ }^{\circ}\text{C}\cdot\text{min}^{-1}$ (Deeming & Biddle 2015), but this difference was almost certainly due to the methodologies used. Instead of having the temperature logger lying in the nest cup, the techniques used by Deeming and Biddle (2015) required the logger to be pushed into the cup lining, which is known to correlate with higher IV values in other species (Deeming *et al.* 2020a). The mean IV values for Willow Warbler and Reed Bunting nests reported by Deeming *et al.* (2020a) were slightly higher than that reported here, whereas values for the Northern Wheatear nests were lower than reported for other chats and robins in the Muscicapidae (Deeming *et al.* 2020a). Although these differences may reflect methodological difference, other studies suggest that they reflect natural variation between species (Deeming *et al.* 2020a), or indicate that nests where a nest is built is important. It is known that latitude significantly affects thermal insulation in a range of species due to differences in nest composition (Mainwaring *et al.* 2012, 2014). New data reported here are within the range of data for IV for nests

Table 3. Results of linear regression analysis that tested for the effect of the log-transformed values for mass of different nest materials as covariates irrespective of species. Significant values are highlighted in bold. For the linear model the F-value and R² = coefficient of determination for the model is included at the base of each relevant column

3. táblázat A lineáris regresszió eredményei, amely a különböző fészekanyagok tömegének log-transzformált értékei mint kovariánsok hatását vizsgálta, függetlenül a fajoktól. A szignifikáns értékek félkövérrel szedettek. A lineáris modell esetében az F-érték és az R², vagyis a modell determinációs együtthatója minden vonatkozó oszlop alján szerepel

Dependent variable	Insulatory value		Water absorbed		Water absorbed as percentage of mass		Minutes to dry	
	Coefficient (SE)	F-value (P-value)	Coefficient (SE)	F-value (P-value)	Coefficient (SE)	F-value (P-value)	Coefficient (SE)	F-value (P-value)
Intercept	-1.648 (0.122)		0.638 (0.185)		2.328 (0.203)		3.569 (0.348)	
Feathers	0.069 (0.147)	42.76 (< 0.001)	-0.002 (0.222)	1.74 (0.199)	-0.515 (0.244)	2.48 (0.128)	0.305 (0.418)	0.49 (0.491)
Hair	-0.074 (0.093)	12.29 (0.002)	0.211 (0.139)	0.72 (0.406)	-0.082 (0.153)	0.40 (0.535)	-0.495 (0.263)	1.80 (0.191)
Silk	-0.176 (0.262)	0.03 (0.875)	-0.428 (0.340)	0.44 (0.513)	-0.317 (0.435)	0.00 (0.967)	-0.346 (0.746)	0.77 (0.390)
Grass	0.065 (0.092)	2.81 (0.106)	0.382 (0.139)	0.56 (0.462)	-0.230 (0.153)	0.94 (0.341)	0.030 (0.263)	1.61 (0.216)
Moss	0.123 (0.180)	2.03 (0.166)	0.560 (0.272)	12.67 (0.002)	0.272 (0.299)	0.06 (0.804)	-0.558 (0.512)	1.84 (0.187)
Leaves	-0.565 (0.174)	3.97 (0.057)	0.178 (0.262)	0.21 (0.654)	-0.145 (0.288)	1.70 (0.204)	0.249 (0.494)	0.20 (0.656)
Lichen	0.147 (0.096)	0.01 (0.935)	0.171 (0.144)	1.64 (0.213)	0.014 (0.159)	0.08 (0.779)	0.038 (0.272)	0.11 (0.748)
Bark	0.489 (0.192)	154 (0.227)	-0.072 (0.290)	0.15 (0.702)	-0.190 (0.319)	0.00 (0.954)	-0.077 (0.546)	0.02 (0.898)
Stems	0.230 (0.069)	11.02 (0.003)	0.125 (0.104)	1.45 (0.241)	-0.157 (0.114)	1.98 (0.177)	-0.128 (0.195)	0.42 (0.521)
Roots	-0.541 (0.151)	11.15 (0.003)	0.012 (0.228)	0.01 (0.941)	-0.204 (0.251)	0.82 (0.374)	0.215 (0.430)	0.25 (0.620)
Mud	0.569 (0.221)	6.62 (0.016)	-0.428 (0.333)	1.65 (0.211)	-0.313 (0.367)	0.73 (0.402)	0.004 (0.629)	0.00 (0.994)
F _{11,25} (P-value)		8.57 (< 0.001)		1.98 (0.084)		0.83 (0.613)		0.68 (0.742)
R ²		0.79		0.46		0.27		0.23

constructed by songbird species of similar body masses and so offer no surprises. Deeming (2016) suggested that as birds get heavier their reliance on the nest to insulate the clutch of eggs is reduced. Further research, therefore, should perhaps focus on measuring the IV of nests built by much larger passerines, e.g. the Corvidae or Cracticidae, than those studied to date to assess the role of the nest in providing nest insulation.

In relation to nest materials the four species studied here had IVs affected by positive relationships for the amounts of feathers, stems, and mud but negative relationships with hair and roots. By contrast, using data for many more species Deeming *et al.* (2020a) showed that insulation related to the increasing amounts of only feathers and moss. These differences between studies may reflect dissimilarity in composition of the four species studied here than was exhibited by the larger sample size of species and nests used by Deeming *et al.* (2020a). Given that different materials will vary in their thermal properties (see Hilton *et al.* 2004, Deeming *et al.* 2020c), further studies could focus on the insulation offered by nests mainly built from materials other than plants or derived from animals, e.g. the mud nests of swallows (Hirundinidae) (Ferguson-Lees *et al.* 2011).

In terms of rainproofing, the nests of the four species studied here had values for water absorbed and minutes to dry within the range reported by Biddle *et al.* (2019). Similarly, despite nests substantially increasing in mass the amount of water absorbed was less than 10% of the mass of water that rained upon them suggesting that the nests had quite effective drainage. Larger domed nests absorbed more water and take longer to dry although, contrary to the report by Biddle *et al.* (2019), for the two species with open cup nests there seemed little effect of nest mass. As was also shown by Biddle *et al.* (2019) the amounts of moss in the nest significantly affected water absorbed, but not as a percentage of dry nest mass. It is acknowledged by Biddle *et al.* (2019) and here that testing rainproofing in a laboratory environment has its limitations because it does not account for other forms of shelter that may be present around the nest *in situ*. Development of a methodology that allows investigation of nests at their construction site would certainly provide a better understanding of how the immediate surroundings affect not only nest function but also how this impacts upon the success of incubation of eggs and rearing of nestlings.

Simulated rainfall reduced the IVs of a range of songbird nests due to a higher internal rate of nest cooling (Deeming & Campion 2018). It is interesting to note that the smallest change in IV was for nests of the Common Chaffinch (*Fringilla coelebs*; Fringillidae) which, compared to the other species studied by Deeming and Campion (2018), has a high proportion of feathers lining its nest cup (Biddle *et al.* 2018a, Deeming *et al.* 2020a). These feathers help contribute to 90% of the thermal insulation of the nest despite the cup lining only being a third of the total nest mass (Deeming & Humphries 2020). Given the hydrophobic nature of feathers (Lui *et al.* 2008) it is possible that a lining of feathers in a nest cup may not only provide thermal insulation but also, they help repel water in the outer nest wall and so keep the cup dry. It would be interesting to explore this possibility in Long-tailed Tit nests and other species, e.g. the European Goldfinch (*Carduelis carduelis*), where the cup lining has a proportion of feathers (Biddle *et al.* 2018a), or to experimentally add feathers to nests.

The results of the present study conflict with the conclusions of previous studies. In particular, Martin *et al.* (2017) suggested that enclosed nests conferred thermal benefits to the

eggs and chicks, that were more important than reduced predation risks. However, Martin *et al.* (2017) drew their conclusions based on interpretation of nest size, attentiveness of parents during incubation, presumed rates of egg cooling and rates of nestling growth, rather than measuring the actual insulation offered by the nests. Other studies that infer advantages to domed nests are also based on indirect measures of nest success (Griffith *et al.* 2016, Duursma *et al.* 2018, Street *et al.* 2022). It is acknowledged that the study described here has a very limited sample but it does suggest that nest architecture may not play such an important role in providing thermal insulation as has been suggested. However, there needs to more research in a wider range of species and nesting locations in order to test this hypothesis further.

This study has confirmed that nest insulation and rainproofing properties varies between species but the data suggested that there is no consistent difference between domed and open nests. Although the dome covering the top of the nest may have little effect on thermal insulation or rain protection, the lack of difference may reflect limitations of the study due to small samples of nests and/or species, nest composition, or geographical variation. During incubation the dome may not have much impact on the thermal profile of the clutch of eggs, but it could confer insulation/rainproofing to the parent during incubation, or to the nestlings during rearing. The presence of a dome may reflect a degree of protection from predators but for many open cup nesting species the construction of a nest in a location surrounded by vegetation may serve the same role. Given that domed nests are commonly built by passerines (Price & Griffith 2017), more research is needed on the functional properties of domed nests to determine whether they differ from those of open cup nests.

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