



MACQUARIE
University

Macquarie University ResearchOnline

This is the peer reviewed version of the following article:

Campbell, B. L., Hurley, L. L., & Griffith, S. C. (2018). Behavioural plasticity under a changing climate; how an experimental local climate affects the nest construction of the zebra finch *Taeniopygia guttata*. *Journal of Avian Biology*, 49(4), jav-01717.

which has been published in final form at:

Access to the published version:

<https://doi.org/10.1111/jav.01717>

This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

1 Author Accepted Version of the article that has now been published as
2 Campbell BL, Hurley LL, Griffith SC (2018) Behavioral plasticity under a
3 changing climate; how an experimental local climate affects the nest
4 construction of the zebra finch (*Taeniopygia guttata*). *Journal of Avian
5 Biology*, 49:

6 The published version can be found at the following link

7 jav-01717. doi:10.1111/jav.01717

8

9

10

11 **Behavioural plasticity under a changing climate; how an experimental local
12 climate affects the nest construction of the zebra finch (*Taeniopygia guttata*)**

13

14 Bridget L. Campbell¹, Laura L. Hurley^{1,*}, Simon C. Griffith¹

15

16 ¹ *Department of Biological Sciences, Macquarie University, Sydney, Australia.*

17

18 *Corresponding author: laura.hurley@mq.edu.au

19

20

21

22 **Key words:** Nest building, climate change, plasticity, hot climate, nest microclimate

23

24

25 **Abstract**

26 Successful reproduction in most avian species is dependent on the construction of a
27 nest that provides protection and a suitable microclimate for the eggs and developing
28 nestlings. Observational studies suggest that climatic variation may affect the
29 structure of the nest, but to date there have been no attempts to experimentally
30 determine the role that local climate plays in the construction of a suitable nest. Using
31 a within-individual counter balanced design we investigated how nest composition
32 and construction differ in zebra finches breeding in ambient conditions of 18°C and
33 30°C. We found that at 18°C birds built nests that were over 20% heavier, and with
34 significantly more thread and less grass than those built at 30°C. Our results highlight
35 the degree of plasticity in nest building behaviour in relation to local ambient
36 conditions. These results suggest that nest building behaviour is one route through
37 which birds can respond to a changing climate and modify the microclimate of their
38 nest in line with projected changes in ambient conditions.

39

40

41

42 **Introduction**

43 The extent to which birds will be able to adapt to a rapidly changing climate, has
44 recently become an important focus of research (reviewed in Møller et al 2010).
45 Beyond altering a suite of phenological, morphological and physiological adaptations,
46 birds can potentially ameliorate the effects of climate change, particularly those
47 effecting reproduction and early development, through the protective qualities of their
48 nests. A taxonomically diverse behaviour, nest construction, is common amongst
49 almost all species of birds, and provides a structure in which to house and care for
50 eggs and nestlings and protect against predation (Collias and Collias, 1984; Hansell,
51 2000, Mainwaring et al. 2014). Whilst overall nest structure (whether domed or open)
52 is remarkably well conserved over evolutionary time (Price and Griffith 2017),
53 variation in structure size and investment into the different structural components,
54 such as the cup and hood, exists within species. Recent work has indicated that some
55 of this variation comes from individual differences in cognitive skills and experience
56 with different materials (Muth and Healy 2011; Muth et al. 2013; Muth and Healy
57 2014). However, some of this differences in nest structure within a population or
58 species may also be driven by climatic variation, and indeed several recent studies
59 have highlighted the role of avian nests in modifying the microclimate surrounding
60 eggs and developing young. For example, the presence of a roof and orientation away
61 from direct sun have been shown to reduce the impact of solar radiation in a hot
62 climate (Griffith et al 2016), while in cooler climates the mass of nest materials has
63 been positively correlated with reproductive success (Gładalski et al. 2016).

64 Increasingly important, in light of climate change, research into how the nest
65 structure can maintain an optimal thermal environment has come from a number of
66 observational studies that have investigated the relationship between nest structure

67 and climatic variables. These studies, examples of which are summarized in Table 1,
68 have found relationships between of nest parameters such as nest mass, and thermal
69 conductance, with latitudinal, altitudinal or climatic variation (see Table 1 for
70 examples). The patterns found by such studies can certainly be explained as an
71 adaptive behavioural response to the local climate, with, for example, larger or thicker
72 nests providing better insulation against the colder climates found at higher latitude or
73 elevation. However, the observational nature of these studies means that their results
74 may be confounded by other sources of variation across the different locations
75 examined. For example, different nest building materials such as moss, may vary in
76 abundance along a latitudinal or altitudinal cline. Furthermore, the spatial
77 heterogeneity in nest structure demonstrated by such studies may be attributable to
78 either fixed cultural or genetic variation amongst populations, rather than behavioural
79 plasticity in response to the local climate. The incidence of behavioural plasticity in
80 nest building behaviour, in response to local conditions is of particular interest
81 because it will provide parents with a greater amount of flexibility in responding to a
82 rapidly changing climate.

83 Here, we utilize an experimentally manipulated climate to examine the degree
84 to which variation in the local climate at the time of nest building affects nest
85 construction. We focused on a captive population of the Australian zebra finch,
86 *Taeniopygia guttata*. In this species, a facultative response to climatic variation is
87 particularly relevant because in the wild, zebra finches breed over an extended period
88 of the year, with mean daily temperatures varying from just 10 °C to over 26 °C
89 during the breeding period (Griffith et al. 2017a), and in the summer, temperatures
90 inside the nest can exceed 50 °C (Griffith et al. 2016). We have used ecologically
91 relevant average temperatures (18 °C and 30 °C) to reflect the average conditions in

92 the cooler period in early spring and the hotter period experienced later in the
93 breeding season (based on descriptions of relevant climate in Griffith et al. 2016 and
94 Griffith et al. 2017a). Nests built under the two different temperature treatments were
95 compared and it was hypothesized that if nest building was behaviourally plastic with
96 respect to climate, then a difference in the mass and composition of nests would be
97 observed. Specifically, the observational studies to date (reviewed above) have found
98 that in cooler conditions, nests are typically constructed with a greater mass of
99 material, and presumably this provides better insulation in any climatic conditions
100 that are below the temperature of thermal neutrality in birds.

101

102 **Methods**

103

104 *Experimental methods*

105 Twenty-four pairs of domestically bred zebra finches were housed in cages measuring
106 70x47x130cm (one pair in each cage) in one of four rooms (six cages to each room),
107 with controlled climates (two set to each of the two experimental temperatures 18° or
108 30°C). All pairs were held in these cages for three weeks at the set temperature prior
109 to the provision of two 13.5 x 15cm rattan nests baskets and *ad lib* nesting material
110 consisting of dried ‘November grass’ (a stiff grass that is very similar to the grass that
111 they use in the wild to build their nests), white cotton thread, and emu feathers. Once
112 nest baskets were supplied, they were monitored daily, as the nests were built and
113 eggs laid. As part of separate work the eggs were removed on the day that they were
114 laid, and replaced with plastic dummy eggs. These dummy eggs were left, and the
115 birds incubated them, until they too were removed, along with the whole nest, nine
116 days after the clutch had been completed. In this way we could be confident that the

117 nest had been completed, because it is likely that pairs will have completed the
118 construction of their nest before incubation begins, and certainly by the mid-point of
119 incubation (after which they were removed). Furthermore, at this stage they are free
120 of nestling waste, and virtually no adult waste was present either at this stage (no
121 more than 3 small dried adult droppings were found in any of the nests). The nests,
122 still within the rattan basket, were labelled and stored for processing. All nests were
123 stored for at least six months before processing during which time they dried under
124 normal indoor laboratory conditions, and they were all stored together.

125 Birds were then allowed to rebuild a second nest and raise chicks to
126 independence (again as part of other work: Andrew et al. 2017). All but two pairs
127 successfully reared chicks and once the nestlings had fledged these nests were taken
128 away (to prevent further breeding at that point). These second nests were not
129 investigated because nest composition was confounded by the number of nestlings
130 and the waste they produced that soiled the nest quite extensively. Birds were then
131 moved between the rooms, so that pairs that had initially bred in an 18 °C room were
132 then moved into a 30 °C room and vice versa. Following another three-week
133 acclimation period with no nest baskets or material, the entire process was repeated.
134 Therefore, this was a balanced design and all birds were subjected to equal treatments
135 with the exception that half of the pairs were exposed to the 18 °C temperature first,
136 and half were exposed to 30 °C treatment first. As each individual pair received both
137 treatments the analysis was a within-individual comparison, removing a number of
138 individual intrinsic confounds.

139 Throughout the period of this work, all birds were maintained on water and dry
140 finch seed ad lib, and supplemented daily with a small amount of greens (mashed
141 frozen peas/spinach), hard-boiled egg and sprouted seed. All work was conducted

142 according to relevant national guidelines and was approved by the Macquarie
143 University Animal Ethics Committee (Animal Research Authority 2013/029).

144

145 *Nest measurements*

146 In total, ten aspects of nest morphology were assessed, measuring the mass of the
147 total nest and also the cup and the hood separately; the thickness of the structure (cup
148 wall and base, as well as the top of the hood), and the composition by mass of the nest
149 with respect to the mass of grass, feathers and cotton string. Structural dimensions
150 were measured using digital callipers (to 0.01mm) and a ruler (to 0.1cm) and nest and
151 nest component masses were measured using a digital scale (to 0.001g). First, the
152 total mass of each nest inside the basket was recorded. The top half of the basket and
153 the hood of the nest were then cut away from the cup and bottom half of the basket
154 and each was weighed.

155 Using callipers, cup diameters (two measurements taken perpendicular to each
156 other) and the thickest and thinnest part of the cup wall were measured. Average wall
157 thickness was then calculated using these two measurements. The thickness of the
158 base of the nest was calculated by subtracting the cup depth (measured from the
159 bottom (base) of the cup to rim of the nest) from the overall height of the cup section
160 (from the bottom of the nest). The material components of the nest – grass, thread and
161 feathers – were then separated out and individually weighed, keeping the hood and
162 cup components separate. Any eggs found buried within the cup of nests were
163 recorded and removed so they were not included in the component mass. Total nest
164 mass was calculated by subtracting the mass of the empty nest basket from the total
165 mass of all nest components. The total mass of each component was calculated from
166 the mass of the given component in the hood and cup. All measurements were made

167 by one person (BLC) blind to the temperature treatment in which the nest was
168 constructed.

169

170 *Data analysis*

171 Data on two nests was recorded for all 24 pairs. All statistical analysis was completed
172 using R Studio (version 1.0.136; RStudio team 2016) with (R version 3.3.2; R Core
173 team 2016) and the ‘*lme4*’ package (Bates et al. 2015). Linear mixed effects models
174 were utilized to determine whether the temperature treatment influenced the total nest
175 mass, the mass of the hood, cup and components- grass, thread, feathers, and hood
176 thickness, base thickness and the average wall thickness of the cup. The temperature
177 of the room (18 °C, 30 °C) and order of room temperature treatments (18 °C -30 °C,
178 30 °C -18 °C) (order) were set as fixed effects and an interaction between room
179 temperature and order was included to determine whether the order in which birds
180 were housed in the two temperatures impacted the effect of room temperature on nest
181 construction. Initial models with the interaction term and order as a fixed effect were
182 run. If either was found to be non-significant it was removed from the model. Order
183 as a fixed effect was removed from all models. The interaction term was removed
184 from all models (due to non-significance) excluding that for hood mass and average
185 cup wall thickness. To control for repeated measures, pair identity was included as a
186 random factor. ANOVA were run to compare models and a backwards elimination
187 approach using the Akaike’s Information Criterion (AIC) was used for model
188 selection. REML was fitted on all finalised models and ANOVA were run to
189 determine statistical significance. All tests were two-tailed and considered significant
190 at $\alpha < 0.05$. Assumptions of normality and homogeneity of variance of residuals were
191 assessed visually (following Zuur et al. 2009).

192

193 **Results**

194 There was a significant difference in the mean total nest mass between the two
195 temperature treatments (Fig. 1, Table 2), with nests built under 18°C being on average
196 23.55% heavier than those built under 30°C (Table 2). The mean mass of both the
197 hood and cup were significantly greater in nests built in 18°C (Table 2). The mean
198 hood and cup mass were 26.60% and 25.21% greater respectively in nests built in the
199 cooler treatment. Overall, average cup walls were 15.96% thicker in nests in the 18°C
200 temperature treatment (Table 2). There was no significant difference between
201 treatment groups in the thickness of the base of the nest, cup depth, or hood thickness
202 between temperatures (Table 2).

203 The total mass of nests built under 18°C and 30°C by pairs subject to the
204 different order of treatments (i.e. 18°C -30°C and 30°C-18°C) did not differ ($F_{1,22}=$
205 0.0006, $p = 0.98$). However, there was a significant interaction between room
206 temperature and the order of room temperature treatment for mean hood mass ($F_{1,22}=$
207 7.04, $p= 0.01$), and the average wall thickness ($F_{1,22}= 7.32$, $p = 0.01$). These
208 interactions indicated that, for these variables, there was only a significant change for
209 the nests built by pairs that started in the 18°C treatment before then experiencing the
210 30°C treatment. For example, there was a significant change in the wall thickness of
211 the treatment group that first nested at 18°C with average wall thickness being 28.2 %
212 greater (30.8mm at 18°C versus 22.1 mm at 30°C mm). By contrast, there was no
213 difference in the thickness of nest walls in the treatment group that were first exposed
214 to the hot climate (25.4 mm at 30°C and then 25.7 mm thick at 18°C).

215 In addition to the difference in the amount of material used in nests built in the
216 different temperatures, there were also some differences in the composition of the
217 nests. Thread mass was significantly greater in nests built under 18°C (Table 2), with

218 nests built in the 18°C conditions containing 77.59% more thread than nests built in
219 the 30°C conditions. While nests built at 30°C contained 18.01% more grass more
220 than those constructed in 18°C conditions (Table 2). The mean total mass of feathers
221 used in nest construction did not differ significantly between the two temperature
222 treatments (Table 2).

223

224 **Discussion**

225 We have demonstrated that the ambient air temperature experienced during nest
226 construction influenced the weight and composition of the zebra finch nests built.
227 Nests built in the 18°C treatment were significantly heavier than those built in the
228 30°C rooms. Both the walls and hood of the nests built in 18°C conditions were
229 constructed with a greater mass of material overall and the walls were significantly
230 thicker. In addition, pairs constructed their nests from a different composition of
231 materials across different temperatures. In 18°C conditions, from the three materials
232 available ad libitum for constructing nests, the birds used a higher proportion of
233 cotton thread, but less grass than birds at 30°C conditions.

234 There are a few possible explanations for the differences that we saw in the
235 construction of nests in different temperature regimes. The adaptive explanation
236 would be that the nests differed in their construction in ways such that the
237 microclimate inside the nest is best shaped by the interaction of the nest structure and
238 the local temperature (e.g. Heenan et al 2015; Mainwaring et al 2014; and other
239 references in Table 1). In cooler conditions, a thicker nest structure will reduce the
240 rate at which heat is lost from within the nest chamber, allowing incubating or
241 brooding parents, or nestlings to keep warm at a reduced energetic cost (as shown in
242 this species and their nests by Zann & Rossetto 1991). Indeed, in a constant

243 temperature chamber, Vleck (1981) found that a grass nest, inside a metal can, was
244 three degrees warmer for a range of temperatures from 8-35°C and led to considerable
245 metabolic savings. At hotter temperatures, perhaps a more lightly woven structure
246 will assist in allowing air to flow through the nest structure and heat to be lost more
247 effectively, or provide a high amount of shading from solar radiation (e.g. Griffith et
248 al 2016).

249 It is however important to note that we have not tested the thermal properties of
250 the different nests, nor the materials that were used. However, now that we have
251 demonstrated this plasticity experimentally, further work could explore how
252 effectively the nest built at cooler or hotter temperatures preserved or lost heat from
253 the nest chamber. As well as considering the mass of material used, further work
254 could examine the benefits of shifting the proportions of different materials, as
255 presumably the grass and string that were provided may confer different structural
256 and thermal properties to the overall nest structure. In previous observational studies
257 nests from different geographic areas have been described to be composed of quite
258 different materials (e.g. Kern and van Riper 1984; Rohwer & Law 2010; Mainwaring
259 et al 2014), which might reflect the local availability of material, but might also
260 contribute adaptive qualities such as thermal conductance and the speed at which they
261 dry after rainfall.

262 The plasticity that we have seen with respect to nest structures built across two
263 different ambient temperatures is consistent with the finding in wild populations of
264 some other passerine species for nests to be constructed significantly differently
265 across different climates (for example the studies summarized in Table 1). In those
266 studies, nest were found to differ in the overall size and mass of material used, but
267 also, in some cases to have different properties such a thermal conductance. Table 1 is

268 not an exhaustive summary of all such studies, but provides some example of studies
269 in which relationships have been found between environmental variables and some
270 element of nest structure. Our experimental findings therefore support the idea that
271 birds are capable of increasing their investment into the amount of material used in
272 nest construction, and also in the composition of the different nest materials, in
273 relation to the ambient temperature. However, it is also important to also consider
274 non-adaptive explanations for the results of our experiment, and indeed the
275 observational data presented in these earlier studies.

276 One viable alternative is that the ultimate nest structure may reflect the
277 energetic constraints of the birds building the nest. Whilst there may be an optimal
278 structure, in conditions in which building a nest is more energetically costly
279 (Mainwaring and Hartley 2013), the nest may be slightly sub-optimal in structure.
280 However, if this were true, then we would probably expect that, if all else is equal,
281 then under colder conditions, the nest should have a lower mass, to reduce the costs of
282 building it. Certainly in our laboratory conditions all else was equal. Food and nesting
283 material were provided ad libitum and within around 1 meter of the location where
284 the nest was constructed. As a result, there should have been a very low cost of either
285 foraging for food or finding and gathering nesting material in both our experimental
286 treatments, and certainly no consistent difference across the two climates. This is an
287 important consideration because in the observational work in the wild populations we
288 would expect consistent differences across cold and warmer climates in a range of
289 ecological variables, which we have controlled for. As it would have been
290 energetically more costly for the birds to thermoregulate in the cooler of our two
291 treatments (in which they invested more in nest building), we can reject the idea that
292 the nests differed for direct energetics reasons.

293 An alternative non-adaptive explanation for the differential investment in nests
294 across climates, is that beyond a certain minimal threshold, nest structure is not under
295 strong selection, and merely reflects the amount of nest building behaviour to a point
296 where the eggs are laid. In the zebra finch, the male is responsible for bringing
297 material to the nest and for the majority of the construction (Zann 1996). It could be
298 that the latency of a female to lay will lead to a greater period of nest building by the
299 male. This could be an explanation if there was a greater latency to lay in cooler
300 climates (where more substantive nests are typically found) (Heenan et al. 2015).
301 However, in this study, the average time between giving a pair a nest basket and the
302 laying of the first egg was $6.13 \text{ days} \pm 0.68$, at $18 \text{ }^\circ\text{C}$, and $8.38 \pm 1.01 \text{ days}$ at $30 \text{ }^\circ\text{C}$,
303 and therefore this idea does not explain the greater amount of material used in cooler
304 nests.

305 Whilst the nests were typically constructed with more material overall in the
306 cooler temperature in our study, for a couple of the measured variables there was an
307 interaction with the order in which the two temperature treatments were presented.
308 This indicates that the overall plasticity in nest construction that we found may partly
309 depend on an individuals' own experience of climate and nest building. To this extent,
310 our work is consistent with other recent findings in the same species that
311 demonstrated the importance of individual nest building experience in refining their
312 nests (Sargent 1965; Muth and Healy 2011). It is also of note that our study
313 demonstrated plasticity in nest structure within individuals across a relatively short
314 time frame (equivalent to the time between different breeding attempts within a single
315 breeding season). All of the studies in Table 1 are focused on variation across
316 different geographic locations, however in their study Mainwaring & Hartley (2008)
317 observed variation in nest structure (nest cup lining depth) within a single population,

318 although different individuals would have been breeding early and late in that season,
319 and study. Again, the pattern observed in that study may have been caused by
320 confounding effects such as the variation in individual quality between early and late
321 breeders. Our study goes beyond this temporal observational approach by
322 demonstrating the extent to which individuals modify their nests in different
323 conditions when all else is equal.

324 The work reported here, focused on domesticated zebra finches, which have
325 been kept for many generations in captivity, and probably in a variety of indoor and
326 outdoor conditions. Domesticated zebra finches are protected from the extremes of
327 climate by the shelter provided by aviaries or cage holding facilities, and in laboratory
328 contexts zebra finches are typically held in temperatures of around 22 °C (Griffith et
329 al. 2017b). It is interesting that they still have a response to the variation in
330 temperature to which we exposed them (18 and 30 °C). In the wild, temperature varies
331 to a much greater extent, and eggs are laid in wild nests in periods with a mean daily
332 minimums of around 12 °C and mean daily maximum temperatures of 26 °C (Griffith
333 et al. 2017a). The absolute maximum temperatures in the arid zone are much greater
334 and, during periods of active breeding, ambient conditions regularly exceed 40 °C
335 (Griffith et al. 2016). In this same study it was found that the temperature within the
336 nest chamber of wild nests largely reflected ambient conditions, but was significantly
337 affected by the orientation towards the sun, and the presence of the roof certainly
338 helped to reduce internal temperatures in hot conditions. It will be interesting to now
339 understand the extent to which the nest structure of wild zebra finches varies over
340 different climatic conditions, and we certainly might expect a larger amount of
341 variation given the greater variability in temperature over the typically long zebra
342 finch breeding season (Zann 1996; Griffith et al 2016). Another interesting point for

343 further work in the wild would be to consider whether the degree of plasticity changes
344 if birds are switched from a cool to a hot condition, rather than the other way around
345 (hot first and then cool). Both conditions are encountered by birds in the wild, the
346 former from spring to summer, and the latter as breeding continues from the hot
347 summer into the cooler autumn (climatic breeding conditions presented in Griffith et
348 al 2016).

349 As discussed above, we believe that our results are consistent with the idea that
350 the variation in nest structure is being tailored to local climatic conditions. This leads
351 to the question of the extent to which nest structure affects the success of different
352 reproductive outcomes. In both the field and the laboratory over 30% of pairs fail to
353 breed successfully when given the opportunity (Griffith et al. 2017b). Whilst this
354 reproductive failure has lots of underlying determinants, our results suggest that the
355 nest structure is worthy of further investigation in this context. While we have shown
356 a degree of plasticity in nest structure that varies across pairs, the fitness
357 consequences of the overall variation in nest structure in both the wild and captivity
358 remain worthy of attention.

359 Finally, there is an increased focus on the importance of plasticity in relation to
360 climate-related behaviour and phenotype, because of its potential importance in
361 conferring resilience to a globally changing climate. It has been well documented that
362 birds around the world are being affected by climate change (Møller et al. 2010), and
363 the avian nest provides an important component in their defence against adverse
364 conditions (Mainwaring et al 2017). Our work provides an experimental
365 demonstration that birds can adjust this important extended phenotype to local
366 climate, and the extent to which this is done across species, and in response to both
367 cold and hot climates is certainly worthy of further work.

368

369 **Acknowledgements**

370 The authors would like to thank Drew Allen for his assistance with the statistical
371 analysis. This work was supported by ARC funding to SCG through a Future
372 Fellowship (FT130101253). Empirical work was run by LLH, nest processed by
373 BLC, and both conducted statistical analysis. All authors contributed to writing of the
374 manuscript.

375

376 **References**

- 377 Andrew, S. C., Hurley, L. L., Mariette, M. M. and Griffith, S. C. 2017. Higher
378 temperatures during development reduce body size in the zebra finch in the lab
379 and in the wild. – *J. Evol. Biol.* 30:2156-2164.
- 380 Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting Linear Mixed-
381 Effects Models Using lme4. – *J. Stat. Soft.* 67:1-48.
- 382 Collias, N. E. and Collias, E. C. 1984. Nest building and bird behaviour. – Princeton
383 Univ. Press.
- 384 Crossman, C.A., Rohwer, V.G. and Martin, P. R. 2011. Variation in the structure of
385 bird nests between Northern Manitoba and Southeastern Ontario. – *PLoS ONE.*
386 6:e19086.
- 387 Gładalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J.,
388 Wawrzyniak, J., Zieliński, P., Cyżewska, I. and Bańbura, J. 2016. Effects of
389 nest characteristics on reproductive performance in blue tits *Cyanistes*
390 *Caeruleus* and great tits *Parus Major*. – *Av. Biol. Res.* 9:37-43.
- 391 Griffith, S. C., Crino, O. L. and Andrew, S. C. 2017a. Commentary: a bird in the
392 house: the challenge of being ecologically relevant in captivity. – *Front. Ecol.*
393 *Evol.* 5:21.
- 394 Griffith, S. C., Crino, O. L., Andrew, S. C., Nomano, F. Y., Adkins-Regan, E.,
395 Alonso-Alvarez, C., Bailey, I. E., Bittner, S. S., Bolton, P. E., Boner, W.,
396 Boogert, N., Boucaud, I. C. A., Briga, M., Buchanan, K. L., Caspers, B. A.,
397 Cichon, M., Clayton, D. F., Deregnaucourt, S., Forstmeier, W., Guillette, L. M.,

398 Hartley, I. R., Healy, S. D., Hill, D. L., Holveck, M. J., Hurley, L. L., Ihle, M.,
399 Krause, E. T., Mainwaring, M. C., Marasco, V., Mariette, M. M., Martin-
400 Wintle, M. S., McCowan, L. S. C., McMahon, M., Monaghan, P., Nager, R. G.,
401 Naguib, M., Nord, A., Potvin, D. A., Prior, N. H., Riebel, K., Romero-Haro, A.
402 A., Royle, N. J., Rutkowska, J., Schuett, W., Swaddle, J. P., Tobler, M.,
403 Trompf, L., Varian-Ramos, C. W., Vignal, C., Villain, A. S. and Williams, T.
404 D. . 2017b. Variation in reproductive success across captive populations:
405 methodological differences, potential biases and opportunities. – *Ethology*
406 123:1-29.

407 Griffith, S. C., Mainwaring, M. C., Sorato, E. and Beckmann, C. 2016. High
408 atmospheric temperatures and ‘ambient incubation’ drive embryonic
409 development and lead to earlier hatching in a passerine bird. – *Roy. Soc. Open*
410 *Sci.* 3:150371.

411 Hansell, M. H. 2000. *Bird nests and construction behaviour*. - Cambridge Univ. Press.

412 Heenan, C.B., Goodman, B. A. and White, C. R. 2015. The influence of climate on
413 avian nest construction across large geographical gradients. – *Glob. Ecol. &*
414 *Biogeog.* 24:1203-1211.

415 Kern, M. D. and van Riper, C. III. 1984. Altitudinal variations in nests of the
416 Hawaiian honeycreeper *Hemignathus virens virens*. – *Condor* 86:443–454.

417 Mainwaring, M.C., Barber, I., Deeming, D.C., Pike, D.A., Roznik, E.A. and Hartley,
418 I.R. 2017. Climate change and nesting behaviour in vertebrates: a review of the
419 ecological threats and potential for adaptive responses. – *Biol. Rev.* 92:1991-
420 2002.

421 Mainwaring, M.C., Deeming, D.C., Jones C. I. and Hartley, I. R. 2014. Adaptive
422 latitudinal variation in Common Blackbird *Turdus merula* nest characteristics. –
423 *Ecol. Evol.* 4:851–861.

424 Mainwaring, M. C. and Hartley, I. R. 2008. Seasonal adjustments in nest cup lining in
425 Blue Tits *Cyanistes caeruleus*. 2008. – *Ardea* 96:278-282.

426 Mainwaring, M. C. and Hartley, I. R. 2013. The energetic costs of nest building in
427 birds. – *Av. Biol. Res.* 6:12.

428 Mainwaring, M. C., Hartley, I. R., Bearhop, S., Brulez, K., du Feu, C. R., Murphy, G.,
429 Plummer, K., Webber, S.,L., Reynolds, S.,J. and Deeming, D.C. 2012.

430 Latitudinal variation in blue tit and great tit nest characteristics indicates
431 environmental adjustment. – J. Biogeogr. 39: 1669–1677.

432 Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M. and Deeming D. C. 2014. The
433 design and function of birds' nests. – Ecol. Evol. 4:3909-3928.

434 Møller, A.P., Fiedler, W. and Berthold P. 2010. Effects of Climate Change on Birds. –
435 Oxford University Press.

436 Muth, F. and Healy, S. D. 2011. The role of adult experience in nest building in the
437 Zebra Finch, *Taeniopygia guttata*. – Anim Behav. 82:185-189.

438 Muth, F. and Healy, S. D. 2014. Zebra Finches select nest material appropriate for a
439 building task. – Anim. Behav. 90:237-244.

440 Muth, F., Steele, M. and Healy, S. D. 2013. Colour preferences in nest-building
441 Zebra Finches. – Behav. Proc. 99:106-111.

442 Price, J. J. and Griffith, S. C. 2017. Open cup nests evolved from roofed nests in the
443 early passerines. – Proc. Roy. Soc. Lond. B. 284:20162708

444 R Core Team. 2016. R: A language and environment for statistical computing. R
445 Foundation for Statistical Computing, Vienna, Austria. URL [https://www.R
446 project.org/](https://www.Rproject.org/).

447 Rohwer, V. G. and Law, J. S. Y. 2010. Geographic variation in nests of yellow
448 warblers breeding in Churchill, Manitoba, and Elgin, Ontario. – Condor
449 112:596–604.

450 RStudio Team. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston,
451 MA, URL <http://www.rstudio.com/>.

452 Sargent, T. 1965. The role of experience in the nest building of the Zebra Finch. –
453 Auk 82:48-61.

454 Schaefer V. H. 1976. Geographic variation in the placement and structure of Oriole
455 nests. – Condor 78:443-448.

456 Vleck, C. 1981. Energetic cost of incubation in the Zebra Finch. - Condor 83:229-
457 237.

458 Zann, R. A. 1996: The zebra finch – a synthesis of field and laboratory studies. –
459 Oxford Univ. Press.

460 Zann, R. A. and Rossetto, M. 1991. Zebra finch incubation – Brood patch, egg
461 temperature and thermal properties of the nest. - Emu 91:107-120.

462 Zuur, A. F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. 2009. Mixed
463 effects models and extensions in ecology with r. – Springer-Verlag.

464

465 **Tables**

466

467 Table 1. Examples of observational studies that have investigated the relationship between nest structure and climatic variables.

468

Species	Environmental parameter	Nest parameter	Relationship	Reference
American Robin <i>Turdus migratorius</i>	Geographic variation across two sites at different latitude	Nest mass and wall thickness	Heavier nests at higher latitude, with colder climate	Crossman et al (2011)
Yellow Warbler <i>Dendroica petechia</i>	“	“	Heavier nests at higher latitude, with colder climate	“
Savannah Sparrow <i>Passerculus sandwichensis</i>	“	“	No significant difference	“
Common Redpoll <i>Carduelis flammea</i> & American Goldfinch <i>Carduelis tristis</i> (combined)	“	“	Heavier nests at higher latitude, with colder climate	“
36 passerine species (combined)	Elevation (altitude)	Thermal conductance	Nests lost heat faster at higher elevation (not significant when climatic variation was accounted for)	Heenan et al (2015)
“	Temperature (and interaction with rainfall)	Thermal conductance	Nests lost heat faster in cooler climate (and more so in wet climate)	Heenan et al (2015)
Common Amakihi <i>Hemignathus virens</i>	Elevation (altitude)	Nest mass	No difference	Kern & van Riper (1984)

“	“	Thermal conductance	Nests lost heat faster at lower elevation	“
Blue tit <i>Cyanistes caeruleus</i>	Temperature variation across a latitudinal gradient (seven sites in the UK)	Thermal conductance	Nests lost heat faster at lower latitudes	Mainwaring et al (2012)
“	“	Mass of the nest cup lining material	Less lining material in warmer locations (lower latitudes)	“
Great tit <i>Parus major</i>	Temperature variation across a latitudinal gradient (five sites in the UK)	Thermal conductance	Nests lost heat faster in warmer locations (lower latitudes)	“
“	“	Mass of the nest cup lining material	Less lining material in warmer locations (lower latitudes)	“
Common blackbird <i>Turdus merula</i>	Geographic variation across a latitudinal gradient (four sites in the UK)	Nest size	Larger nests at higher latitudes	Mainwaring et al (2014)
“	“	Thermal conductance	Nests lost heat faster at lower latitudes	“
Yellow Warbler <i>Dendroica petechia</i>	Geographic variation across two sites at different latitude	Nest size	Larger/thicker/ deeper nests at higher latitude, with colder climate	Rohwer and Law (2010)
“	“	Thermal conductance	Nests lost heat faster at lower latitude	“
Orchard Oriole <i>Icterus spurius</i>	Geographic variation across multiple sites with climatic variation	Size of nest opening	Larger nest opening in warmer areas	Schaefer (1976)

Northern Oriole
Icterus galbula

“

Placement in tree and nest size

Geographic variation in placement in
tree and nest size

“

469

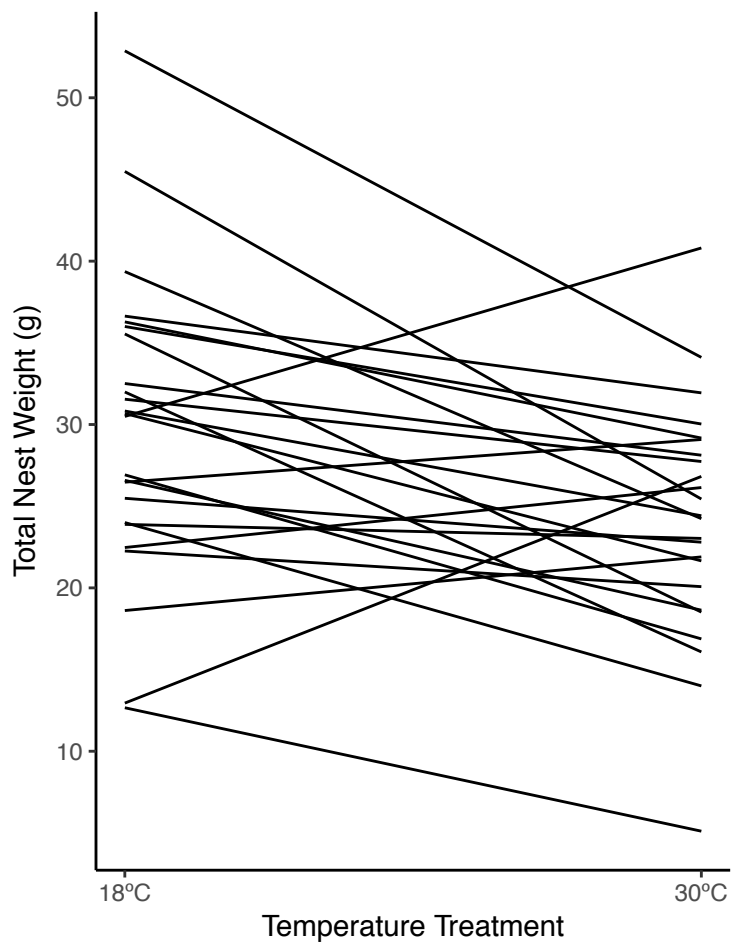
470 Table 2. The average values of the different variables from nests built in the two
 471 temperature treatments, along with the results of ANOVA run on the linear mixed
 472 effects models, including the F and p-values for the fixed effect of room temperature,
 473 alongside the p-value for the interaction between room temperature and order of
 474 temperature treatment for the nest variables where the interaction was significant. *
 475 indicates a significant p-value of <0.05.

476
 477
 478
 479

Nest variable	18°C mean ±SE	30°C mean ±SE	F-value	df	p-value	Interaction p-value
Total mass (g)	29.69 ±1.89	24.03 ±1.50	10.48	1,23	0.004*	
Hood mass (g)	8.52 ±0.84	6.73 ±0.57	7.67	1,23	0.011*	0.014*
Cup mass (g)	20.96 ±1.51	16.74 ±1.11	8.52	1,23	0.007*	
Average cup wall thickness (mm)	28.26± 1.71	23.74±1.37	8.56	1,22	0.007*	0.01*
Base thickness (mm)	34.13 ±0.26	30.17 ±0.19	1.65	1,23	0.212	
Cup depth (cm)	4.66 ±0.26	5.01 ±0.19	1.79	1,23	0.194	
Hood thickness (mm)	32.10 ±2.47	33.34 ±2.91	0.12	1,23	0.728	
Thread mass (g)	15.93 ±2.06	8.97 ±1.12	10.55	1,23	0.003*	
Grass mass (g)	10.99 ±0.72	12.97 ±0.74	10.56	1,23	0.003*	
Feather mass (g)	1.93 ±0.21	1.61 ±0.18	1.89	1,23	0.182	

480

481 **Figure**
482



483 **Figure 1.** Comparison of the total mass of each of the two nests built under 18 °C and
484 30 °C by each of the 24 breeding pairs.
485