

Reproductive consequences of material use in avian nest construction

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Highlights

- We tested if material rigidity affects birds' nest-building and/or breeding performance
- For stiff-string builders, fledgling success increased with decreasing use of this material
- For flexible-string builders, fledgling success increased with increasing use of this material
- Physical differences in nest material can differentially affect avian reproduction

Abstract

Birds' nests represent a rich behavioural 'fingerprint', comprising several important decisions—not the least of which is the selection of appropriate material. Material selection in nest-building birds is thought to reflect, in part, builder-birds' use of the 'best' material—in terms of physical properties (e.g., rigidity)—refined across generations. There is, however, little experimental evidence to link the physical properties of nest material to *both* birds' nest building and breeding performance. We examined individual-level material-use consequences for breeding zebra finches by manipulating the kind of material available to laboratory-housed pairs: stiff or flexible same-length string. We show that higher fledgling numbers were related to (i) fewer pieces used in nest construction by stiff-string builders; and conversely, (ii) more pieces used in nest construction by flexible-string builders. Together, these data suggest that physical differences in nest material can affect avian reproduction (here, the trade-off between nest-construction investment and fledgling success), highlighting the adaptive significance of nest-building birds' material selectivity.

1. Introduction

To reproduce, most birds need to construct a nest. Avian nest construction involves the selection of, first, a site, and then, material, which a bird manipulates into a structure—the nest—that is often typical of their species within a given area (Briggs and Deeming, 2016; Hansell, 2000; Healy et al., 2015; Mennerat et al., 2009). Such material ‘choosiness’ by nest-building birds is presumably based, in part, on physical affordance(s) of the material favoured by natural selection (Hansell, 2000; Mainwaring and Hartley, 2013; Wallace, 1867). Cape Weavers (*Ploceus capensis*), for example, seem to select stronger, stiffer, and thicker material to enhance nest structural integrity (Bailey et al., 2016). Indeed, the impact of material physical properties, such as size, mass and/or rigidity, on avian reproduction, is likely to be substantial, as a bird that uses the ‘wrong’ material could incur one, or multiple, costs. The currency of the cost(s) incurred might be in the energy and/or time expended on material collection, nest construction, and/or the number of chicks fledged (reviewed in Mainwaring and Hartley 2013). To our knowledge, however, no experimental data yet exist to confirm a link between the physical properties of nest material and *both* nest building and breeding performance in birds, likely due to logistical constraints inherent to field studies.

Here, we manipulated the material available to birds breeding under laboratory conditions, to directly examine links between material use, nest construction, and ultimately, how these two traits together affect avian reproduction. We used a model species (Breen et al., 2016) for experimental study on nest construction in the laboratory: the zebra finch (*Taeniopygia guttata*). In the wild, zebra finches are a nomadic, opportunistically breeding species; thus, builder-males need to be able to quickly identify suitable material—typically, stiff grass stems—for species-typical

domed nest construction (Zann, 1996). Because they are sensitive to the physical properties of different kinds of material in the laboratory (reviewed in Breen et al. 2016), it seems that male zebra finches are capable of minimising unprofitable material-use decisions. For example, males (i) choose paper of the same colour as the environment in which they build (i.e., they camouflage their nest; Bailey et al. 2015); (ii) change their preference for one of two coloured material-types based on previous breeding success (Muth and Healy, 2011); (iii) initially select material of the appropriate length for a particular nest site (e.g., short and not long material for a nestbox with a small entrance hole; Muth & Healy 2014); and (iv) learn to prefer more rigid ('stiff') string over less rigid ('flexible') string of identical lengths after building and breeding in nests of either string type (Bailey et al. 2014).

The experience-driven preference for stiff over flexible same-length string seen in laboratory-housed zebra finches is thought to reflect males' sensitivity to the number of pieces used in nest construction (stiff < flexible; Bailey et al. 2014), as energetic expenditure during nest construction appears related to the number of material collection trips (Hansell, 2000; Mainwaring and Hartley, 2013; but see Deeming et al., 2019). This supposition is supported by observational data showing that material-use patterns in wild nest-building birds correspond to the flight-distance required to collect material (Cantarero et al., 2015; Surgery et al., 2012), and by experimental data showing that a forced increase in nest-construction investment is linked to a decrease in reproductive success (Haywood, 1993; Lambrechts et al., 2012; Winkel, 1970). Based on this evidence, we provided male-female pairs of zebra finches either stiff or flexible pieces of string of identical lengths, and we recorded their breeding progress, beginning with nest construction through to the fledging of chicks, to probe the ultimate consequences of breeding birds' material use. If physical differences in nest material

influence avian reproduction, we expected stiff-string builders to use less pieces (i.e., energy) for nest construction, and, consequently, fledge (with the help of their female partner) more chicks, compared to pairs that build with flexible string.

2. Material and methods

2.1. Subjects and housing

Sixty-seven adult (age range: >90 days to ~2 years of age) non-sibling male-female zebra finch pairs participated in the study. All birds were bred at the University of St Andrews. The males of the breeding pairs were the experimental subjects: because they are the builders in this species (female participation is limited to within-nest manipulation of material brought by the male; Zann 1996). All of the males had previous nest-construction experience, and all of the females were experienced breeders. The birds were housed in same-sex colony cages (140 × 71 × 122 cm) on a 14:10 light:dark light cycle with humidity at ~50% and temperature ~20° C; they were also provided *ad libitum* access to seed (Johnston & Jeff Ltd., UK), oystershell grit, calcium, vitamin block, and vitamin supplemented water, and fresh spinach (three × per week).

2.2. Experimental treatments and set-up

There were two treatment groups: we provided pairs with either 15 cm lengths of stiff string ($n = 35$ pairs) or 15 cm lengths of flexible string ($n = 32$ pairs) with which to construct their nest (Fig. 1a; both string types were obtained from James Lever Co., London, UK). We used string rather than natural material (e.g., grasses) as this allowed us to control for differences in string rigidity across treatments. Indeed, when hung over a horizontal wire at midpoint, the stiff and flexible string differ in rigidity (as

measured from the distance between the string-ends) by 1 cm (Bailey et al., 2014). All string was coloured off-white with a diameter of 3 mm. None of the pairs had previously encountered these kinds of string.

Each of the 28 experimental cages (100 × 50 × 50 cm) always contained six perches, one food and one water bowl, as well as one food and one water hopper, cuttlefish bone, oystershell grit, and vitamin block (Fig. 1b); and we hung a white curtain between each cage column to reduce between-cage distraction to pairs. Admittedly, this test environment does not mirror—in terms of space and resource availability/proximity—the natural environment; hence, any detected effects should be considered *conservative*.

2.3 Experimental protocol

We carried out the experiment in three blocks: (Block 1: $n = 28$ pairs; Block 2: $n = 28$ pairs; Block 3: $n = 11$ pairs). Which string type pairs received, and thus which treatment we assigned each to, was balanced across pairs within each experimental block, with the exception of Block 3 (stiff string: $n = 7$; flexible string: $n = 4$). Six days before the start of each experimental block, we placed non-related birds in male-female pairs in the experimental cages, which allowed adequate time for pair bonds to form. None of the birds were paired with a previous partner. At light on-set on the seventh day we attached a wooden, open-box nestbox (11 × 12 × 4.5 cm) midway along the back-cage wall, and we then provided each pair with 400 pieces of treatment-specific string (stiff or flexible), placed in four piles ($n = 50$ pieces per pile) in a row across the cage floor ~20 cm apart (for an example of the material and set-up, see Fig. 1b). We provided a further 400 pieces of the same string type each subsequent day unless >5 pieces of string remained from the previous day or a female had laid at least one egg

in the nest. We provided the string in blocks of 400 pieces because laboratory-housed zebra finch males can build a species-typical domed nest with this amount of 15 cm lengths of material (Breen et al. 2019). Once a female laid her first egg, we removed all material not used for nest construction. From when we placed material into their cage, females of each pair were allowed 35 days to lay their first egg, and, if an egg was laid, pairs were allowed a further 35 days to hatch chicks, before we classified these pairs as having failed and returned them to their respective colony cages, following Bailey et al. (2014). We removed the nest (or nests; see below) of successful pairs five days after their first chick had fledged (to allow adequate time for all chicks to fledge; Zann 1996), and, for those pairs that failed, we removed their nest(s) immediately after we returned each bird to group housing. Offspring of successful pairs remained housed with their parents until 45 days post-hatching, after which, we fitted each juvenile bird with an identification ring (A C Hughes Ltd., UK), recorded their sex, and moved them and their parents to same-sex colony cages.

For all pairs, we monitored their breeding progress once per day, recording whether we observed the following behaviours: (I) nest construction; (II) egg laying; (III) hatching; and (IV) fledging; we also recorded cases ($n = 5$) where a chick died (each of these behaviours are defined in Table S1). For each pair we further recorded, from collected nests, where the nest had been constructed (in the nestbox or on the cage floor), its structure (here, we classified structure based on the presence or absence of a roof), and, after we disassembled each nest, the total number of pieces and unhatched eggs each contained. If a pair constructed more than one nest, we did not count the pieces each contained or include the pair in our analyses, as detailed below.

Unexpectedly, thirty-seven (stiff: $n = 20$; flexible: $n = 17$) of the 67 males in the current experiment constructed at least one additional nest (mean number of additional nests constructed: stiff, 2.85 ± 0.28 ; flexible, 3.35 ± 0.30) either before (stiff, $n = 8$; flexible, $n = 7$) or after (stiff, $n = 6$, flexible, $n = 6$) his female had laid her first egg in a nest, or the 35-day egg-laying cut-off criterion was reached (stiff, $n = 6$, flexible, $n = 4$). In doing so, these multi-nest builders re-used some or all of the provided string, rendering count data for the number of pieces used in nest construction inaccurate: because we could not count pieces in nests that no longer existed, or track the amount of material moved back-and-forth between nests. For example, it was not uncommon among multi-nest builders for an individual to: (i) build a nest; (ii) use some of the material from that first nest for a second nest; and then, (iii) use some or all of the material from the first and second nest to build a third nest. Thus, we excluded the data from all males that built more than one nest from our statistical analyses. We also excluded data for three single-nest builders (stiff, $n = 2$; flexible, $n = 1$) since their nests were prematurely thrown-away before the pieces within were counted. Of the remaining 27 single-nest builders, three were paired with a female who did not lay an egg (stiff, $n = 2$; flexible, $n = 1$), and these pairs were also excluded from our analyses to avoid confounding any effect of treatment with possible physiological defects (e.g., calcium deficiency) in female egg-laying capacity. The final dataset thus included data on 24 single-nest builders (stiff, $n = 11$; flexible, $n = 13$), highlighting some of the challenges of data collection despite laboratory conditions. Nonetheless the experimental setting allowed us to greatly reduce the amount of random variation in our data—a prerequisite of sample size economisation (Taborsky, 2010).

2.4 Statistical analyses

To determine the effect of both string rigidity and builder investment on pairs' reproductive success, we examined whether the type and/or amount of string used by males in nest construction was related to the number of chicks they (plus their partner) fledged. As the act of producing a fledgling can be effectively considered a successful event (and not producing a fledgling, a failure), we analysed these fledgling data using a binomial generalised linear model (GLM; Model 1) in R (R Core Team, 2017). The fixed-effects structure of our model included string type (stiff or flexible), the number of pieces used in nest construction (Tukey-transformed to normalise residuals; Tukey 1977), and their interaction. The response variable of our model was the proportion of chicks successfully fledged per clutch. We used this measure of fledgling success as our response variable because it allowed us to account for failures at both the incubation and rearing level (hatching and fledging failures, respectively; although we note that fledging failures were nearly non-existent: $n = 5$ chick deaths across two stiff- and one flexible-string nest(s)). Because not all of the females laid identical clutch sizes, in Model 1 we accounted for this variation in sampling across pairs by specifying model 'weights' as the total number of eggs laid i.e., the number of potential fledging events or 'trials' (King and Zeng, 2003).

At least one study suggests that birds (female magpies *Pica pica*) can adjust the number of eggs they lay based on experimental manipulation (the removal or addition of some roofing material) of their partner's nest construction (Soler et al., 2001). Thus, we also examined if the type and/or amount of string used by the builder-males in our study were related to female clutch size. To do this we fitted an additional GLM (Model 2) with a Poisson error structure for count data. Accordingly, the response

variable in our second model was the number of eggs laid by each female in her clutch. The fixed-effect structure of Model 2 was identical to that of Model 1 (described above).

For both Model 1 and 2, we used: (i) the 'testUniformity' function from the 'DHARMA' package (Hartig, 2017) on the scaled model residuals to confirm the model goodness-of-fit (both $p > 0.05$); and (ii) Type II likelihood-ratio chisquare tests from the 'car' package (Fox and Weisberg, 2011) to assess model significance (Langsrud, 2003). Because the majority of pairs constructed a nest of the same structure (non-roofed: stiff, $n = 8$; flexible, $n = 11$; roofed: stiff, $n = 3$; flexible, $n = 2$) in the same location (nestbox: stiff, $n = 11$; flexible, $n = 10$; floor: stiff, $n = 0$; flexible, $n = 3$), we did not include either of these variables as a mixed effect in our models to prevent model overfitting.

3. Results

String rigidity and pieces used for nest construction *together* affected breeding pairs' fledgling success (material rigidity, $\chi^2 = 0.44$, $n = 24$, $p = 0.509$; builder investment, $\chi^2 = 0.50$, $n = 24$, $p = 0.480$; interaction term: $\chi^2 = 9.27$, $n = 24$, $p = 0.002$; Model 1); a result that was robust to data truncation (see supplementary analysis). For stiff-string builders (Fig. 2a, top panel), the fewer pieces used by males to construct their nest, the more chicks per clutch they (plus their partner) fledged (Fig. 2b, top panel). Conversely, for flexible-string builders (Fig. 2a, bottom panel), fledgling success increased with increasing use of this material by males for nest construction (Fig. 2b, bottom panel). Females of breeding pairs did not adjust the number of eggs they laid within a nest based on the string type and/or the number of pieces used for its construction (material rigidity, $\chi^2 = 1.63$, $n = 24$, $p = 0.202$; builder investment, $\chi^2 =$

0.02, $n = 24$, $p = 0.883$; interaction term: $\chi^2 = 0.67$, $n = 24$, $p = 0.412$; Model 2; Fig. 2c).

4. Discussion

For decades, popular belief has it that nest-building birds largely base their choice of appropriate material on particular physical properties of that material (for example, its rigidity), because natural selection has favoured the use of those material properties over others (Hansell, 2000; Mainwaring et al., 2014; Wallace, 1867). Any such evolutionary refinement in nest-building birds' use of material would require differential breeding outcomes between physically distinct types of material. To our knowledge, the current data provide the first experimental demonstration of a link between a physical property of nest material and aspects of birds' nest building *and* breeding performance. When laboratory-housed pairs of zebra finches were provided either stiff or flexible pieces of same-length string for nest construction, we found: (i) that, consistent, in part, with our expectation, higher fledgling numbers were related to *fewer* pieces used in nest construction by stiff-string builders; (ii) that, conversely, the flexible-string builders that used *more* pieces in nest construction also fledged (with help from their female partner) more chicks; and (iii) that the differences in pairs' reproductive success cannot be explained by differences in female egg-laying: the number of eggs that a female laid in a nest was unrelated to the string type, or the number of pieces, within that nest—or the two together. Collectively, these data imply that physical differences in nest material influenced the trade-off between energetic investment (that is, the number of pieces used) in nest construction and pairs' fledgling success.

It has been proposed that a learnt preference to use stiff and not flexible string in male zebra finches is a cost-cutting response—in terms of energetic expenditure—to differences in the number of pieces required for nest construction (stiff < flexible; Bailey *et al.* 2014). The current study thus provides substantial albeit indirect support for this hypothesis but with one addendum: the stiffer string allows males to maximise reproductive success through lower energetic expenditure (that is, fewer material collection trips/deposits). Such energy savings should confer later benefits to pairs, in both their current breeding attempt (with, for example, shared incubation and/or chick-rearing duties—both tasks are demanding; Vleck 1981; Lemon 1993), and any subsequent breeding attempts (which, in the wild, since zebra finches are opportunistic breeders, can range up to six attempts in a single breeding period; Zann 1996), but future work is required to test this hypothesis. Nevertheless the current data indicate (based on our observation that only five of the 66 chicks that hatched then failed to fledge) that differences in the reproductive success of pairs originated before the hatching stage, during fertilisation or incubation or both. To improve incubation conditions (perhaps by incorporating a nest cup; Heenan 2013; Fig. 2a), flexible- but not stiff-string builders, then, may have needed to use more string, likely at the expense of future breeding efforts. If zebra finches trade-off the energetic costs of nest construction and incubation between successive reproductive events, selection should favour the ability to learn, both individually and socially, which are appropriate material for building.

In conclusion, the differential impact of string rigidity on builder-bird investment, suggested here, provides a possible proximate explanation for why material-use patterns in nest-building birds appear to respond to differences in the structural efficacy (pieces invested in nest construction) of material (Bailey *et al.*, 2014).

Together these data from zebra finches imply that, unlike nest structure (Krause and Schrader, 2016; Price and Griffith, 2017), nest material might not be as stable a trait over evolutionary time. Recent experimental evidence shows that adult zebra finches have the capacity to shape which material juvenile conspecifics will later prefer for constructing their first nest (Breen et al., 2020), and so it seems plausible that shifts in material use could happen within a generation (Breen, 2021). Zebra finches thus present a useful system to increase understanding of the adaptive potential of nest-building birds—a topic of increasing importance in the face of climate-change driven shifts in material availability (Mainwaring et al., 2017).

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Authors' contributions

A.J.B., S.D.H, and L.M.G. conceived of and designed the study. A.J.B. carried out the experiment, and collected, processed, analysed, and visually presented the data. A.J.B. wrote the manuscript, and S.D.H. and L.M.G. contributed to manuscript edits. All authors read and approved the final manuscript.

Data and code availability

Data and R script for this study are available as electronic supplementary material.

Competing interests

The authors declare no competing interests.

Ethics approval

The study described here was conducted with the approval of the University of St Andrews Animal Welfare and Ethics Committee.

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Fig. 1

Experimental materials and set-up. (a) Photograph of the two string types used in the current experiment: 15 cm lengths of polished stiff cotton string (left) and 15 cm lengths of unpolished flexible cotton string; both with diameter of 3 mm. (b) Top-down photo of the experimental test-cage layout including an example of the string presentation when placed within the cage (here, stiff string is pictured).

Fig. 2

Reproductive consequences of material use differ between material types. (a) Two nests constructed by two different male zebra finches in the laboratory using ca. 100 pieces of either stiff or flexible string cut to 15 cm lengths. (b) Proportion of chicks successfully fledged per clutch and (c) number of eggs per clutch, for pairs given 15 cm lengths of stiff or flexible string as a function of builder investment (the number of pieces used in nest construction—Tukey-transformed for scaling purposes). For panels (b) and (c), each symbol corresponds to an individual observation (square, stiff-string treatment; circle, flexible-string treatment); lines indicate linear least squares regression ‘trends’. In all panels: stiff-string treatment = blue; flexible-string treatment = orange. Panels with untransformed string-count data are available in the electronic supplementary material.

Fig. 1

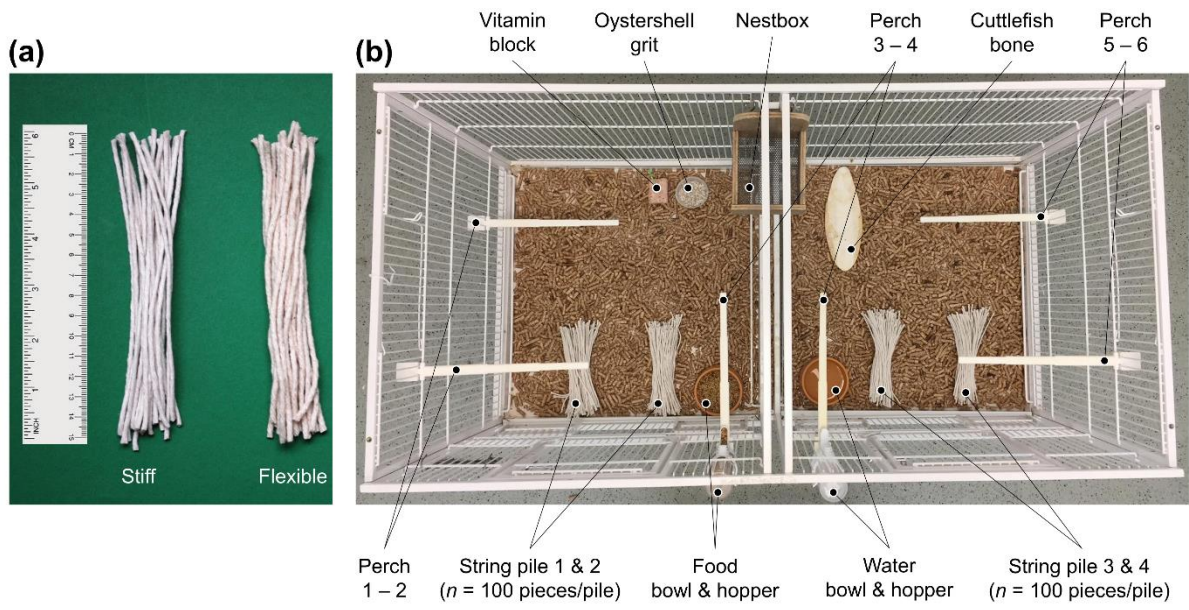


Fig. 2

