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Repeatability of nest morphology in African weaver birds

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It is generally assumed that birds build nests according to a genetic 'template', little influenced by learning or memory. One way to confirm the role of genetics in nest building is to assess the repeatability of nest morphology with repeated nest attempts. Solitary weaver birds, which build multiple nests in a single breeding season, are a useful group with which to do this. Here we show that repeatability of nest morphology was low, but significant, in male Southern Masked weaver birds and not significant in the Village weavers. The larger bodied Village weavers built larger nests than did Southern Masked weavers, but body size did not explain variation in Southern Masked weaver nest dimensions. Nests built by the same male in both species got shorter and lighter as more nests were constructed. While these data demonstrate the potential for a genetic component of variation in nest building in solitary weavers, it is also clear that there remains plenty of scope in both of these species for experience to shape nest construction.

Keywords: experience; nest building; repeatability; weaver bird

1. INTRODUCTION

Nest building in birds is a widespread, commonly observed behaviour, and yet we understand rather little about how birds construct what appear to be species-specific nests. Simple, stereotyped building rules seem to explain even seemingly complex constructions in invertebrates (Hansell 2005), but how relevant such rules are to avian nest construction is unclear. While it is generally assumed that nest building in birds is largely innate (e.g. Hansell 2000; Moller 2005; Raby & Clayton 2009), there are some species that build nests which seem beyond such simple rule-governed, innate construction. Striking examples come from the weaver birds (Family Ploceidae), which weave and knot plant material in a way that has been likened to weaving in humans (Collias & Collias 1984).

A key to understanding how nest construction is achieved is to determine the degree of repeatability of nest morphology, as repeatability sets an upper limit on the heritability of a trait, i.e. the potential genetic variation in a trait (e.g. Lessells & Boag 1987; Boake 1989). As such, it has been used to demonstrate significant potential for genetic control over nest building in sticklebacks, penduline tits and barn swallows (Schleicher *et al.* 1996; Moller 2005; Rushbrook *et al.* 2008). The other side of the construction coin is the contribution made by previous experience, including that associated with learning and memory (Healy *et al.* 2008). Little is known about the importance of experience, but it is from weaver birds that there is most evidence for a role for experience in changing nest structure: the nests of first-year males are untidy and loosely woven compared with those of mature males (Collias & Collias 1964). It is unclear, however, to what extent the variability of weaver bird nests may be genetic in origin.

In order to determine the repeatability of nest morphology (width, length and height) in solitary weaver birds, we collected series of nests built by male Southern Masked weavers *Ploceus velatus* in Botswana and by the larger bodied male Village weavers *Ploceus cucullatus* in Nigeria.

2. MATERIAL AND METHODS

Completed nests were collected (November–December 2008) from colour-ringed Southern Masked weavers in south-eastern Botswana (Atholl Holme 11-KO, Gaborone) approximately 30 days after they were built. By this time the chicks had fledged. In total, 66 nests were collected: three to eight (mean $\pm$ s.e.m.: 4.71 ± 0.40) nests each for 14 different males. We used wing length (11 of the 14 males) as a proxy of male body size (Gosler *et al.* 1998).

We also collected 27 nests (June–July 2008) from Village weavers in central Nigeria (Laminga Village, Jos, Nigeria), after males completed building the nest: three to six (4.33 ± 0.42) nests each for six males. No body size measurements were available for the Village weavers.

For both species, the order in which the nests were built was determined by periodic observation of males' territories, daily in the case of the Southern Masked weavers and three times a week for Village weavers. However, as some nests were destroyed before collection, the nest data are analysed in sequential, rather than numerical, order.

To measure each nest, digital images were captured using a 10 mega-pixel digital camera and analysed using image analysing software (Measuring Vegetation Health). Photographs were taken from a camera on a fixed tripod, with each nest placed 1 m away in front of A3 (420×297 mm) 1 cm grid graph paper to provide a scale for the images. Each nest was photographed from two different views: (i) a lateral side (the same side for all nests) provided nest length and height (figure 1), and (ii) the posterior side, which provided the nest width. Each nest was measured four times with the mean value used in the analyses. Nests were weighed using an electronic balance (± 0.1 g).

The date of nest construction and the sequential order in which the nests were constructed were highly correlated ($\rho = 0.62$, $p < 0.0001$), so Pratt's measure of relative importance (PRI; Pratt 1987) was used to determine that nest order (PRI = 1.156) was substantially more important than was date of construction (PRI = −0.156). Therefore, analyses of nest size included sequential nest order rather than date of construction. The repeatability of nest size within males and species was analysed using the three nest size variables in a multivariate ANOSIM (ANalysis Of SIMilarity), with 10 000 permutations, in the PAST statistical package (Harper 1999). Variation among males was determined using linear mixed models, in SPSS v. 17, with nests as a repeated measure and male as a random factor. Analyses were performed on log-transformed data.

3. RESULTS

The length (L) and width (W) (L: $F_{13,51} = 2.32$, $p < 0.05$; W: $F_{13,51} = 3.26$, $p < 0.005$; figure 2*a*) of nests constructed by Southern Masked weavers varied across males, but nest height (H) did not ($F_{13,51} = 1.410$, $p = 0.19$). The dimensions of nests built by

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Figure 1. A series of six nests from a single Southern Masked weaver male (ordered by date of construction from left to right).

the same male were significantly repeatable ($R = 0.21$, $p < 0.0001$). Neither variation in nest size among males nor number of nests was explained by body size (L: $F_{1,10} = 0.31$, $p = 0.59$; W: $F_{1,10} = 0.35$, $p = 0.57$; number of nests: $F_{1,10} = 2.28$, $p = 0.17$). Nests were marginally, but not significantly, different in weight among males ($F_{13,51} = 1.71$, $p = 0.09$; mean: 33.66 g $\pm$ 0.66 s.e.m.). Earlier nests built by male Southern Masked weavers were significantly longer ($F_{1,51} = 8.59$, $p < 0.005$) and tended to be heavier ($F_{1,51} = 3.17$, $p = 0.08$) and taller ($F_{1,51} = 3.30$, $p = 0.08$) than were later nests. Nest width did not vary in this species ($F_{1,51} = 3.36$, $p = 0.07$). The nest size decrease was not explained by wing length ($F_{1,46} = 0.51$, $p = 0.48$) or the total number of nests that a Southern Masked male constructed in the season ($F_{1,62} = 0.10$, $p = 0.76$).

Among Village weaver males, there was a significant difference only in nest length (L: $F_{5,26} = 4.44$, $p < 0.01$; W: $F_{5,26} = 1.13$, $p = 0.378$; H: $F_{5,26} = 0.92$, $p = 0.49$; figure 2*b*). The dimensions of nests built by individual Village weaver males were not repeatable ($R = 0.06$, $p = 0.227$). Additionally, nests varied in weight across males ($F_{5,26} = 3.79$, $p < 0.05$; mean: 50.83 g $\pm$ 2.65 s.e.m.). The earlier nests of Village weavers were longer ($F_{1,26} = 7.20$, $p < 0.05$) and heavier ($F_{1,26} = 5.94$, $p < 0.05$) and tended to be taller ($F_{1,26} = 3.44$, $p = 0.08$) than were later nests. Nest width did not vary with nest order ($F_{1,26} = 0.35$, $p = 0.56$).

The nests constructed by Village weavers were significantly longer ($F_{1,92} = 15.71$, $p < 0.0001$), wider ($F_{1,92} = 246.43$, $p < 0.0001$), taller ($F_{1,92} = 156.29$, $p < 0.0001$) and heavier ($F_{1,92} = 76.91$, $p < 0.0001$) than were the nests of the smaller Southern Masked weavers.

4. DISCUSSION

Repeatability of nest dimensions was significant in male Southern Masked weaver nests but not in Village weaver nests. Village weavers, the larger of the two species (Hockey *et al.* 2005), built nests that are larger in all three dimensions (L, W & H) and heavier than those built by Southern Masked weavers. In both species, nest length decreased across the season, a decrease that was, in Southern Masked weavers, independent of the total number of nests built and of body size.

The repeatability of nest dimensions in Southern Masked weavers confirms that there is potential for a genetic component to nest building in these birds, as seen with nest size (measured from top to bottom) in penduline tits (Schleicher *et al.* 1996). However, as repeatability was only 0.21 in Southern Masked weavers and 0.06 in Village weavers, there remains considerable within-male variation in both species, and with it scope for plasticity in the face of nest-building experience. Nest construction in Village weavers, especially, may be considerably more responsive to environmental influences than is typically considered to be the case for nest building in birds. Indeed, repeatability itself may be a reflection of a learning process such as imprinting, as copying of parental nest building could also lead to greater among- than within-male variation in nest dimensions.

Unlike penduline tits, which build relatively complex nests that do not vary systematically across the season (Schleicher *et al.* 1996), nests in both weaver species changed as the male constructed more nests: they got shorter in both length and height and weighed less. This change may be in response to changes in the weather conditions, although is not in the direction that would be predicted if that response is to enhance thermoregulation (Hoi *et al.* 1994, 1996) as weaver nests became smaller as rainfall increased and ambient temperature decreased. Alternatively, nest materials may change across the season in such a way that nest construction is altered, a possibility we are currently exploring. Changes in the size and weight of nests within the season may be an indicator of male quality (Moller 2005). Although we have not explicitly measured aspects of ‘male quality’, all of the Southern Masked weaver nests we measured were occupied by females that successfully raised offspring. In addition, male size, at least in Southern Masked weavers, does not explain the sequential decrease in nest size, as the nests of all the males decreased and the decrease was independent of the number of nests build by each male. Rather, it seems plausible that increasing nest-building experience leads to smaller nests. This interpretation may be consistent with the observation that experience leads to changes in nest structure in Village weavers in captivity: first-year male Village weavers build loose nests compared with the compact, tightly woven nests made by older, experienced males (Collias & Collias 1964).

In conclusion, although the repeatability of the dimensions of the complex nests of Southern Masked weaver birds is significant, the nests built by solitary weavers owe considerably more to the birds’ experience of their environment, physical and/or social, than has been previously considered. This leaves open the possibility that nest construction by weaver birds requires cognitive abilities not dissimilar to those used in behaviours currently described as

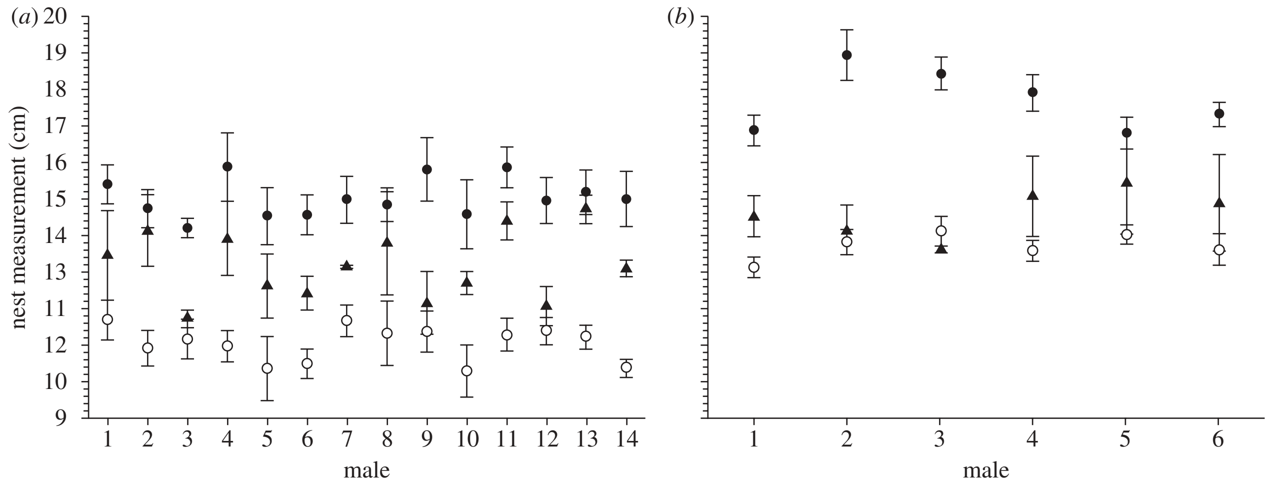

Figure 2. Mean (± s.e.m.) length (filled circles), width (open circles) and height (filled triangles) of nests built by (*a*) male Southern Masked weavers ($n = 14$) and (*b*) male Village weavers ($n = 6$).

requiring 'physical cognition' such as tool construction and tool use (Seed *et al.* 2006; Healy *et al.* 2008; Bird & Emery 2009).

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