



Individuality in nest building: Do Southern Masked weaver (*Ploceus velatus*) males vary in their nest-building behaviour?

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ARTICLE INFO

Article history:

Received 27 February 2011

Received in revised form 13 June 2011

Accepted 20 June 2011

Keywords:

Behaviour
Laterality
Nest building
Repeatability
Variation
Weaverbird

ABSTRACT

We currently have little understanding of how birds know what nest to build and what little we do know has been gained largely from investigations of the completed structures (morphology of finished nests) or of material selection. Here we looked at the behaviours performed by male Southern Masked weaverbirds when building their nests. During the two earliest phases of construction individual males varied in the direction in which they carried and inserted grass into their developing nest, the speed at which they completed phases of nest construction and in the frequency with which they dropped grass during weaving. Behaviours performed during the initial attachment phase, when grass is being secured to a bare branch, were not repeatable within males, whereas during the subsequent “ring” phase behaviours tended to be repeatable. Some males were biased as to which side of the nest they inserted grass blades and strongly lateralized individuals completed phases of nest-building more quickly. The lack of repeatability of most nest-building behaviours and the changes in those behaviours as males build more nests seems most readily explained by increasing dexterity. Further work is required to confirm any role for cognition in these experience-dependent changes.

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1. Introduction

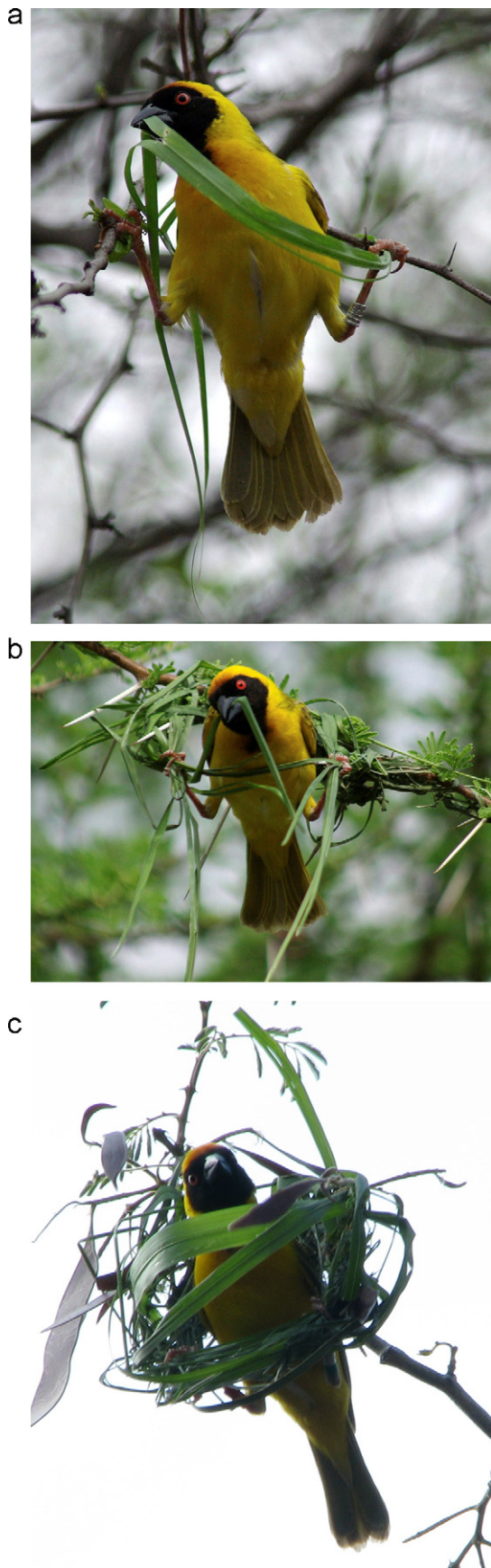
Many animals perform behaviours that are seemingly complex, such as animal building, exemplified by the intricate nests of some bird species (Gould and Gould, 2007; Hansell, 2000) and social insects (Hansell, 2005) and by the tool manufacture of the New Caledonian crows (e.g. Hunt, 1996; Weir and Kacelnik, 2006) and non-human primates (e.g. McGrew, 1974). Although it appears that relatively simple rules can explain how invertebrates produce elaborate structures, such explanations do not seem adequate for describing tool construction and use by birds and mammals (e.g. Seed and Byrne, 2010, but see Ruxton and Hansell, 2011). In addition to tool manufacture, birds and mammals also construct nests, which vary considerably in structural complexity, especially across bird species. Although it is typically assumed that nest building in birds is essentially governed by rules similar to those underlying construction behaviour in the invertebrates, rather than involving the cognitive processing involved in tool manufacture (e.g. Raby

and Clayton, 2009; Seed and Byrne, 2010), there are, in fact, few data to support this assumption (Healy et al., 2008). To date, our understanding of how birds know what nests to build have come from examining completed nests (Crook, 1963; Schleicher et al., 1996; Mennerat et al., 2009; Metz et al., 2009; Walsh et al., 2010), qualitative descriptions of species-typical nest building behaviours (Collias and Collias, 1973, 1962; Crook, 1960, 1964) and investigations of choice of nest material (Collias and Collias, 1964; Sargent, 1965), with few examinations of individual behaviour (Metz et al., 2007).

Reaching an understanding of how invertebrates produce elaborate constructions required knowledge of the constituent actions individuals use to produce the final structure (Brockmann, 1980; Downing, 1992). Here we collected data on the constituent behaviours used by male Southern Masked weaver birds (*Ploceus velatus*) when building their nests so as to investigate whether such data could allow us some insight into the mechanisms leading to the building of bird nests, and in particular, bird nests considered to be complex. Southern Masked weaver males each construct multiple woven nests in a single breeding season, which allows for comparisons of nest-building actions within and among individuals. Greater variation among conspecific individuals in behaviours used during animal construction has been proposed to be related to the role of experience or cognitive function (Heiling

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and Herberstein, 2000; Weir, 2005) although intra-species genetic variation might still explain these individual differences (Weir, 2005). One way to attempt to address the genetic component is to examine the repeatability of behaviours within an individual, as repeatability sets an upper limit on the heritability of a trait (Boake, 1989; Lessells and Boag, 1987). Changes over time, or with greater experience, in the actions performed or in their efficiency would indicate a role for experience in nest building (Downing, 1992).

We examined whether the actions performed (e.g. grass carrying, grass insertion, quadrant where weaving was conducted, and dropping of grass) or the duration of different nest building phases varied within or among individuals. The dropping of grass may also reflect an ineffective sequence of movements (Collias and Collias, 1964). If nest building is achieved by fixed action patterns or predominantly under genetic control as is often assumed (e.g. Hansell, 1984; Nicolakakis and Lefebvre, 2000; Raby and Clayton, 2009), then these behaviours should show little inter-male variation and significant repeatability.

2. Materials and methods

2.1. Study species and procedures

The nest building of seven colour-ringed male Southern Masked weaver birds (*P. velatus*) was digitally recorded in southern Botswana (Athol Holm Farm, Gaborone) using Sony Handycam DCR SR210E camcorders mounted on adjustable height (up to 2 m) tripods. The cameras were set up so that they were either directly facing or behind the bird when building the nest, so that all footage was taken from points perpendicular to the nest.

The nesting territories of males were searched daily during active building periods between 0530 and 1845 h to ensure that nests were found at the beginning of construction. Nests were recorded until the egg chamber, where the eggs would be housed, was closed off and it was no longer possible to see into the nest. The building of three nests by each of the seven males was recorded. The total number of nests built by each male during the season was also recorded, as was the number of days between the onset of building of the filmed nest and the start of the subsequent nest, which we termed 'nest completion time'. As males continue to add material to 'completed' nests, nest completion was not as clear as might be expected. Hence, we took the beginning of a new nest as a measure that the previous nest was sufficiently complete and could be used by a female.

We looked at the first two key phases of nest building (adapted from descriptions provided by Collias and Collias (1984): the initial attachment (IA) phase and the ring (R) phase. The initial attachment phase was considered to extend from the first piece of grass added to a branch (Fig. 1a) until two pieces were joined across the bottom of the structure forming the central ring of the nest (Fig. 1b). For the ring phase we combined 'ring' and 'roof' phases described by Collias and Collias (1984) because building gradually progresses between the two phases with no discrete event to mark the separation between the two. For our study, we took the beginning of the ring phase to be at the end of the initial attachment phase and to end when two pieces of material had been run across the front

Fig. 1. Photographs indicating the beginning (a) and end (b) of the initial attachment phase and the end of the ring phase (c). In (b) the end of the initial attachment phase is demarcated by the two blades of grass running beneath the male and completing the formation of a ring. In (c) the end of the ring phase is demarcated by the two blades of grass projecting in front of the male, which form the start of the egg chamber. The photographs are only to indicate the different phases of building and were not taken from the same positions or angles as the video footage. Courtesy of Felicity Muth (a) and (b) and Rachel Walsh (c).

of the ring projecting outwards from the plane of the central ring (Fig. 1c).

2.2. Video analysis

Analysis of the video footage was performed using Observer XT v7 (Noldus, Wageningen, Netherlands) with the researcher blind to the identity of the male and date of building. We coded the side of the beak from which the blade of grass protruded, the side of the nest into which the first end of a grass blade to be woven was inserted, the part of the nest into which the male wove the grass, the duration of total time spent weaving and the amount of time the male spent weaving in each part of the nest. The measurement of time spent weaving was restricted to the actual time spent at the nest manipulating material. These actions were chosen since they offered clear, quantifiable measures of the actions used by males during nest building. Each of these measures was taken for each visit to the nest. The developing nest was divided into four parts (quadrants): top, bottom, left and right. We also recorded those instances in which males lost hold of, or completely dropped, the grass while weaving.

2.3. Statistical analysis

We analysed the directionality of carrying and inserting grass, the total time spent weaving, the nest completion time, the time (corrected for total weaving time as a covariate) spent weaving in each of the quadrants, and the frequency of dropping grass using Linear Mixed Models (LMM) with male included as a random factor and nest order as a repeated measure.

Whether the insertion of grass into either the left or right side of the nest deviated from being 1:1 was determined with a repeated *G*-test for goodness of fit (McDonald, 2009). We designated directional laterality as a right-bias, which was the proportion of behaviours directed to the right-hand side of the nest minus 0.5. Thus, -0.5 represents a 100% bias to the left while 0.5 represents a 100% bias to the right. 0 represents no bias. We used the absolute value of the right bias scores to determine the strength of laterality, independent of directionality. This could range from 0 (no lateralization) to 0.5 (strong lateralization).

To determine whether the duration of nest building was affected by the strength of laterality, the absolute bias score was included as a covariate in the total time males spent weaving and nest completion time LMMs mentioned above. The total number of nests was analysed in a general linear model (GLM), with male as random and absolute bias score as a covariate. LMM and GLM analyses were performed using PASW v18.

Repeatability of lateral preference in carrying and inserting grass, losing grass, time spent weaving and the pattern of weaving in each quadrant within males was analysed in separate multivariate ANOSIM (ANalysis Of SIMilarity), with 10,000 permutations, in the PAST statistical package (Harper, 1999). In repeatability analyses, all measures were represented as a single figure for each nest for each male ($n = 21$).

3. Results

3.1. Inter-male variability and intra-male repeatability

Males did not vary among themselves in the direction that the blade of grass protruded from their bill during the initial attachment phase ($F_{6,12} = 1.13$, $p = 0.40$) but they did vary during the ring phase ($F_{6,12} = 3.00$, $p = 0.05$). During the initial attachment males switched from being marginally right biased to marginally left biased in the direction they carried grass as they built more nests

($F_{2,12} = 6.63$, $p = 0.01$). However, during the ring phase the directionality of carrying grass did not change and it did not change as they built more nests ($F_{2,12} = 0.99$, $p = 0.40$). The directionality of carrying grass was not repeatable within males during either phase of construction (IA: $R = -0.11$, $p = 0.89$; R: $R = 0.13$, $p = 0.10$).

Males varied in their bias for inserting grass into the right side of the nest during both the initial attachment ($F_{6,12} = 6.17$, $p = 0.04$; Fig. 2) and the ring phase ($F_{6,12} = 3.57$, $p = 0.03$; Fig. 2). The bias expressed was not repeatable within males during the initial attachment phase ($R = 0.08$, $p = 0.20$) but was repeatable within males during the ring stage ($R = 0.44$, $p = 0.0005$). The directional bias of inserting grass did not change, in either phase of construction (IA: $F_{2,12} = 0.98$, $p = 0.40$; R: $F_{2,12} = 2.10$, $p = 0.17$), as males built more nests.

The total time spent weaving the initial attachment phase did not vary among males (mean: 773.06 s (± 99.95 s.e.); $F_{6,11} = 0.60$, $p = 0.72$). Males did, however, differ in the total time spent weaving the subsequent ring stage (mean: 999.00 s ± 92.30 s.e.; $F_{6,11} = 5.73$, $p = 0.006$). The time taken to complete the initial attachment phase was highly variable within males ($R = -0.12$, $p = 0.91$) but the time taken to complete the ring phase was significantly repeatable within males ($R = 0.30$, $p = 0.006$). The time spent weaving during each phase did not change as males built more nests (IA: $F_{2,11} = 1.39$, $p = 0.29$; R: $F_{2,11} = 0.05$, $p = 0.96$). Across males there was no variation in how long they took to complete a nest ($F_{6,11} = 0.34$, $p = 0.90$), although there was considerable within-male variation ($R = 0.01$, $p = 0.40$). Males did not complete nests sooner as they built more nests ($F_{2,11} = 1.44$, $p = 0.28$).

The amount of time spent weaving in each of the four quadrants differed during both the initial attachment phase ($F_{3,52} = 8.76$, $p < 0.0001$) and the ring phase ($F_{3,52} = 4.24$, $p = 0.009$). Males wove at the top of the developing nest structure for longer than at any other place and carried out very little weaving at the bottom of the nest. No more time was spent weaving on one side relative to the other (post hoc tests IA: $p = 0.98$; R: $p = 0.74$; Fig. 3). This pattern of weaving was similar for all males during both the initial attachment phase ($F_{18,24} = 0.47$, $p = 0.96$) and the ring phase ($F_{18,52} = 0.77$, $p = 0.72$) and did not change with nest order (IA: $F_{3,52} = 0.41$, $p = 0.99$; R: $F_{3,52} = 0.22$, $p = 0.88$). The duration of weaving in each quadrant was not repeatable within individuals during the initial attachment phase ($R = -0.03$, $p = 0.58$) but it was during the ring phase ($R = 0.21$, $p < 0.05$).

Males varied in the frequency with which they dropped grass during the initial attachment phase ($F_{6,12} = 3.23$, $p < 0.05$) but not

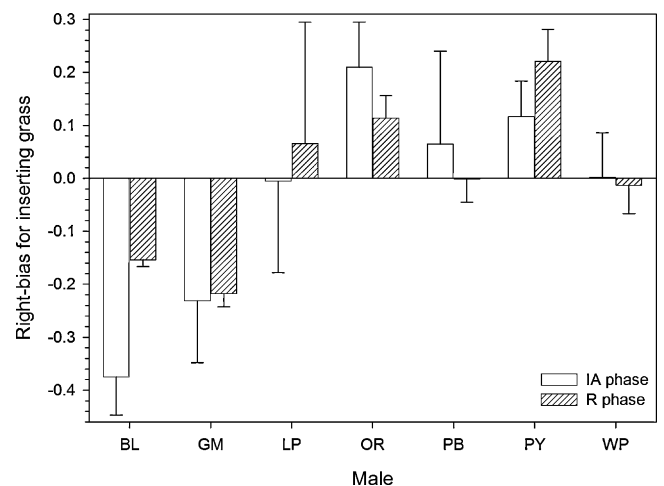


Fig. 2. The mean (\pm s.e.) right bias for inserting grass into the nest for each of the seven males during the initial attachment and the ring phase. Positive values indicated a right bias and negative values a left bias, 0.0 represents no bias.

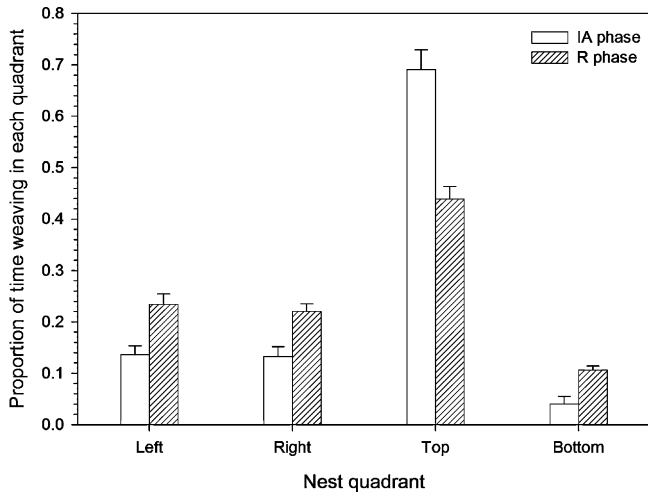


Fig. 3. The mean (\pm s.e.) proportion of time spent weaving in each quadrant of the nest during the initial attachment and ring phases of construction.

during the subsequent ring phase ($F_{6,12} = 0.88$, $p = 0.54$). The frequency of dropping grass was not repeatable within individuals during either the initial attachment phase ($R = 0.03$, $p = 0.37$) or the ring phase ($R = 0.10$, $p = 0.16$). The frequency with which males dropped grass decreased as they built more nests during the initial attachment phase ($F_{2,12} = 7.53$, $p < 0.01$) but not the ring phase ($F_{2,12} = 0.15$, $p = 0.86$; Fig. 4).

3.2. Laterality

None of the males consistently held blades of the grass to the right or to the left of their bill when returning to the nest (7 G -tests, all $p > 0.1$).

Across males there was no bias as to the side of the nest in which they inserted the first end of a blade of grass during either the initial attachment phase ($G = 0.06$, $n = 161$, $p = 0.81$) or during the ring phase ($G = 0.00$, $n = 439$, $p = 0.96$). However, two of the seven males typically inserted the first end of the grass into the right of the nest (PY: $G = 4.38$, $n = 24$, $p < 0.05$; OR: $G = 13.81$, $n = 21$, $p < 0.0005$) and two typically inserted the first end of the grass into the left side (BL: $G = 11.89$, $n = 21$, $p < 0.001$; GM: $G = 7.80$, $n = 23$, $p < 0.01$) during the initial attachment phase (Fig. 2). This bias was also evident in the following ring phase (to the right: PY: $G = 16.19$,

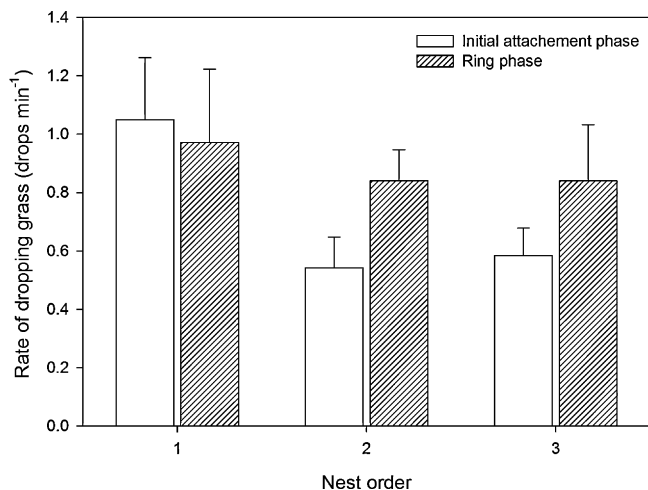


Fig. 4. The mean (\pm s.e.) rate with which males dropped grass during the initial attachment and ring phases of construction.

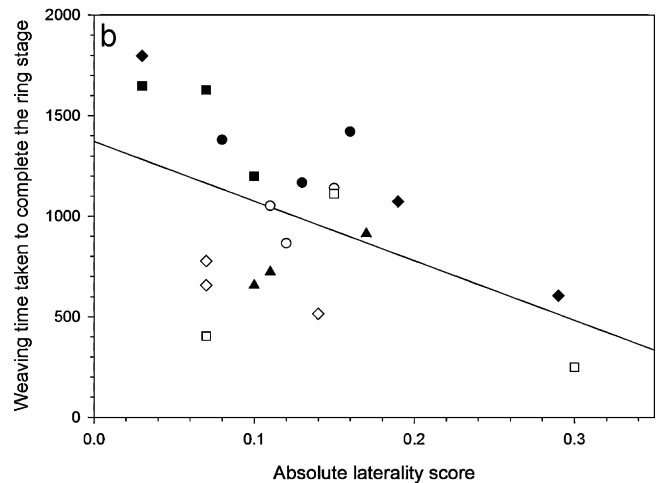
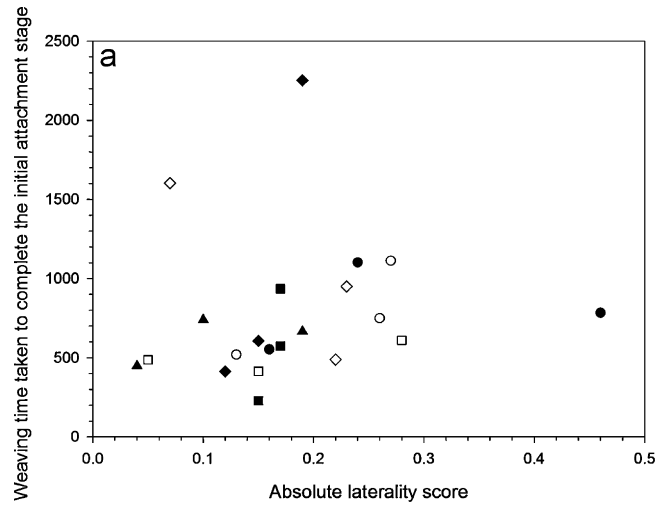


Fig. 5. The relationship between the strength of laterality, expressed as the absolute difference from neutral, and the time (s) spent weaving to complete the initial attachment (a) and ring (b) phase of nest construction for the seven males (●: BL; ○: GM; ◆: LP; ◇: OR; ■: PB; □: PY; ▲: WP).

$n = 41$, $p < 0.0001$; OR: $G = 11.13$, $n = 38$, $p < 0.001$; to the left: BL: $G = 7.51$, $n = 78$, $p < 0.01$; GM: $G = 15.03$, $n = 75$, $p < 0.0001$; Fig. 2). The remaining three individuals did not have a side bias (6 G -tests, all $p > 0.4$).

The strength of lateralization was not significantly related to the time spent weaving during the initial attachment stage ($F_{1,11} = 2.48$, $R^2 = 0.02$, $p = 0.14$; Fig. 5a). However, the more lateralized the male's behaviour at the ring stage, the faster he completed that stage ($F_{1,11} = 8.46$, $R^2 = 0.25$, $p = 0.01$; Fig. 5b). The strength of lateralization was not associated with the total number of nests a male built in the season ($F_{1,6} = 2.30$, $p = 0.19$) or with the time he took to complete a whole nest ($F_{1,11} = 0.10$, $p = 0.76$).

4. Discussion

Male Southern Masked weavers vary in some nest-building behaviours. For example, some males were more likely to insert new blades of grass into the left side of the nest than to the right, some more likely to insert grass into the right side while other birds had no side bias of this kind. Other behaviours were less variable such as the time birds spent weaving in the different quadrants of the developing nest. Males did not perform behaviours repeatably during the initial attachment phase but, with the exception of the directionality of carrying grass and the frequency of dropping

grass, were significantly repeatable in their behaviours during the ring phase. The strength of the lateral bias for inserting grass was associated with faster nest-building performance in the completion of the ring phase but not with any other measure of building performance. While most of the nest-building behaviours we examined did not change as males built more nests, they did drop grass less often and they tended to switch the side of the beak in which they carried grass to the nest.

If the birds were building their nests using fixed action patterns or according to a genetic template (Healy et al., 2008), we would have expected high repeatabilities across all the behaviours we measured. In fact, during the initial attachment phase no behaviours were repeatable, with the directionality of inserting grass and frequency of dropping grass being especially variable across males. Two out of the five behaviours during the ring phase were also not repeatable (directionality of carrying grass and frequency of dropping grass) and males varied in the directionality of carrying and of inserting grass, and total time spent weaving.

During the initial attachment phase the directionality of carrying grass, total time spent weaving and the preference for weaving in a particular quadrant were all highly variable within males. We suggest that males are responding flexibly to variation in the grass they are collecting (in the length and flexibility) and to the structure of the site to which they are attaching their nest (Hansell, 2000). This flexibility in building behaviour with increasing building experience is also consistent with the experiential-dependent variation we have observed in the morphology of the complete nests (Walsh et al., 2010). However, as orb-web weaving spiders also appear to respond in a flexible fashion to variation in attachment sites during the initial period of web building (Eberhard, 1990; Zschokke, 1996), we are cautious as to the interpretation of this flexibility in our birds.

Not only did the movements the birds used to build change the more nests a male built, they also appear to have become more competent at building, as seen in the decreasing rate at which they dropped grass while building in the initial attachment phase. Like the other behavioural changes, this can be readily explained by increasing dexterity as the birds have more practice at building. Such an effect has been seen previously in changes in nest building from juvenile to adult Village Weavers: more experienced birds build neater and more tightly woven nests than do inexperienced birds (Collias and Collias, 1964).

Male behaviour was more repeatable during the ring phase of construction, compared with the initial attachment phase. This is, perhaps, not surprising as there is inherently less variability in the problem the bird deals with at this stage than there is during the initial attachment phase.

Both the lateral preference for inserting grass and the time taken to complete the ring phase varied among males and had moderate repeatabilities, of 0.44 and 0.30 respectively. This lateralization of inserting grass during the ring phase appears to provide a benefit (Rogers, 2000), with more strongly lateralized males completing this phase more quickly than weakly lateralized males. Whether there is any other benefit to this lateralization cannot be determined from this study. However, since not all males have a side preference and, those that did, did not have the same side preference, it seems unlikely that such preferences confer a cognitive benefit in this system (Dadda and Bisazza, 2006a,b; Gunturkun et al., 2000; Magat and Brown, 2009; McGrew and Marchant, 1999; Rogers et al., 2004).

In conclusion, we have shown that the actions contributing to nest building in Southern Masked weavers vary among individuals and, particularly during the initial attachment phase, show little or no repeatability. Furthermore, we suggest that the individual differences among males, their lateral bias and the reduction in dropping grass change with experience. Whether

those experience-dependent changes are due to more than enhanced dexterity is not yet clear.

Acknowledgements

We thank Remi Borello for his hospitality and support, those people who banded the weavers at this site, Peter Jones for suggesting the site, Rachel Walsh for assistance in the field, Felicity Muth for photographs, two anonymous reviewers for their useful comments on an earlier version of the manuscript and The Leverhulme Trust for funding this project. Permission for the field work was provided by the Botswana Department of Wildlife and National Parks.

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