

Are elaborate bird nests built using simple rules?

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ABSTRACT

Determining how animals achieve seemingly complex behaviours is central to our understanding of the evolution of cognition. Complexity in behaviour is itself not sufficient for confirming a role for learning and memory. For example, although the nests some birds build appear structurally complex, they may, like the structures built by ants and termites, be achieved through relatively simple building processes. We attempted to use observations of nest building by male Southern Masked Weavers to determine whether one aspect of nest building, the completion of a nest, could be described usefully by either of two rule-based explanations that explain the construction of complex physical structures by invertebrates. The first possibility, stigmergy, is that birds use feedback from local nest cues to determine the building sequence and nest completion. The second possibility is that birds follow a stereotypical series of behaviours. We found that male Southern Masked Weavers returned to work on apparently complete nests even when they had begun to build a new nest. Neither stigmergy nor stereotypy explains our observations of nest building behaviour in Southern Masked Weavers. If weaverbirds do complete their nests using a set of rules, those rules are not the simple ones that have been used to describe building by invertebrates. This leaves open the possibility that learning and memory play a greater role in nest building than is currently thought to be the case.

Keywords: fixed-action patterns, nest building, stereotypy, stigmergy, weaverbird

1. INTRODUCTION

Many of the behaviours that we observe in animals are described as being complex, such as tool-making (Jones and Kamil, 1973; Boesch and Boesch, 1990; Hunt and Gray, 2004; Sanz *et al.*, 2009) or bower building (Marshall, 1954; Madden, 2001), vocal mimicry (Pepperberg, 1999; Kelley *et al.*, 2008), and patterns of social affiliation and manipulation (Whiten and Byrne, 1997; Bugnyar and Kotrschal, 2004; Seed *et al.*, 2007). It can be tempting to assume that the more complex a behaviour seems to us, the more likely it is that cognitive processes underlie that behaviour (Lefebvre *et al.*, 1997, 2002; Madden, 2001; Reader and Laland, 2002; Day *et al.*, 2005). While the definition of cognition may vary, here we consider it to include learning, memory and decision-making (Pearce, 1997; Shettleworth, 1998; Dukas, 2004).

Animal constructions range in perceived complexity. For example, many tools are structurally simple while the nests of many bird species appear far from simple (Healy *et al.*, 2008; Hansell and Ruxton, 2008). On the other hand, the cognitive processes thought to underpin these two kinds of constructions are typically characterised in the opposite fashion: tool making is thought to require

'advanced' cognitive capacities while it is considered that nest building requires little or no cognitive ability, as defined above (Hansell, 1984; Nicolakakis and Lefebvre, 2000; Lefebvre *et al.*, 2004; Moller, 2005; Hunt, 2005; Sherry, 2006; Bluff *et al.*, 2007; Raby and Clayton, 2009). There are at least two non-cognitive mechanisms that animals could use to achieve structurally complex nests: 1) animals could use a series of sequential stereotypical movements that followed in the appropriate order lead to the construction of the nest (Healy *et al.*, 2008); 2) the animal's behaviour could be stigmergic, *i.e.* the animal uses direct, local sensory feedback from the emerging nest to determine which, of a pre-determined set of potential behaviours, is to be the next movement (Grasse, 1959; Collias and Collias, 1984; Theraulaz *et al.*, 1998; Theraulaz and Bonabeau, 1999; Hansell, 2005). As with stereotyped behaviours, stigmergy in its simplest form leads to complexity without learning, memory or decision making since it is driven entirely by predetermined stimulus-response reactions (Theraulaz and Bonabeau, 1999).

Here we attempted to determine whether one of these two simple rules could explain the completion of a structurally complex bird nest. We observed nest building by male Southern Masked Weavers (*Ploceus velatus*),



Figure 1 Photograph of a typical southern masked weaver territory with six completed nests and one (top right corner) nest in the ring phase of construction, which is green with fresh grass.

which build multiple woven nests over a breeding season (Figure 1), using several knot types that have been likened to those used in human basket weaving (Collias and Collias, 1984; Ingold, 2000). If males use simple rules for building we would expect to see clear phases of nest construction that would progress in a sequential, non-overlapping pattern, particularly with respect to nest completion (Downing and Jeanne, 1988; Karsai and Penzes, 1993; Theraulaz and Bonabeau, 1995). Nest completion, and the starting of a new nest, is such a clear and distinct point, which makes it particularly accessible to the examination of simple rule use. If a male uses a set sequence of stereotyped actions to build, this would result in him working through the nest-building sequence until it was complete before starting another. Similarly, if a male uses only direct, local stimuli, he is expected to work on a single nest at a time, responding to feedback at every stage from the developing nest until he reaches completion. He would then embark on a new nest, building at that nest only, until completion, due to the lack of direct stimuli to return to that completed nest. We recognise these interpretations of the rule-based behaviour during nest building may represent an extreme level of simplification. However, it seems useful to address these possibilities because this level of simplicity appears to explain some of the construction of apparently complex structures by various invertebrates (Hansell, 1968; Theraulaz *et al.*, 1998; Hansell, 2005) and are often assumed to be sufficient for explaining avian nest building (Lefebvre *et al.*, 2004; Hunt, 2005; Raby and Clayton, 2009).

2. MATERIALS AND METHODS

The nest building of 18 colour-ringed male Southern Masked Weavers was observed in South-Eastern Botswana (Atholl Holme Farm, Gaborone, Latitude: -24.753,

Longitude: 25.859) between October and November 2008. Southern Masked Weavers are a long-lived (up to 20 years), polygynous species in which the males maintain individual territories and build individual nests within a breeding colony. Observations were conducted between 0600 and 1800 hours during an early, clearly observable phase of the construction of a new nest, referred to as the “ring” phase (Collias and Collias, 1962; Theraulaz *et al.*, 1998). The ring is the central structure around which the rest of the nest is constructed and the ring phase is reached approximately three hours into nest construction at this study site. This phase was selected because the beginning and end can be clearly defined, providing a consistent point in the construction of a new nest to conduct observations. The phase begins when the male first weaves blades of grass together into a ring and ends when he begins to weave the first blades of grass that project outwards to form the egg chamber (Walsh *et al.*, 2011). In total, one-hour long observations were made for three nests for each of the 18 males, a sum of 54 observations.

Observations began when males had already built at least one nest (mean number of nests per bird was 3.63 ± 0.24 SE), excluding the one under construction. At the start of each observation period we recorded the date, time of observation and the total number of nests within the males’ territory. During the course of the observation we recorded which of his nests the male visited and the type of activity he performed at that nest. Visits were classed as being of one of four different types: (1) bring new material to and incorporate it into a nest; (2) work on a nest without the addition of new material (“tidying”); (3) display at a nest; and (4) neither work nor display and did not visibly interact with the nest. Both building activities [(1) and (2)] were mutually exclusive and visit type 4 was exclusive of the other three behaviours. However, displaying could be performed in conjunction with either building action or independently and was scored separately under both scenarios.

Replicated G-test for goodness of fit were calculated according to McDonald (2009) on counts of nest visits from each individual to avoid pseudoreplication. Pooled results are reported where heterogeneity among individuals was not violated. We arcsine-transformed the proportion of the visits to an old nest for each category of nest visitation and analysed these data using Linear Mixed Models (LMM) in PASW version 18 for the number of nests at the time of the observation. The date and time of day were included as covariates and the male under observation as a random factor. As there were no significant interaction terms the interaction terms were excluded from the presented analysis. Correlations between the number of different old nests visit and the number of old nests present at the time of the observation period were analysed in PASW.

To determine whether males returned to old nests according to a fixed pattern, for each observation period we calculated the mean number of new-nest visits: (1) between visits to the same old nest; and (2) between

visits to any two old nests. These values were analysed separately using LMM in PASW, with male as a random factor, the order in the observation period sequence as repeated measure and the number of old nests at the time of observation as a covariate. Males that did not visit old nests twice in at least two observations were excluded from the analyses, excluding three males. Repeatability, or the degree of within male variation in the number of new-nest visits between old nest visits, were performed by ANOSIM (ANalysis Of SIMilarity), with 10,000 permutations, using the PAST statistical package (Hammer *et al.*, 2001). Data are presented as means \pm SE.

3. RESULTS

Males made on average 33.78 ± 1.57 visits to nests within their territory during a one hour observation period. They visited from one to five different nests (mean: 2.61 ± 0.17) per hour, inclusive of the new nest under construction. The behaviour performed during a nest visit did not differ among males ($F_{17,33} = 1.25, P > 0.25$), with regard to date ($F_{1,33} = 1.26, P > 0.25$) or to the time of day ($F_{1,33} = 2.57, P > 0.10$).

Males brought and incorporated new material to the new nest on most of those visits (Figure 2). Addition of new material occurred almost five times more frequently than did tidying ($F_{1,17} = 243.27, P < 0.0001$; Figure 2). Working visits, where new material was incorporated or the nest was tidied, were made much more frequently to the new nest under construction than to any older nest ($Gp_1 = 1371.01, P < 0.00001$), while most of the visits to the older nests did not entail building or tidying (Figure 2). Across all 54 observations males did not visit their nests at random and visited the nest under construction most frequently (all $G_{1-7} > 11.09, all P < 0.05$). Males varied in the kind of behaviour performed when visiting the older

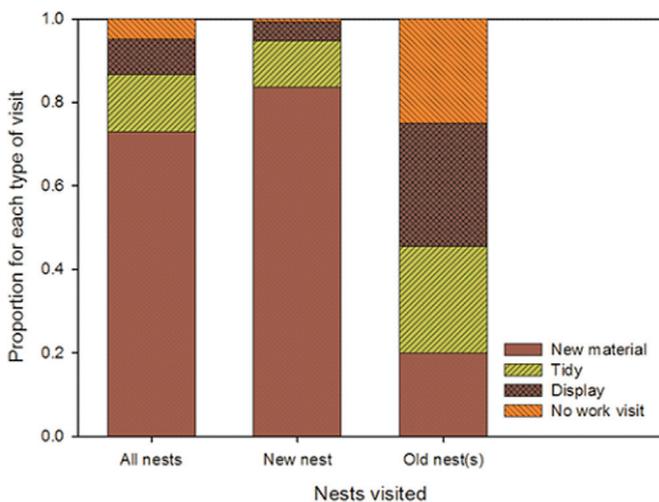


Figure 2 Mean proportion of each visit type to all nests, new nests alone and old nests alone.

nests ($Gh_{33} = 136.12, P < 0.0001$): 13 males divided their number of visits equally among incorporating new material, tidying, displaying and visiting without visibly interacting with the nest (all $G_2 < 5.55, all P > 0.15$; Figure 2), four males were more likely to tidy or do nothing when visiting older nests (all $G_2 > 11.58, all P < 0.009$) and one male always brought new material when visiting his old nests ($G_2 = 27.73, P < 0.00001$). However, the number of different old nests visited differed among actions ($Gp_3 = 8.82, P = 0.03$): males displayed at only 24 out of 196 different old nests but performed work on 57 different old nests. They visited 43 old nests without adding material, tidying or displaying during the visit.

The more nests a male had, the more visits he made to older nests ($F_{1,33} = 11.07, P < 0.005$; Figure 3) and the greater the number of different old nests he visited ($r_s = 0.42, n = 56, P < 0.005$). The more nests a male had, the more visits he made to tidy an old nest ($F_{1,33} = 4.77, P < 0.05$; Figure 3). Furthermore, males did not just tidy the same old nest more, but visited more different old nests in order to tidy them ($r_s = 0.50, n = 56, P < 0.0001$). However, males did not increasingly take new material to older nests when they had more nests ($F_{1,33} = 2.44, P = 0.13$; Figure 3). Males incorporated new material into 1.32 (± 0.11) different older nests per observation period.

Males did not differ in the schedule that they visited old nests (new nest visits between: the same old nest: $F_{14,18} = 1.12, P = 0.40$; any two old nests: $F_{14,20} = 1.24, P = 0.32$). However, within males their individual behaviour was highly variable and they did not have a fixed schedule for visiting older nests (returning to same old nest: $R = 0.01, P = 0.27$; any two old nests: $R = -0.06, P = 0.95$).

4. DISCUSSION

Male Southern Masked Weavers did not complete a nest before beginning the construction of a new one. Rather,

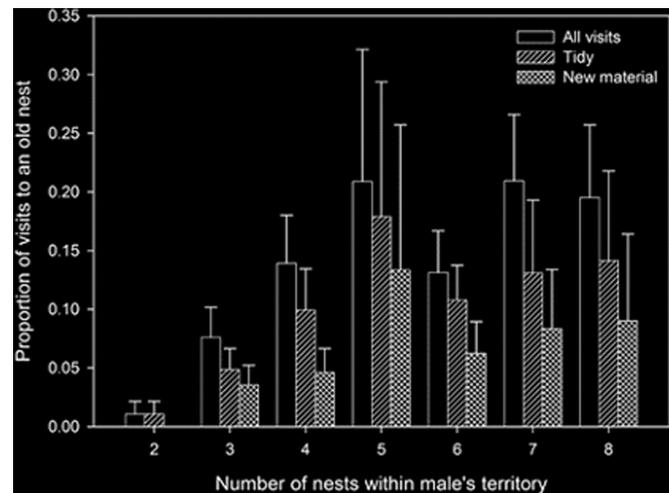


Figure 3 Mean proportion (± 1 SE) of the type of visit based on the number of total nests within the males' territory at the time of the observation period.

they revisited and continued to add material to, and to tidy, older nests, even when those nests contained females and eggs. The more nests a male had, the more he visited older nests when in the early stages of constructing a new nest. He did not, however, visit those older nests in a fixed pattern.

These data are not compatible with the commonly-held idea that all stages of nest building are achieved by either stereotyped or stigmergic rules (Lefebvre *et al.*, 2004; Hunt, 2005; Raby and Clayton, 2009). The extent to which stereotyped or stigmergic rules may explain other parts of their nest building remains to be seen (Collias and Collias, 1962). However, as there appears to be significant variability in the completed nest structures (Walsh *et al.*, 2010) and in several individual nest-building behaviours (Walsh *et al.*, 2011), in weaverbirds at least, this may seem unlikely.

There are alternative, relatively simple, ways to explain the work on multiple nests during the construction of a new nest. Firstly, visits, both working and otherwise, to old nests may be mistakes, reflecting imperfect knowledge or speed-accuracy trade-offs (Reed, 1973; Chittka *et al.*, 2009; Latty and Beekman, 2010). Indeed, birds do on occasion take fresh grass to an older nest and attempt to weave it into that nest before taking the grass to the new nest. However, as they are just as likely to attempt to weave fresh grass into the new nest, before removing the grass and taking it to an older nest (Walsh, personal observation), it seems unlikely that incorporating new material to an older nest or tidying an old nest is a mistake. Removing new material from the new nest to an old nest also makes a simple stimulus-response rule like stigmergy unlikely, since there should be no local stimulus at the new nest to indicate that work was needed at an older nest (and certainly not which of those older nests). Secondly, males may simply return to old nests on a fixed schedule, irrespective of the actions required at nests. A regular patrol, akin to trap-lining (Janzen, 1971; Feinsinger and Chaplin, 1975), might allow males to determine that work is required on an older nest. Alternatively, they may return to their nests at random, adding new material or tidying as necessary during these random visits. We did not observe males behaving in either of these ways.

Finally, males may simply respond to cues from females to determine when and what type of visits to make to older nests. Southern Masked Weaver males appear to begin nest building following interactions with a female (Walsh and Healy, personal observation), which would be consistent with males being stimulated by external cues to begin building a nest, for example as observed in domestic Canaries (*Serinus canaria domestica*; Warren and Hinde, 1959), Red-billed Quelea (*Quelea quelea*; Butterfield and Crook, 1968), and Ring Doves (*Streptopelia risoria*; Cheng, 1973; Martinez-Vargas and Erickson, 1973). However, we have no quantitative data to address the question as to whether females cue males to return to build, to finish building or to tidy their nests.

Here we defined simple to be represented by stereotypy or stigmergy as these are the two most common 'simple' explanations both invoked (Lefebvre *et al.*, 2004; Hunt, 2005; Raby and Clayton, 2009) and known to explain nest building by other animals, chiefly invertebrates (Karsai and Theraulaz, 1995; Theraulaz and Bonabeau, 1995). Nest completion, the most recognisable facet of nest building, does not conform to the predictions of either simple rule, and appears to require more flexibility than expected, at least in Southern Masked Weaver males. Whether or not this flexibility involves cognition, complex or otherwise, is not yet clear. However, working concurrently on multiple nests does suggest an additional level of organisation than that required for working on a single nest. Additional organisational levels have been proposed to indicate greater complexity (Sambrook and Whiten 1997).

Our observation that males increase their visits to old nests as they build more nests, and to more of those old nests, suggests that males retain information about the number and location of nests that they have built as well as its status of nests. This is supported by the observation that males remove nests after a breeding attempt fails or the chicks have fledged (Collias and Collias, 1984; Walsh, personal observation). Similar to other polygynous mating systems, male weaverbirds may be required to retain episodic-like information (Clayton *et al.*, 2001), such as the status of different nests (e.g. under construction, damaged, completed but unoccupied, completed and occupied) and the progression of particular breeding attempts (e.g. mated female, mated female with eggs, mated female with chicks, fledged chicks or failed breeding attempt). However, to determine whether this species remembers this information in a 'what', 'where' and 'when' manner (Clayton and Dickinson, 1998; Clayton *et al.*, 2001; Healy *et al.*, 2008) would require experimental testing.

While rejecting stereotypy or stigmergy does not confirm that learning and memory are involved in nest building, based on our data, we suggest that the possibility merits investigation. Further detailed observations of nest building behaviour itself as well as experimental manipulations during, for example, early development will help us to determine whether, or to what extent, cognition plays a role in the construction of the elaborate weaverbird nest.

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