1 Nest building, the forgotten behaviour

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12 Key words: Animal cognition, Building, Construction, Nests, Physical cognition, Tool
13 making

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17 Abstract

18 In the last decade tool manufacture in birds has transformed the landscape of animal
19 cognition. As tool manufacture, however, is rare and practised by species that are not
20 commonplace it is not a particularly useful model for investigating the evolution of physical
21 cognition. Based on recent evidence, we argue that nest building, which bears considerable
22 phenotypic resemblance to tool making, is more useful for examining not only the role that
23 cognition may play in construction behaviours, but also the neural underpinning of those
24 behaviours and, ultimately their evolution. We substantiate our view with recent evidence
25 that building by birds involves changes in dexterity, is experience-dependent and involves
26 activity in, at least, motor, reward and social network brain regions as well as in the
27 cerebellum.

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30 Introduction

31 Building by animals is a surprisingly neglected behaviour, surprising because it is key to
32 reproductive success for many species and, of more recent relevance, because it bears a
33 striking phenotypic similarity to tool making [1,2]. For a behaviour with such a broad
34 taxonomic spread across orders of animals (e.g. birds [3], reptiles [4], rodents [5], primates
35 [6], fish [7,8], and many social insects [9]), we still know remarkably little about how these
36 animals know what structure to build. These structures include beaver dams, caddis larvae
37 cases, antlion larvae pits, bowers, fish, chimpanzee and bird nests. In striking contrast, a
38 considerable amount of research effort has been addressed to another form of construction
39 behaviour, tool manufacture and use. Although much of this effort is based on the apparent
40 value of tool making for our understanding of the evolution of physical cognition (how
41 animals acquire, process and use information about the physical world [10–13]), the rarity of
42 tool making does not, in our view, make it a system of general applicability. Although tool
43 making has been explicitly separated, by definition, from all other building behaviours
44 [14,15] we contend that due to the significant phenotypic similarity that tool making shares
45 with nest building, nest building, due to its greater amenability to experimental manipulation,
46 to neural investigation and to phylogenetic analyses, may prove a more useful ‘model’
47 system.

48

49 Recent empirical evidence

50 In the 19th century several observers, including Alfred Russel Wallace, concluded that
51 building by birds (of nests), like that of man, was dependent on their experience [16].
52 Despite supporting evidence from the Collias’ and a few others in the 1960’s [17–19],

however, the common view, even in the 21st century, is that nest building by birds is innate [19–23]. Firm and widespread though this view may be, it has been held in the face of little to no evidence. That is, until relatively recently. Data are now steadily accumulating to show that birds modify where they build, what they build and how they build it, in response to experience.

Field evidence for a significant component of experience-dependence in nest building comes largely from observations that, after suffering predation on their nest, birds will move to a different site to build their next nest [25]. The structure of the nests of some birds also varies depending on their geographical location [26,27], although it is not clear whether this variation is due to real-time responses by individuals to local conditions or to selection. That selection can act on nest morphology is shown by the evolution of the addition of domes to nests built by those babbler species that build their nests on the ground, thought to be a response to increased predation risk [28].

The demonstration that there is low to no repeatability of the morphology of nests built by male Southern Masked weavers (*Ploceus velatus*, Botswana) and male Village weavers (*P. cucullatus*, Nigeria [29,30]) strongly suggest that the building of these nests is not achieved by a fixed-action pattern or behaviour that is ‘hard-wired’ rather, that individual builders do modify their behaviour depending on their experience/their environment (see Figures 1 and 2). This interpretation is further supported by the observations that male Southern Masked weavers rarely complete a nest before they begin the construction of the next [31] and that these males improve their material handling skills as they drop fewer pieces of grass the more nests they build.

Although weavers have significant appeal because they build a beautiful, apparently complex multi-knot nest (Figure 3), they are not the best system, at this point, for addressing the key

questions in building because experimental manipulations of building behaviour in the field are not straightforward. Zebra finches, *Taeniopygia guttata*, however, which breed essentially on demand in the laboratory [32], are a useful model for building behaviour. And, importantly, while a zebra finch nest may not be a thing of beauty to the untrained eye, data are accumulating to show that zebra finches learn multiple components of their nest building (Figure 4). For example, adult males learn to associate their own reproductive success with the colour of the material with which they build the nest: males that successfully reared chicks from a nest built with material of a colour they did not like, subsequently switched their preference to the colour of the successful material, when given another opportunity to build [33].

Furthermore, and importantly for a builder, male zebra finches also learn both how to manipulate material and about the structural properties of the material with which they build. Both these features were shown by nest-building male zebra finches provided with a nest-box that had either a large (10cm diameter) or small entrance (5cm diameter), and with nest material of two different lengths, short (20-22cm with 4.5-5.5cm stiff middle section) and long (25-27cm with 11.5-13.5cm stiff middle section). Birds with a box of either entrance-size could carry the short material directly into the box but only the birds with the large nest-box entrance could readily use the long material. From the outset, males with the large entrance nest box took materials of both lengths into their box while the males with the small nest-box entrance preferred to take the short material. Over the course of the experiment, however, the small nest-box entrance males modified the way in which they held the material so that they could take both lengths of material into the nest box [34]. This change in material handling shows firstly that dexterity with physical objects changes with experience but also that by changing the way they manoeuvred the material through the entrance these builders could solve the problem of access to only half of the available building materials. Zebra

finch males also learn to select among nest material that is most suitable for their nest: builders given several experiences of building with either flexible or stiff string, all eventually preferred the stiffer material, which is also the most efficacious building material (see Figures 5-7). It takes nearly twice as many pieces of flexible string to build a complete nest than it does to build a nest with the stiff material [35]. Builder zebra finches will also modify the colour of material with which they prefer to build depending on the colour of environment in which they build so as to camouflage their nest [36].

Although these data all show that builders learn from their own experience, social learning also has at least some part to play. For example, migratory flycatchers (*Ficedula albicollis* and *F. hypoleuca*) use information provided by resident tit species (*Parus major* and *P. caeruleus*) when choosing where to build their nest [37–39]. The migrants used at least two kinds of information, firstly with regard to the location of nest building. The flycatchers chose, from two possible boxes each marked with an arbitrary geometric symbol, to build in those boxes marked with the same geometric symbol as that marking a nearby box occupied by a tit nest [37]. The propensity of the flycatchers to nest near to the nest occupied by tit nests also increased as the number of offspring in those nests increased [40]. It is plausible, then, that birds may also pay attention to conspecifics when deciding what material to use or the structure to build.

Nest building in the brain

As the zebra finch is the iconic system for examining the neural and hormonal underpinnings of song learning [41], the wealth of data on its neuroanatomy [32] means that it is also a useful species in which to begin investigating the neural bases of building behaviour. Early data show that there is differential expression of the immediate early gene *c-fos* in the

126 anterior motor pathway, which is typically implicated in motor learning and sequencing [42],
127 the dopaminergic reward circuit, and social behaviour network in zebra finch builders [43],
128 specifically in relation to the number of times builders picked up and deposited material into
129 the growing nest and time spent in the nest by the female [43]. Nest building, itself, also
130 appears to be rewarding as targeted neuronal populations in implicated brain areas show: (1)
131 activity increases in mesotocinergic populations of builders compared to controls; (2) activity
132 is higher in vasotocinergic populations and dopaminergic populations the longer a builder
133 spends in the nest with his mate; and (3) activity is also higher in vasotocinergic cells the
134 more material a builder picks up [44]. Of the additional brain areas that may be involved in
135 building behaviour [45,46], the cerebellum holds especial promise: a phylogenetic analysis
136 shows that nest complexity increases with cerebellar foliation (the amount of surface folding
137 [47]). Given that the cerebellum is involved in cognitive processes such as learning, memory
138 and language ability in humans [48] and tool-use in birds [49] and primates [50,51], it will be
139 useful to determine its role in nest building.

140 The male zebra finch and weaver builders are, however, just the beginning to the possible
141 value nest building might hold for our understanding of physical cognition. For example, sex-
142 differences in physical cognition in the brain and behaviour can be elucidated because who
143 builds the nest (the male, the female, or both) varies among species. Moreover, one might
144 explore the ontogeny of nest building by manipulating the features of the nest into which a
145 chick hatches and the materials to which it is exposed in early life, one could investigate the
146 function of the nest structure [52,53] and the degree to which natural and sexual selection
147 have acted on the structure [54,55], as well as exploring a whole range of mechanistic
148 underpinnings, including the role of hormones.

149 In sum, we propose that nest-building behaviour is a useful model system to examine the
150 evolution of physical cognition. Birds, in particular are an excellent taxa in which to examine

nest-building behaviour, because in this group the behaviour is ubiquitous, with variation in the identity of the builder, in material use, in the physical manipulations required to build a nest as well as in the final nest structure (e.g., ranging from scrapes on a beach to self-incubating mound nests and hanging baskets of weavers [56]) and is very amenable to experimental manipulation. Thus nest-building can be examined using both existing frameworks [13] for the study of comparative cognition: behaviour of closely related species that face different ecological pressures where different cognitive abilities may be favoured and the behaviour of more distantly related species that face similar environmental pressures where we might expect convergence in cognitive abilities.

Acknowledgements

We thank the BBSRC (BB/I019502/1, SDH; Anniversary Future Leader Fellowship BB/M013944/1, LMG) for funding. Thanks to Eira Ihalainen for providing photographs of zebra finches and Ida Bailey and Kate Morgan for providing photographs of cape weavers and to Ida Bailey for providing a previously unpublished graph (Fig. 5).

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258 a female) when they had begun to build subsequent nests, the simple rules consistent with
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270 small or large and with nest-material that was either long and short. Birds initially chose the
271 most appropriate material for their nest box type: males with a box with a small entrance hole
272 selected the short nest material, while males with a box with a large entrance hole were
273 indifferent to material choice. With experience, males with a box with a small entrance hole
274 changed their material handling technique: they initially carried material to the nest by
275 holding the material in the middle, but changed to holding the material at one end. They
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284 stiffer material. As the nests that were built with only flexible material required, on average,
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303 entrance hole of the nest boxes in which these nests were built were marked with an arbitrary
304 geometric symbol. A second empty nest box, marked with a different symbol, was put up
305 next to the occupied box. Two additional nest boxes, bearing symbols that corresponded to
306 those on the two existing boxes, were put up some distance away. When migratory female
307 flycatchers returned to the breeding area, they chose the nest box type that matched the great
308 tit nest box when the clutch size was large, but not when the clutch size of the tits was small.
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A combination of immunohistochemistry for Fos and vasotocin, mesotocin and tyrosine hydroxylase were used to investigate neuronal activity in nest building and non-nest building male and female zebra finches. There was increased immunoreactivity in three neuronal populations in nest-building males: in a mesotinergetic neuronal population relative to that in non-building males, in a vasotinergetic neuronal population dependent on the amount of material they picked up and in both a vasotinergetic and a dopaminergic neuronal population dependent on the time they spent together in the nest with their mate. These data are the first to show that the social behaviour network and the dopaminergic reward system are active during nest building.

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For 87 species of bird for which data on the volume of the cerebellum (a part of the brain thought to correlated with complex motor abilities), the degree of cerebellar foliation (cerebellum surface folding) and complexity of nest structure were available, cerebellar folding is greater the more complex the nest. Nest complexity was categorised into cup building, platform building or no nest. This correlation is consistent with the cerebellum acting in increasingly manipulative skill in nest-building birds.

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Figure captions

Figure 1. A series of six nests from a single Southern Masked weaver males. Photos ordered by date of construction from top left to right. The picture originally appeared in [29] and appears here with permission.

Figure 2. Mean $\pm$ s.e.m nest measurements (y -axis) for length (filled circles), width (open circles), and height (filled triangles) of nests built by individual male Southern Masked weavers (x -axis), $n = 14$. This figure originally appeared in [29] and appears here with permission.

Figure 3. Clockwise start top left - cape weaver (*Ploceus capensis*) male that has just completed the ring phase, more complete nest, tearing down an old nest with another nest in the background, completed new nest.

Figure 4. Clockwise start top left – zebra finch (*Taeniopygia guttata*), male selecting short nest material (~ 5 cm), selecting long nest material (~ 10 cm) with female in background, late stage of nest building working on roof with the entrance hole in the bottom right, early stage of nest building.

Figure 5. The percentage of stiff string chosen by males that has no ($n = 7$), one ($n = 10$), or two ($n = 7$) experiences building with flexible string (mean $\pm$ s.e.m). The dashed line indicated 50%. This figure originally appeared in [35] and appears here with permission.

Figure 6. The associated costs of building measure by the number of pieces of sting in the final nest (y -axis), for nests built with different material types (x -axis) for zebra finches in [35].

409 Figure 7. Cup-shaped nests build by zebra finches in [35] with different material types:
410 flexible string (pictured left) and stiff string (pictured right)

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