Nest building, the forgotten behaviour

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Abstract

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

Introduction

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

Recent empirical evidence

In the 19th century several observers, including Alfred Russel Wallace, concluded that building by birds (of nests), like that of man, was dependent on their experience [16]. 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 in 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 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 anterior motor pathway, which is typically implicated in motor learning and sequencing [42], the dopaminergic reward circuit, and social behaviour network in zebra finch builders [43], specifically in relation to the number of times builders picked up and deposited material into the growing nest and time spent in the nest by the female [43]. Nest building, itself, also appears to be rewarding as targeted neuronal populations in implicated brain areas show: (1) activity increases in mesotocinergic populations of builders compared to controls; (2) activity is higher in vasotocinergic populations and dopaminergic populations the longer a builder spends in the nest with his mate; and (3) activity is also higher in vasotocinergic cells the more material a builder picks up [44]. Of the additional brain areas that may be involved in building behaviour [45,46], the cerebellum holds especial promise: a phylogenetic analysis shows that nest complexity increases with cerebellar foliation (the amount of surface folding [47]). Given that the cerebellum is involved in cognitive processes such as learning, memory and language ability in humans [48] and tool-use in birds [49] and primates [50,51], it will be useful to determine its role in nest building.

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

In sum, we propose that nest-building behaviour is a useful model system to examine the 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.

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Phylogenetic analyses were used to test wehther Old World babblers (*Timaliidae*) that build domed nests are more likely to build them on the ground than in trees. Babbler species that build cup-shaped nests build their nests higher from the ground than do babbler species that build domed nests. It is presumably the increased predation pressure suffered by birds building on or near the ground that lead to the evolution of domed nests. This was the first study to formally identify the evolutionary pathways leading to diversity in nest structure in this group of birds.

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Observations of nest building by male Southern Masked Weavers were used to distinguish between two explanations that could explain the production of the structurally complex nest built by these birds. As males continued to work on apparently complete nests (occupied by a female) when they had begun to build subsequent nests, the simple rules consistent with stigmergy or stereotypy are not sufficient to explain building in this species. These data suggest that building weavers can identify when the nest is sufficiently functional rather than complete, a degree of building flexibility previously unrecognised

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Male zebra finches were presented with a nest-box with an entrance hole that was either small or large and with nest-material that was either long and short. Birds initially chose the most appropriate material for their nest box type: males with a box with a small entrance hole selected the short nest material, while males with a box with a large entrance hole were indifferent to material choice. With experience, males with a box with a small entrance hole changed their material handling technique: they initially carried materal to the nest by holding the material in the middle, but changed to holding the material at one end. They could, then, carry both the short and long material through the small entrance. This shows that male zebra finches attend to physical properties of nest material and learn to handle novel nest material efficiently.

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Male zebra finches were given several experiences building a nest using nest material that varried in rigidity. With increasing nest building experience, males increasingly preferred the stiffer material. As the nests that were built with only flexible material required, on average, over twice as many pieces of material to complete a nest it appears that birds select nest material based on one of its structural properties: rigidity, and that male zebra finches learn to prefer the more efficacious nest material.

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Male zebra finches were given two nest materials of different colours with which to build: one colour matched the colour of the nest cup and surrounding cage walls, the second colour material did not. Males predominantly built using the material of the colour that matched the background colour of the nest cup and cage walls. This study shows that male zebra finches select nest material to camouflage their nest relative to the background.

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Great tit nests were experimentally manipulated to contain either five or 13 eggs. The entrance hole of the nest boxes in which these nests were built were marked with an arbitrary geometric symbol. A second empty nest box, marked with a different symbol, was put up next to the occupied box. Two additional nest boxes, bearing symbols that corresponded to those on the two existing boxes, were put up some distance away. When migratory female flycatchers returned to the breeding area, they chose the nest box type that matched the great tit nest box when the clutch size was large, but not when the clutch size of the tits was small. Flycatchers can, then, use information about the fitness of heterospecics when deciding where to build a nest.

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In this study, immediate early gene expression was used to identify brain regions that are active during nest building by male zebra finches. Activity was identified specifically in motor sequencing, social behaviour, reward and motivation pathway relative to the number of times males picked up or deposited nest material and the amount of time the female spent in the nest. These data provide the basis for investigation of the neural basis of construction behaviour

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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 mesotinergic neuronal population relative to that in non-building males, in a vasotinergic neuronal population dependent on the amount of material they picked up and in both a vasotinergic 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 ± 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 (~5cm), 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 ± 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].

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

Figure 1.

Figure 2.

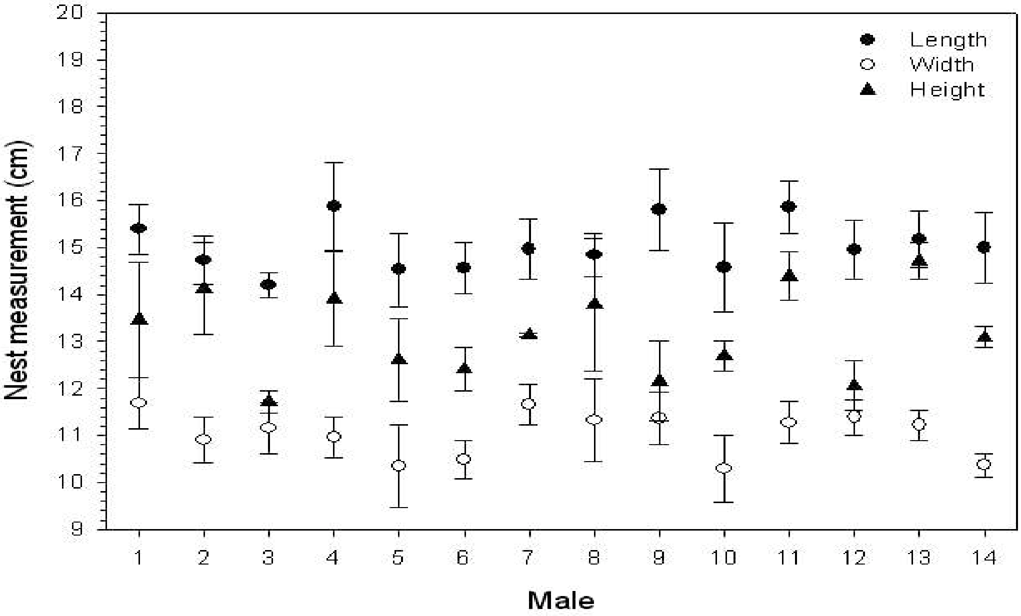
Nest measurement (cm)
20
19
18
17
16
15
14
13
12
11
10
9
● Length
○ Width
▲ Height
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Male

Figure 3.

Figure 4.

Figure 5.

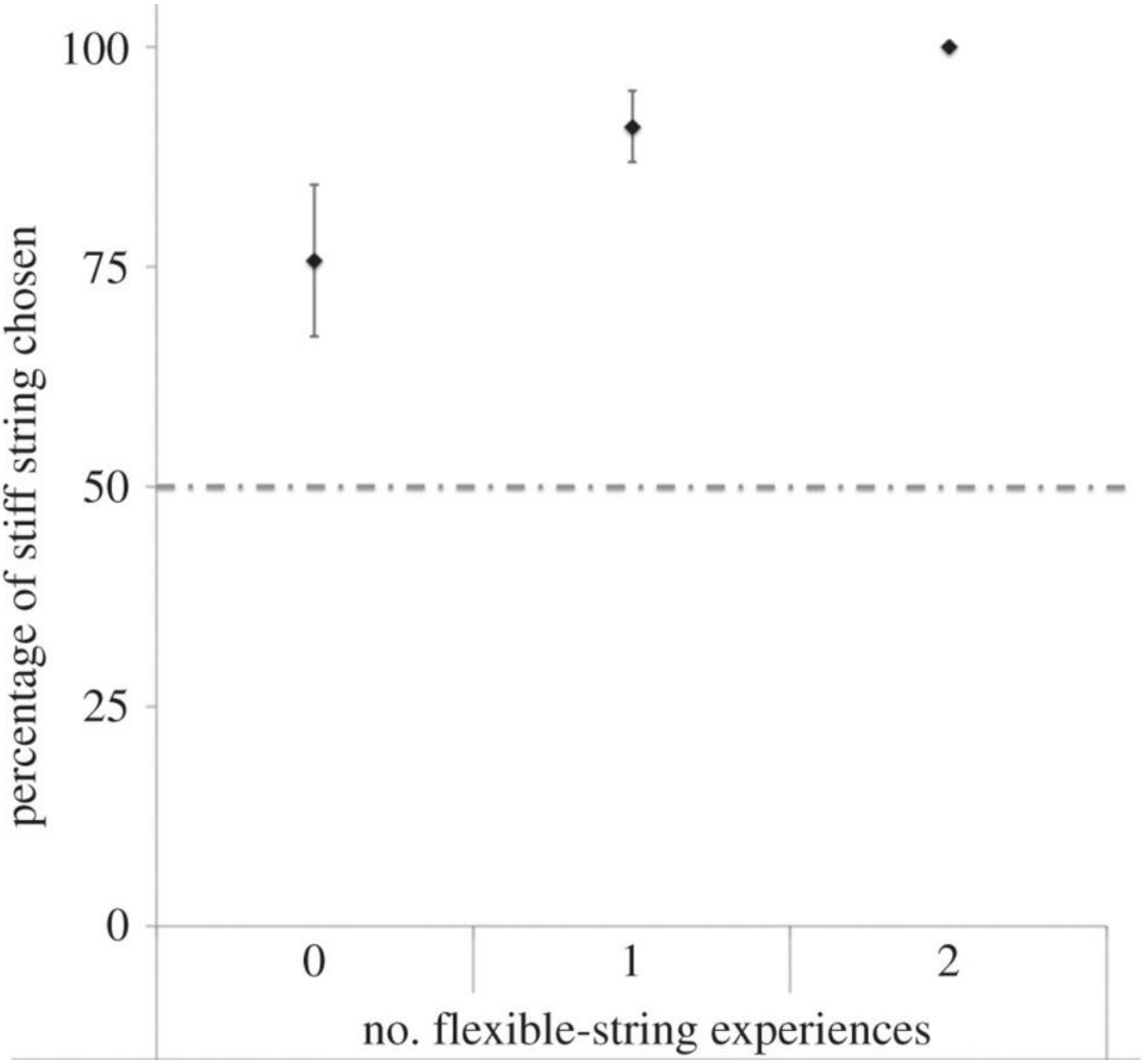
percentage of stiff string chosen
100
75
50
25
0
0
1
2
no. flexible-string experiences

Figure 6.

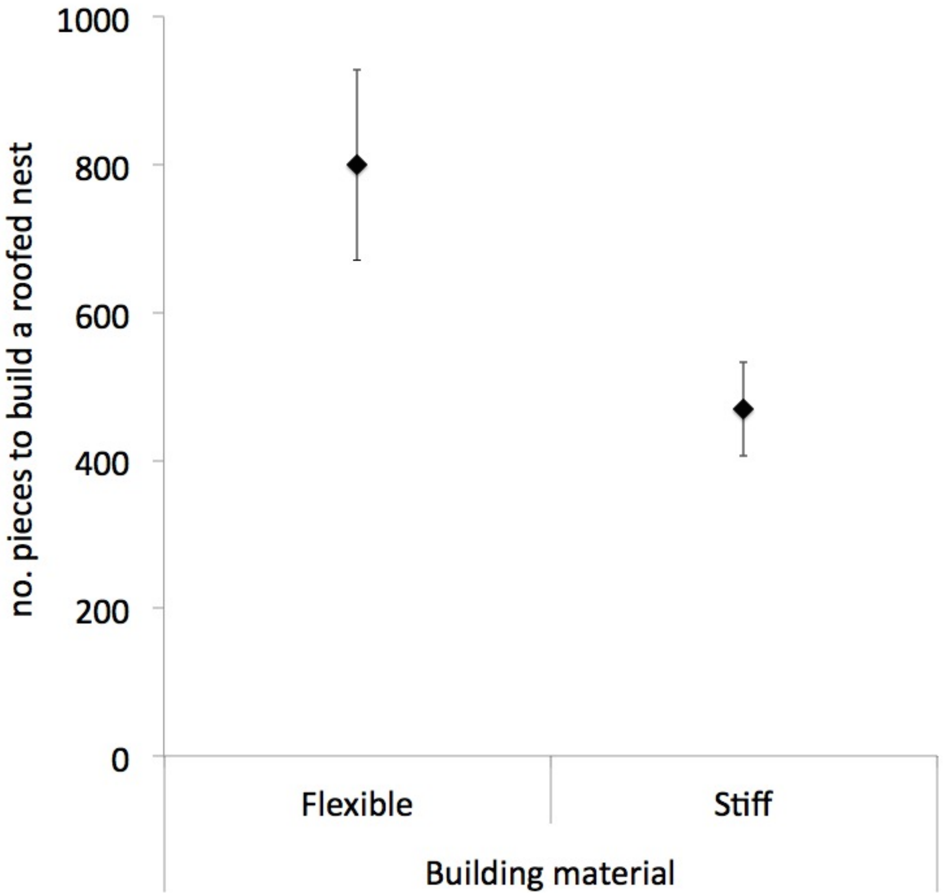
1000
800
600
400
200
0
no. pieces to build a roofed nest
Flexible
Stiff
Building material

Figure 7.