3.1 Introduction

‘I believe, in short, that birds do not build their nests by instinct’ (Wallace 1867). It may have taken some time but one of Alfred Russel Wallace’s lesser known ideas finally appears to be bearing fruit. There is increasing evidence that birds build nests that are more variable than once thought and that they will change the material they use to build their nests, depending on their experience. Therefore, birds do not rely entirely on instinct to build their nests. Not only would we argue that the accumulating evidence shows that nest building by birds is not all instinctual but also that the recent data on nest-building behaviour and decision-making are beginning to help us to answer a question that remains, perhaps surprisingly, unanswered, which is why birds build the nests they do.

Birds are one of the best-studied taxa in the world, so it is not surprising that, for the approximately 9,000 species of bird worldwide, there is a plethora of descriptions of the nests they build (e.g. Ferguson-Lees et al. 2011). Although many fewer, there are also multiple descriptions of how different species go about building their nests. In Table 3.1 we provide examples of species for which there are detailed descriptions of the behaviours used by different species when building their nests (for more examples see Hansell 2000; Goodfellow 2011). Importantly, for our purposes, it is difficult to know whether descriptions of nest-building behaviours are typical for a species as usually they have been described only for just one or two individuals per species. In general, birds may either sculpt a nest by removing material from a site or assemble a nest by adding material to a site (Hansell 1984). During nest assembly, material may be piled up, moulded, stuck together, interlocked, sown or woven (for more detail and examples see Hansell 1984). Detailed experimentation investigating how birds know which building techniques to use is rare. Hence, we have little information on how they make choices of materials or whether birds copy the nest-building process and material choice of a parent. We know nothing about whether birds can learn how to manipulate building materials. From recent work, however, it is becoming clear that not only do birds within a species vary in their building behaviour but individuals can be flexible in that building behaviour, variation that can lead to significant variation in the nest produced. These data are increasingly showing that learning has an important role to play in both building dexterity, choice of nest materials and the making of a number of other nest-building decisions. These topics are covered in this chapter.

3.2 Background

Unlike his rather more famous ideas concerning natural selection, the view of Wallace (1867) that it was simply implausible that all of the information required for appropriate nest building was instinctive has languished for over 100 years; it remains both scientific and popular belief that a species’ knowledge about nest design, construction, location etc. was all ‘in’ their genes. We think it most likely that nest-building behaviour is rather more like most other behaviours in that it is shaped both by genes and experience. Here, then, we begin by describing the historical background to the understanding of avian nest-building behaviour and then go on to examine more recent data that begin to provide some of the first evidence for acquisition by birds of nest-building knowledge.

Classical methods to examine the causal basis of a behaviour involve two approaches: 1) deprive the juvenile bird of access to adults so that it has no opportunity to see/experience the behaviour performed by experienced individuals. This is usually done by hand-rearing young birds, sometimes coupled with the isolation of each bird from same-aged conspecifics; and
2) restrict the bird from any opportunity whereby it might ‘try out’ the behaviour. This can be difficult but in the case of nest building it can be achieved by ensuring that the bird has no access to material that may constitute appropriate nest material (this may, in practice, be a little more difficult than it sounds, see below). At a later date, one then assesses whether, in the presence of suitable nest material and, possibly a potential mate, the bird attempts to use the material to form a nest and, if so, what shape that nest takes. Wallace (1867) wrote of such deprivation experiments, describing birds that were raised in cages from eggs, which even when given appropriate nest-building material did not produce a nest that was characteristic of their species. He also suggested that the ‘fair’ testing of what the birds actually did was to ‘turn out a pair of birds so brought up into an enclosure covered with netting, and watching the result of their untaught attempts at nest making.’

Early deprivation experiments with hand-reared rose-breasted grosbeaks (Pheucticus ludovicianus) and American robins (Turdus migratorius), which had had no experience of nesting materials, resulted in birds that were totally unable to produce a nest when presented with suitable material at adulthood (Scott 1902, 1904). Yet, other species appear to be more capable when deprived in an apparently similar way: domestic Atlantic canaries (Serinus canaria), for example, without early experience with appropriate nest-building materials apparently were later able to build a nest of species-typical form (Hinde 1958). Canaries with either restricted access, i.e. material was provided for only 30 minutes per day, or deprived entirely of material were also observed to perform odd behaviours, including plucking their own feathers, unlike those birds that had had continuous access to building materials (Hinde 1958).

There is more than one reason why lack of early experience may result in first-time builders attempting to build a nest that is not species-typical or failing to build a nest at all. The first of these is that, rather than not ‘knowing’ what nest to build, the bird lacks the ability to manipulate material in appropriate fashion. That dexterity and practice of manipulating material makes a contribution to the shape of the final nest, and is affected by deprivation, comes from both observational data and deprivation experiments performed on captive, hand-raised village weavers (Ploceus cucullatus). Collias and Collias (1964) described a range of actions that young birds raised by their parents had to practice before being as capable as an experienced adult in tearing strips off suitable plants. Those actions, which included where to perch, which part of the grass to begin tearing, which direction to tear, how much to tear off, and so on, all appear to be behaviours that might be required for successful building.

Collias and Collias (1964) also described how young birds, whether deprived of suitable materials or not, begin mandibulating objects from a very early age. In the birds deprived of suitable materials this mandibulation sometimes took the form of weaving their own feathers or those of other birds (Collias and Collias 1964). The plucking of their own feathers by nest material-deprived canaries may also have occurred in lieu of learning the mechanical components required for nest building (Hinde and Harrison Matthews 1958). It is possible that it was the deprivation of materials suitable for mandibulating that caused young birds deprived of usual nest-building materials (palm strips or giant reed grass) to be less capable of ripping off strands than were undeprived conspecifics.

The possibility that young weavers may also learn about nest building (whether material choice, method of weaving or both is not clear) from watching the behaviour of nest-building adult males also came from observational data collected by Collias and Collias (1964). They described the establishment by these immature birds of ‘play colonies’ where they attempt to build nests (Collias and Collias 1964) and young male weavers will also visit nests of adult males as they build, often removing material. It is still unclear, however, why the young males do this and whether they remove the material from the nest of a related male.
who may be more tolerant of the learning of a young relative. Thus far, these observational data form the only evidence that social learning may play a role in some component of nest-building behaviour, perhaps even in shaping the specifics of the nest structure itself (but see below for a role for social learning in nest-building decision-making).

That early experience has an impact on nest-building decision-making was also provided by a series of experiments conducted by Sargent (1965). These were designed to test the specific suggestion of Wallace (1867) that young birds while in the nest and when recently fledged, have the opportunity to examine the detail of their natal nest and the materials from which it was built. As the young birds forage near to the nest in the early post-fledging days, Wallace (1867) also suggested that this provided an opportunity to compare available material with that contained within the nest. Sargent (1965) considered that there were three different sources of information that might be both available and used by a young bird learning how to build a nest: 1) the materials and the construction of the nest; 2) the substrate immediately surrounding the nest; and 3) the wider habitat in which the nest is located. He included these two latter manipulations because there had been reports of small groups of individuals choosing unusual nesting substrates over multiple generations. For example, western yellow wagtails (Motacilla flava) were observed nesting in shrubs rather than on the ground (Schiermann 1939) and redheads (Aythya americana) were seen to be nesting on marshland rather than in emergent vegetation over water (Hochbaum 1955). More evidence (including some experimental data) that apparent innate preferences for nest habitats could be modified by experience (Klopfer 1962, 1963) is provided by detection that the natal philopatry of birds following ‘transplantations’ of eggs or young from one place to another was to sites in which they were reared rather than to those in which they hatched (Välikangas 1933; Löhrl 1959).

Sargent (1965) manipulated each of the three sources of information in turn by providing nest-building captive zebra finches (Taeniopygia guttata) with strands of burlap of one of three colours (green, brown, or red) with which to build the nest. The birds also had access to a plywood box or a wire-mesh canary nest cup in which to build, which was located either inside the birds’ cage or outside the cage in an enclosed extension accessible from their cage. Sargent (1965) compared the choices birds made when building their first nests with the features of their natal nest. Although birds raised in nests of each of the three colours preferred brown burlap, the preference for brown of those birds that had been raised in green nests was much less than it was for birds in the other two groups. That natal nest colour need not affect material colour preference, however, was evidenced by birds raised in red nests: they preferred brown burlap as strongly as did the birds raised in brown nests.

Rearing experience also appeared to affect habitat choice: zebra finches of Sargent (1965) preferred to nest in the habitat type in which they were raised although their choice of nest location was not apparently so flexible. All birds preferred to nest in cups rather than boxes, although the strength of this effect seemed variable, depending on the combination of experience and the way in which the options were presented in the test conditions, i.e. at first nesting. The effect of habitat usually overwhelmed the effects of preferences for substrate type.

Sargent (1965) set an early high standard in experimental design, not least in his thorough exploration of sources of information the birds might use in their nest-building decisions. He also differentiated between experience gained from hatching and nestling periods to that gained during the fledgling stage. Although he did not test all the possibilities, Sargent (1965) provided some compelling evidence that experience gained during the fledgling stage has a significant impact on habitat preferences at first nesting. He also looked at the choices of birds building their second nests. Although birds appeared to choose options much as they had for their first nests, they tended to choose more ‘natural’ or species-characteristic nest materials and situations. This latter result may have helped to shape his ultimate conclusion that for nest building, experience played little role relative to innate predispositions. We have described the work of Sargent (1965) in detail not only because his thorough experimental exploration of the assertions of Wallace (1867) regarding the role of instinct, or lack thereof, on nest-building behaviour is a model of experimental design, but also because his data were the last substantial examination of the influence of experience, i.e. learning and memory, on nest-building decision-making.

By the mid-1960s the work of Collias and Collias (1964) on behaviours such as the weaving of weaverbirds involved in the building of a nest and that of Sargent (1965) on the decisions involved in nest building had both produced evidence of experience-dependent effects. It is perhaps ironic, then, that both studies probably helped to cement the then widespread, and now trenchant, view that nest building by birds is ‘instinctive’, ‘innate’ and entirely ‘genetic’ (each of these labels
is used). This is because those data do not allow exclusion of a significant genetic contribution to the observed building behaviours and decisions. Evidence of the hormonal control of nest building by various species, i.e. red-billed quelea (*Quelea quelea*; Butterfield and Crook 1968), Atlantic canaries (Warren and Hinde 1959; Hinde and Steel 1972), pigeons (common pigeons, *Columba livia*, Cheng 1973; ring doves, *Streptopelia risoria*, Martinez-Vargas and Erickson 1973), and zebra finches (Rochester et al. 2008), which showed that testosterone, oestrogen, and progesterone all contribute to motivating birds into nest building, only added further weight to this view. As did the outcome of administering one or other of these hormones, which may lead to the initiation of nest building in the mate of the sex that is not the usual nest builder (Steel and Hinde 1972).

### 3.3 Habitat choice

Contrary to the assumption that there is little or no flexibility in the behaviour of nest building or in the structure that results, there is one aspect of nest building for which there soon came overwhelming evidence that birds will often modify their behaviour with experience. As Sargent (1965) showed with his experiments, alongside the data from others before him, birds will change the location of their nests based on their experience of the success, or not, of their own previous nest-building attempts. Predation is thought to be the key factor in whether or not birds raise their young successfully (Ricklefs 1969; Martin 1995; Lima 2009) and there is evidence that birds move their nest sites in response to a realized predation risk to their eggs and nestlings (Shields 1984; Sonerud 1985; Haas 1998). Following depredation of a nest a bird may disperse for the next attempt (Howlett and Stutchbury 1997) or for the following season (Dow and Fredga 1983; Doligez et al. 1999). Sometimes birds will both disperse and change nest-cover type (Greig-Smith 1982). Sometimes birds do not go so far as to leave their territory and will reuse a nest site but not in the same season (Styrsky 2005).

Birds may also choose nest sites that reduce the perceived predation risk to their eggs and nestlings. For example, Siberian jays (*Perisoreus infaustus*) respond to taped calls of corvids (egg and nestling predators) by moving to build their nests to safer but cooler sites (Eggers et al. 2006). Moreover, migratory passerines did not settle in a habitat sprayed with water containing American mink (*Neovison vison*) urine and faeces to simulate an increased mammalian predator presence (Forsman et al. 2013). In some cases the apparent predation risk originates from the presence of humans: black redstarts (*Phoenicurus ochruros*) shifted their nests deeper into nest cavities after researchers had disturbed them (Chen et al. 2011).

Predation is not, of course, the only hazard for nest-building parents and birds also choose their initial nest location, and may change it subsequently, so as to mitigate against environmental challenges to their eggs and offspring (see further details in Chapter 5). For example, dabbling ducks (*Anas* spp.) in west-central Montana build their nests so that the surrounding vegetation does not block the sun in the morning but offers shade in the afternoon when the temperatures are considerably higher (Hoekman et al. 2002). Whether these birds learn to do this is not yet clear.

At least some birds can respond to variation in more than one factor causing nest failure. Pinyon jays (*Gymnorhinus cyanocephalus*), for example, will move their nests away from exposed sites (these are warmer due to higher exposure to the sun) only after a nest has failed due to predation. Those birds that first nest in a concealed site will only move to an exposed site when their concealed nest has failed due to the impact of snowfall (Marzluff 1988).

Finally, some species respond to positive memories rather than just by avoiding their previous failures. Mountain bluebirds (*Sialia currucoides*), when given a choice of nestbox type, prefer to return to nest in box types in which they have previously successfully raised a brood (Herlugson 1981).

Success or failure estimates may also be gained from observing heterospecifics’ choice of nestbox, even when the characteristics that are copied or avoided appear to be arbitrary. Seppänen and Forsman (2007) showed that European pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*Ficedula albicollis*) will choose nestboxes with either a white triangle or square painted around the nest box entrance based on whether the boxes are occupied, or not, by great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), or coal tits (*Periparus ater*). A follow-up study showed that this preference appeared to be based on the success of the tit parents as the more offspring their box contained, the more likely the flycatchers were to choose a box of a similar type (Seppänen et al. 2011). These flycatchers continue to acquire information regarding nesting success of conspecifics through inspecting conspecific nests after a simulated predator visit (Thomson et al. 2013). A more commonplace use of social information is seen in black-legged kittiwakes (*Rissa tridactyla*), which nest on cliffs that vary in their quality across time. New birds will recruit to nest on the cliffs that had been the
most productive the previous year. Furthermore, the success of surrounding birds seems to have a greater impact on cliff choice than does a bird’s own reproductive performance in any one year, with birds being much more likely to disperse from the cliff on which they had a poor reproductive event when others on the same cliff also bred poorly (Danchin et al. 1998).

Slagsvold et al. (2013) used cross-fostering to show that some part of the preference for nestbox type in tits, at least, is due to imprinting. Although blue tits reared in a small nestbox by blue tit or great tit parents preferred small over large nestboxes when they nested themselves, blue tits cross-fostered by great tits in a large nestbox much preferred to nest in a large nestbox. Great tits fostered to blue tits also preferred the size of the nestbox in which they were raised.

3.4 Material choice

Typically, although not without exception, birds’ nests are layered structures consisting of (an) outer shell(s) of coarser material and (an) inner layer(s) of
finer, lining material (Hansell 2000). The function of the outer part of the nest is to act predominantly as a container to prevent eggs and birds from falling out and perhaps also to provide some protection against adverse effects of climate and predation (Dixon 1902; Collias and Collias 1984; Hansell 2000). The lining of the nest probably provides further insulation against the climate (Mainwaring et al. 2014a), may in some instances provide cushioning to prevent eggs from moving around and cracking against each other or against harder nest materials, and may also aid in nest hygiene (Winkler 1993; McGowan et al. 2004; Dawson et al. 2011; Suárez-Rodríguez et al. 2013; Biddle et al. 2015).

Although nest structure may be roughly species-specific (Ferguson-Lees et al. 2011), there may also be considerable intraspecific variation in nest composition and morphology (Allen 1878; Brewer 1878; Cresswell 1997; Walsh et al. 2010; Britt and Deeming 2011; Álvarez et al. 2013; Chapter 4; Figures 3.1 and 3.2). There is an untested suggestion that there is greater intraspecific variation in the constitution and structure of nests built in vegetation above the ground or adherent to walls or cliffs than are nests built by ground-nesting species (Nickell 1956). In some cases, regional variation in intraspecific nest morphology may simply reflect the abundance of different materials in the local habitat (Álvarez et al. 2013). In other instances, individuals appear to be more selective about their nest materials. For example, killdeers (*Charadrius vociferus*) prefer to use white material to build their nests even when in limited availability (Kull 1977). Other species add pieces of particular species of aromatic plants to their nests. The variability in preference for plant species does not seem to reflect plant species’ abundance (Gwinner and Berger 2008; Dykstra et al. 2009; Mennerat et al. 2009a), but rather they have other functions (see Chapters 4 and 7).

It is still unclear what causes variation in preference for plant materials by birds. Like Sargent (1965), others have since suggested a role for imprinting (Muth and Healy 2013). However, material preferences may be based on genetic predispositions, reflect innate responses to climate conditions, or be due to a bird learning the structural or functional features of the material. This may be either through experience of manipulating the material, or associating the outcome of using one material or another with subsequent reproductive success (Muth and Healy 2011, 2014; Bailey et al. 2014).

There are a number of observations from free-living birds in which nest composition and structure vary

**Figure 3.2** Six nests built by different male zebra finches (*Taeniopygia guttata*). These males built these nests when they had been provided with four different types of string (all 15 cm long), string that varied in flexibility from stiff to very flexible. Although the males each had access to similar quantities and types of nesting material (i.e. stiff string), these nests demonstrate variation in the nests built by different zebra finch males. (Photo: K.V. Morgan).
intraspecifically with the climate in which the nest was constructed as influenced by latitude (Kern and van Riper 1984; McGowan et al. 2004; Mainwaring et al. 2012, 2014b; Chapter 4) or altitude (Kern and van Riper 1984). These data do not, however, allow us to differentiate between a number of possible explanations for why birds choose different materials: 1) materials differ in their availability as habitat changes; 2) birds have a population-specific genetic predisposition for choosing different materials; or 3) birds learn which materials ‘work’ best for them. We also do not yet know whether this variation enhances reproductive success.

At least some species can also learn through experience which materials are best for nesting. For example, zebra finches will learn to avoid nest material if it has structural properties that make it difficult to use for building (Bailey et al. 2014; Figure 3.3). They will also learn to choose nest material of a non-preferred colour once they have successfully produced a brood from a nest of that colour (Muth and Healy 2011; Figure 3.4). Some preferences are more difficult to explain. Although zebra finches often strongly prefer material of one colour over another, preferences are not repeatable across populations. Sargent (1965) found that zebra finches much preferred brown over green material while those studied by Muth and Healy (2011) much preferred green over brown when offered a choice. Muth et al. (2013) also found that while zebra finches strongly preferred blue over yellow or red nest material, they did not have any colour preferences when they were offered a choice of food of the three different colours.

![Figure 3.3](image-url)

**Figure 3.3** The mean number of pieces of either flexible or stiff string male zebra finches (*Taeniopygia guttata*) use to build nests. Modified from Bailey et al. (2014).

![Figure 3.4](image-url)

**Figure 3.4** In an experiment in which male zebra finches (*Taeniopygia guttata*) built their first nest using material of a colour they did not prefer (preference before breeding), the birds that raised chicks subsequently switched their preference to this initially non-preferred colour (filled symbols). Birds that failed to raise chicks did not switch their preference for material colour (open symbols). Modified from Muth and Healy (2011).
3.5 Nest composition

3.5.1 The outer shell

The composition of the outer shell of the nest may be made almost entirely of a single material type or may be a composite structure made of multiple material types (Hansell 2000). The most basic of nests are shallow scrapes on the ground, such as those built by least terns (Sterna antillarum; Stucker et al. 2013), little ringed plovers (Charadrius dubius; Hanley et al. 2013), and common ostriches (Struthio camelus; Kubelka et al. 2014). In these cases nest-site and material selection are much the same thing as little or no material is moved from elsewhere and added to the nest. Substrate type and shelter are important to such nesting decisions; black-tailed gulls (Larus crassirostris) that lay eggs in those locations concealed by vegetation have low rates of egg loss (Lee et al. 2010). Camouflage partly explains this success because eggs are a better match to their background allowing higher egg survival than in areas with low vegetation and poor concealment. Under experimental conditions Japanese quail (Coturnix japonica) can select among locations based on the colour of the substrate, as they will lay their eggs in locations that are the best possible match to the colouration of their eggs (Lee et al. 2010; Lovell et al. 2013; Chapter 11). This suggests that the birds learn the colour of their own eggs and choose the nest substrate that will best camouflage them. Alternatively, birds exhibit a preference for nest-substrate colour and the colouration of their eggs that are both genetically determined and genetically linked.

Numerous species build a nest with the outer part of the nest formed from only one material type. Some of the structurally simplest of these are mound or platform nests of Adelie penguins (Pygoscelis adeliae), which build unlined mounds of gravel (Williams 1995), or James’s flamingoes (Phoenicoparrus jamesi), which build mounds of mud (Johnson et al. 1958). At the other end of the continuum of structural complexity, the hanging basket nests built by weaverbirds (Ploceidae) have an outer shell built entirely of long and strong vegetation, usually reed, grass or sedge although some species use strips of palm frond or fine twigs (Crook 1963). The village weaver prefers to build using long green material, a preference that seems to be at least partially learnt. In captivity younger birds are more accepting of less appropriate building materials, such as tooth picks and raffia, than are older more experienced nest builders (Collias and Collias 1962a, 1964). This preference for long fine material can be fatal when the weavers build with synthetic materials such as string, which can entangle both adults and young alike (Oschadleus 2012).

Why these species-specific preferences develop, or have evolved, is not clear. Although the assumption is that they are fixed, there are instances in which it appears that nest-building birds assess the structural properties of the materials with which they choose to build (Bailey et al. 2014). This is especially so when birds use human-produced materials. For example, although barn swallows (Hirundo rustica) typically build a cup-shaped nest out of balls of mud, they will also build with a mix of cement, sand and gravel (Al-Safadi and Al-Aqas 2006). While the usual interpretation would be that this choice is accidental, it is also possible the birds learn that the cement dries harder and stronger than other materials and so choose it preferentially. Similarly, the addition by common house martins (Delichon urbicum) of polysaccharides delivered in their saliva to the clay with which they build their nest increases the compressive strength of the clay. Nest strength may be an important building criterion for these birds and they may learn how to enhance that component of their nest (Silva et al. 2010).

Many species build a nest with an outer shell containing a mix of materials, which may vary widely. For example, the structural components of nests of many small species, such as hummingbirds (Trochilidae), are built using moss and spiders’ webs (Calvelo et al. 2006). Spider’s web looped around the moss seems to act like Velcro® might to hold the structure together (Hansell 2007). The nests of larger species such as thrushes (Turdus spp.) are, on the other hand, made largely of mud and dried grass, which may in the case of the common blackbird (Turdus merula), at least, increase insulation (Mainwaring et al. 2014b).

To date, there is, however, rather little information on whether using a mixture of building materials affects the mechanical properties of nests and that birds choose a combination of materials for this reason. Analysis of the co-occurrence of the most common material types (silk, grass stems, grass leaf, and sticks) used by species of the Fringillidae, Tyrannidae and Corvidae in building their nests did not reveal any distinct categories of material type (Hansell 2000). Such a categorization would have suggested that birds used groups of materials with complementary structural properties. As Hansell (2000) pointed out, however, the lack of such evidence might have resulted from coarse nest dissection protocols rather than whether birds choose an appropriate structural mix of materials (see Chapter 4).
3.5.2 Nest lining

Nest lining consists of material(s) on the inside that differ from those in the outer layer(s) (Hansell 2000). While not all nests are lined, those that are vary greatly in the material used. The song thrush (*Turdus philomelos*) builds a nest with an outer layer of grass, moss and mud but lines the nest with a thin layer of well-decomposed wood or bark (Ferguson-Lees et al. 2011). The nest of the common blackbird, however, which is very similar externally to the song thrush nest, is typically lined with fine grasses (Ferguson-Lees et al. 2011; Mainwaring et al. 2014b). In some nests it may be difficult to determine whether the inner layer fulfils a lining or structural role. For example, in weaver bird nests, the inside of the nest roof may consist of overlapping leaves, which act in much the same way as do roof slates by allowing rainwater to run off. These leaves may also play a structural role by helping to hold the nest walls apart (Crook 1960, 1963).

Many small birds will also add wool or artificial wool-like fibres to their nest linings, the use of which appears to be opportunistic as birds building closer to the source use more artificial material than do those building further away (Surgey et al. 2012). Long-tailed bushtits line their nests only with feathers, which constitute 41% of the overall nest mass. They also respond to variation in air temperature with a smaller mass of feathers being used while a mixture of materials could aid a nest’s structural properties, it is also possible that using a mixture of nest materials in the outer shell may aid nest crypsis via disruptive camouflage as the different colours and textures of the materials could help to break up the nest outline (Hansell 2000; Bailey et al. 2015). Although there is much evidence that birds respond to predation risk by choosing appropriate locations, which results in improved concealment of either the nest (Westmoreland and Best 1985) or the eggs (Lovell et al. 2013), it is perhaps surprising that there are few data to show that birds choose materials to camouflage their nests. There is some anecdotal evidence such as the addition by long-tailed bushtits (*Aegithalos caudatus*) of a thin, apparently decorative, layer to the outside of their nests, which is composed of pale reflective materials such as lichen, spider cocoons and polystyrene. This may help the nest to blend into its background (Hansell 1996). The addition of carnivore scat to nests by common waxbills (*Estrilda astrild*) may also play a role in reducing nest predation either by masking the scent of the nest or by repelling nest predators (Schuetz 2005; Chapter 5). To our knowledge, however, the only experimental evidence to date is provided by zebra finches building with coloured paper in the laboratory: the birds preferred to build with material that was a colour match to their nest site than to build with material of a contrasting colour (Bailey et al. 2015; Figure 3.5).

![Figure 3.5](image-url) In an experiment in which the nest cup and background of the cage were covered with coloured paper, nest-building male zebra finches (*Taeniopygia guttata*) typically preferred to build their nests with materials that matched the colour of the background to nests (dark portion of bars). The colours of background and material were pink, yellow, blue, green or cream and males were presented with materials that either matched the background or were of a contrasting colour (light portion of bars). Modified from Bailey et al. (2015).
in nests built later in the season when it is warmer (McGowan et al. 2004). In an experimental manipulation of the number of feathers in the nests of tree swallows (Tachycineta bicolor), chicks from featherless nests grew more slowly and had more parasites than did chicks from feathered nests (Chapter 8). This is possibly because the young birds were colder and had less energy available for growth and immune responses (Winkler 1993). The colour of the feathers chosen by barn swallows appears to be important, as birds prefer white feathers and nests containing more white than dark feathers have a higher hatching success (Peralta-Sánchez et al. 2011). There may be a trade-off between the benefit of feathers for increasing insulation and a cost of increasing predation risk because they increase the conspicuousness of the nest; this idea is supported by the greater incorporation of feathers by hole-nesting than by cup-nesting species (Møller 1984). It is not clear, however, that conspicuousness alone explains any effect of feather lining on predation risk. The addition of breast feathers of common pheasants (Phasianus colchicus) to the lining of open cup nests, but not to nests in cavities, increased the predation risk compared to nests without feathers. The addition of fur of European hares (Lepus europaeus) to the same nests, on the other hand, had no effect on predation (Møller 1987).

Birds may also trade off the predation risk associated with the conspicuousness of the material with which they line their nests if the materials act as a signal of adult quality to conspecifics. For example, black kites (Milvus migrans) add bright white material, often pieces of plastic, to nests. Although decorated nests are more visible and therefore more vulnerable to predation, conspecifics intrude less often into territories containing highly decorated nests than they do into territories with undecorated nests (Sergio et al. 2011).

Birds may also include aromatic substances, usually green plant material but on occasion even material like cigarette butts (Dykstra et al. 2009; Suárez-Rodríguez et al. 2013; Tomás et al. 2013; Chapter 8), when lining their nests. These substances contain chemicals with anti-parasitic and anti-microbial properties that, when added to nests, can improve chick survival (Gwinner and Berger 2008, Suárez-Rodríguez et al. 2013). The choice of species of aromatic materials that common starlings (Sturnus vulgaris) and blue tits add to their nests appears to be learnt as birds do not choose herbs relative to their abundance, do not all choose the same herbs, and tend to choose herbs they experienced in their natal nests (Gwinner and Berger 2008; Mennerat et al. 2009a).

### 3.6 Nest structure

In his review of the roles played by predators on breeding birds, including their nest-building decisions, Lima (2009) noted that there was little evidence that birds changed the structure of the nest they built in response to a perceived risk of predation. Comparative evidence, however, suggests that predation has been a selection pressure not just on choice of where to locate the nest but also in shaping the nest structure itself (Chapter 5). Collias (1997) suggested that those species forced to move to the ground because of competition for nest space would face a greater risk of predation from ground predators. Collias (1997) also proposed that these species would be expected to add a dome to their original cup nest. Indeed, in the babblers (Timaliidae), those species that build on the ground are highly likely to add a dome roof to the basic cup nest, which is not true for those babbler species that build their nests in trees (Hall et al. 2015). Furthermore, it appears that the ancestral state was to build a cup nest off the ground.

Although there are still no data (to our knowledge) that birds will respond to depredation of their own nest by modifying their nest structure, the often long (up to 30 cm) tube entrances to the nests built by some African weavers have often been considered to provide protection from a range of predators, including snakes. This is, in part, because the nest is often pendant from a single relatively fine twig. When Crook (1963) described 62 species of ploceine weavers from Africa, India and the Seychelles, he included anecdotes of snakes slipping off the ends of nest tubes and raptors pulling apart the ends of nest tubes but failing to reach the egg chamber. He concluded, however, that the intraspecific variation in the length of the nest tube was not obviously correlated with variation in predation risk. We suggest that there is more work to be done on explaining nest structure in the weavers.

House wrens (Troglodytes aedon) may make structural changes in response to perceived predation risk. Stanback et al. (2013) showed that birds that built in boxes with relatively large entrance holes built up a taller pile of sticks between the entrance hole and the nest cup than did wrens nesting in boxes with relatively small entrance holes. It appears that these birds, at least, can use the size of the entrance hole to assess their vulnerability to possible sources of nest failure, such as predators or brood parasites, and adjust their nest morphology appropriately.
There is increasing evidence for intraspecific structural variation in nests that correlate with variation in weather conditions (Britt and Deeming 2011; Crossman et al. 2011; Mainwaring et al. 2012, 2014b). It is not clear yet whether this variation is due to the responses of individuals to the weather they experience or to natural selection. The construction of a well-insulated nest can reduce both the energetic expenditure required during incubation and the rate at which eggs cool when the parents are away from the nest (Drent 1975; Collias and Collias 1984; van Dijk et al. 2013). It appears that birds usually manage this not by changing the materials they use but by simply adding more material (Crossman et al. 2011; Mainwaring et al. 2014b).

Whether social information plays any role in birds building the nest remains a mystery. It may be that some species modify their nest structure in response to others and the use by great tits of hair to cover their eggs may be such an example. In Finland great tits that have European pied flycatchers as near neighbours fledge fewer offspring than do great tits without such heterospecifics nearby (Loukola et al. 2014). Furthermore, the more offspring in a great tit’s nest, the more likely it is that the flycatchers will choose to nest nearby. Loukola et al. (2014) suggested that to reduce the ability of the flycatchers to assess the number of eggs in the nest and therefore to dissuade them from becoming neighbours, great tits cover their eggs with hair. It is unclear, however, whether this function only as a deterrent to harmful neighbours as great tits will also cover their eggs in areas free from flycatchers.

If there are relatively few data on intraspecific structural variation in nests, there are even fewer concerning what birds do in order to produce that structure. Since the studies by Collias and Collias (1962a, 1964) on weavers, and by Thorpe (1956) on long-tailed bush-tits, provided detailed observations on the specific behaviours these birds perform when building their nest, there has been little work to investigate how birds ‘know’ what structure to build. This is perhaps because detailing nest-building behaviour requires high definition video recordings accompanied by a prodigious effort in their analysis. Determining whether or not birds use a stereotypic sequence of movements when nest building also requires recording of birds building more than one nest. Solitary weavers are a very useful taxon in this regard because they will build multiple nests in a single season. Zebra finches in the laboratory are also useful as they will build ‘on command’, i.e. as soon as paired and provided with nest material. The logistic issues surrounding the requisite data collection may mean that describing and quantifying the building behaviour of species that build a single nest in each breeding season will prove much more elusive.

Using such detailed video data, however, Walsh et al. (2013) provided a possible explanation for their finding (Walsh et al. 2010) that, for both village weavers (Ploceus cucullatus) in Nigeria and southern masked weavers (Ploceus velatus) in Botswana, nests built by individual male weavers decreased in size as the season progressed. Walsh et al. (2010) proposed that this was either a response to changing weather conditions or to smaller clutch sizes. The video data showed that the birds also became more dextrous with more building resulting in them dropping diminishing quantities of grass (Walsh et al. 2011; Figure 3.6). Nest-building males may also have woven the grass more tightly as their weaving improved but there are no data to confirm this. The video data also provided an explanation for the lack of repeatability of nest structural characteristics within and across male weavers because individual birds were not stereotypic in the movements they used to build. When building, males also do not follow any obvious behavioural sequence from the beginning to the finishing of a nest as they continue to add new material and to work on older nests. This is the case even when nests are sufficiently complete that they are occupied by adult females and young (Walsh et al. 2013).

![Figure 3.6](image-url) The mean rate (± 1 S.E.) at which male southern masked weavers (Ploceus velatus, n = 7) dropped pieces of grass during the attachment phase for three successive nests. Modified from Walsh et al. (2011).
3.7 Neural basis of nest building

Concomitant with the recent increase in effort addressing the behaviour and decision-making involved in building nests, work is also beginning on the neural underpinnings of nest building. In zebra finches, at least, activity (as measured by expression of the immediate early gene c-fos) increases in several brain regions the more nest-building activity a male undertakes: the anterior motor pathway, the social behaviour network, and the dopaminergic reward system (Hall et al. 2014). Increased activation, however, is not observed in the posterior motor pathway. The differential gene expression in the anterior but not posterior motor pathway suggests that nest building differs from other motor actions as the anterior motor pathway is specifically involved in motor learning and sequencing (Feenders et al. 2008). More general motor actions are represented by activity in the posterior motor pathway. Gene expression data also suggest that while taking material to the nest and spending time in the nest with his mate is a rewarding behaviour for a nest-building male zebra finch, tucking the material into the growing nest is not. Activation in dopaminergic cells in the ventral tegmental area decreases the more males tuck material into the nest (Hall et al. unpublished data).

The cerebellum, a much-folded brain region involved in complex motor actions, especially manipulative skills, also seems to have a role in nest building. A significant proportion of the variation in the degree of cerebellar folding across species is explained by the complexity of the nest built (Hall et al. 2013; Figure 3.7). How the cerebellum is involved when birds are building their nests is not yet clear. This is just one of the many questions still to be answered with regard to the relationship between the brain and nest-building behaviour.

Figure 3.7 Regression lines of cerebellar foliation index on cerebellum volume (log transformed) and CFI for bird species that build a cup nest (filled circles, solid line), a platform nest (open circles, dashed line) or no nest (open circles, dotted line). Modified from Hall et al. (2013).
3.8 Conclusions

For such an important component of a bird’s reproductive success, we are still some distance from a full understanding of the behaviours and decision-making of nest-building birds. While there is much evidence showing that birds make decisions over where to locate the nest, modifying their choices with respect to their own experience and with regard to the choices of both conspecifics and heterospecifics, we know much less about the sources of information and decisions birds make over material choice and construction of the nest. It is still unclear, for instance, the extent to which individual birds can use environmental and social cues to fine tune the morphology of their nest to prevailing conditions. It is possible that dependence on learning some or all nest-building attributes is high in some species but not in others. We also need more data on the informational feedback (e.g. building success or reproductive success) that drives whether birds learn about nest design or the value of some materials over others. These are all questions concerning an individual’s own experience of nests or nest building but nest building is also a behaviour that might be shaped by observation of others or of the nests of others. We have much to learn about the role of social learning and whether (and if so, what) birds can learn about nest building from watching others build and inspecting the products of their nest-building efforts. We also know nothing at all with regard to the decision-making of birds that build in pairs or groups and how they coordinate their building efforts.

Given the apparent phenotypic similarity between tool use and manufacture in birds and nest building, we suggest that there may be merit in comparisons of the cognitive demands imposed by tool manufacture and those imposed by nest building. Perhaps the first obstacle to overcome is the still trenchant view that while tool manufacture is a product of complex cognition, nest building is entirely genetic. Although we are some considerable distance from fully understanding which aspects of nest building are entirely genetically predetermined and which involve learning from experience, there is increasing evidence that learning plays a role in multiple aspects of nest building. Finally, it may be surprising how little we understand about the structure of the nest itself. For example, how birds might use different materials and combine materials to refine properties of their nest such as insulation, rigidity and waterproofing (see Chapter 4). We will need a combination of both carefully designed field and laboratory experiments with long-term observational data to address these myriad questions.