Behavioural Processes 164 (2019) 59–64

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Experimental evidence of non-random nest material selection in pied flycatchers

Kevin B. Briggs[a], Mark C. Mainwaring[b,*]

[a] 1Washington Drive, Warton, Carnforth, LA5 9RA, UK
[b] Division of Biological Sciences, University of Montana, Missoula, MT, 59812, USA

ARTICLE INFO

Keywords:
Ficedula hypoleuca
Nest building
Nest material
Pied flycatcher

ABSTRACT

Nest building is a taxonomically widespread behaviour that consists of the construction of a suitable receptacle with collected materials for the incubation of eggs and sometimes for the raising of offspring. The use of specific nest materials has important fitness consequences for avian parents and offspring because they help to determine the thermal, parasitic and bacterial environment within nests and may also influence parental investment via intraspecific signalling. However, we presently know very little about the process by which nest materials are selected from the wider environment and specifically, it is unclear whether wild birds randomly or non-randomly select nest materials in relation to their local availability. Here, we report an experiment in which we provided experimental pairs of pied flycatchers (*Ficedula hypoleuca*) with wool, feathers and deer hair – commonly used nest materials found in their woodland habitats – close to their nests during the nest building period whilst control pairs were not provided with any materials. We found that females at experimental nests showed very clear preferences for deer hair, whilst almost completely avoiding the wool and feathers, thereby demonstrating that females exhibited very strong preferences for certain nest materials but not others. We therefore conclude that birds select nest materials in a non-random manner and do not simply use the materials most commonly available to them.

1. Introduction

Nest building is a taxonomically widespread activity with invertebrates and vertebrates building nests of some form or other in which to lay eggs and for some species, raise offspring (Collias and Collias, 1984; Hansell, 2000, 2005). Nest building consists of the collection of materials from the wider environment and the subsequent arrangement of them within the nest structure to help provide a suitable environment for offspring development towards independence (Hansell, 2005; Mainwaring et al., 2014; Healy et al., 2015). In birds, considerable interspecific and intraspecific variation exists in nest building behaviours and also in the materials incorporated into their nests (Mainwaring et al., 2014; Deeming and Mainwaring, 2015). For example, intraspecific variation in the presence or amount of certain materials within nests varies in relation to the phenotypic quality of the builder (Sergio et al., 2011), the phenotypic quality of the builder's reproductive partner (Polo and Veiga, 2006), the abundance of ectoparasites (Tomás et al., 2012; Suárez-Rodríguez et al., 2013), environmental conditions (McGowan et al., 2004; Mainwaring and Hartley, 2008) and rapid land use changes such as those caused by urbanization (Wang et al., 2008; Lambrechts et al., 2017).

Nesting materials used by birds can have profound effects on the fitness of developing offspring (Deeming and Mainwaring, 2015). They can, for example, modify the thermal (McGowan et al., 2004; Mainwaring et al., 2017), bacterial (Peralta-Sanchez et al., 2010) and parasitic (Tomás et al., 2012; Suárez-Rodríguez et al., 2013) environment within nests and can also influence parental investment by nonbuilding reproductive partners through signalling processes (Polo and Veiga, 2006; Mainwaring et al., 2008). Illustratively, a study of spotless starlings (*Sturnus unicolor*) showed that the experimental addition of green plants and feathers, both of which are commonly used materials by the starlings, to nests subsequently increased and decreased the rates of telomere attrition, respectively (Soler et al., 2017). As the length and attrition of nestlings' telomeres were accurate predictors of their future survival prospects, then there was evidence that nest materials directly influenced the nestlings' telomere length and dynamics (Soler et al., 2017). More broadly, this means that the materials used to construct nests have important consequences for offspring fitness.

Despite the importance of selecting appropriate nesting materials, we presently know very little about the selection of nest materials by

---

* Corresponding author.
E-mail address: mark.mainwaring@mso.umt.edu (M.C. Mainwaring).

https://doi.org/10.1016/j.beproc.2019.04.008
Received 9 November 2018; Received in revised form 7 February 2019; Accepted 9 April 2019

wild birds. A notable exception comes from Surgey et al. (2012) who provided nesting materials of different colours for great tits (*Parus major*) in dispensers throughout their woodland habitat and found that they generally collected material from the closest dispenser in an opportunistic manner. Another study of great tits supports this conclusion because birds breeding in nestboxes attached to pine trees used pine needles as nest materials more often than conspecifics in nestboxes attached to other tree species (Lambrechts et al., 2017). Whilst these studies suggest that nesting materials are used in relation to their local availability, there is also evidence that birds use some nest materials preferentially over others (McGowan et al., 2004; Sergio et al., 2011) with perhaps the best known example coming from the incorporation of green plant materials into nests by passerine birds despite the assumption that such herbs are only infrequently available in their woodland habitats (e.g. Mennerat et al., 2009; reviewed by Dubiec et al., 2013).

Studies therefore strongly suggest that some nest materials are preferred over other nest materials (Deeming and Mainwaring, 2015), but it remains unclear if wild birds show a preference for some materials over others and whether or not such preferences are related to the local availability of those materials. Evidence from captive birds indicates that birds do select nest materials in a non-random manner when alternatives are also available (e.g. Muth and Healy, 2014; Bailey et al., 2014, 2015) but here, we address this issue in wild birds. We report an experiment in which we provided experimental pairs of pied flycatchers (*Ficedula hypoleuca*) with wool, feathers and deer hair, all of which are materials commonly found and used by the species in their woodland habitat (Lundberg and Alatalo, 1992; Briggs and Deeming, 2016). Each of the materials were provided close to their nests of experimental pairs during the nest building period, whilst control pairs were not provided with any materials. After the birds had finished breeding, we dissected the nests and quantified the materials collected by female flycatchers to construct their nests. We test the prediction that experimental pairs will exhibit clear preferences for some of the provided nest materials (following Bailey et al., 2015) and thus confirm that pied flycatchers collect nest materials in a non-random manner that is unrelated to their local availability.

2. Material and methods

2.1. Study area and study species

We studied pied flycatchers breeding in seven deciduous woodlands that consisted largely of sessile oak (*Quercus petraea*) and downy birch (*Betula pubescens*) trees with an understory largely consisting of wood sorrel (*Oxalis acetosella*), which is classified as ‘W11’ by the National Vegetation Classification (Rodwell, 1991). The woodlands were grouped around Roeburndale West in the Forest of Bowland Area of Outstanding Natural Beauty in Lancashire in northwest England (54°05′N, 2°36′W, altitude = 100-190 m above sea level). Our study was performed in the 2016 and 2017 breeding seasons in seven woodlands that covered about 120 ha in size (Briggs and Mainwaring, 2017). Pied flycatchers have been breeding in a total of 685 nestboxes in those seven woodlands since 1968, with just over 100 pairs now regularly nesting and being routinely monitored as part of a British Trust for Ornithology ‘Ringing Adults for Survival’ project (Briggs and Deeming, 2016). Following well established protocols (Lambrechts et al., 2010; Møller et al., 2014), wooden nestboxes of standardised dimensions (internal floor = 140 × 95 mm; distance from floor to hole = 105 mm) were placed about 1.5 m above the ground and about 50 m apart on tree trunks and faced in either a southerly or easterly direction unless local topographical features prevented us from doing this.

Old nests were removed from nestboxes at the end of each breeding season and so when the flycatchers arrived back from their sub-Saharan wintering grounds, empty nestboxes were ready for them to breed inside. Female pied flycatchers build nests made primarily of dead leaves, moss, bark, fibres and grass (Lundberg and Alatalo, 1992; Briggs and Deeming, 2016) collected within˜40 m of the nest site (Stjernberg, 1974) shortly after their arrival. Females then incubate the eggs alone before both parents provision the offspring with caterpillars (Lundberg and Alatalo, 1992) and a wide variety of invertebrates (Betts, 1954).

2.2. Providing nesting materials

Prior to the flycatchers arriving on their breeding grounds from their sub-Saharan wintering grounds, all of the nestboxes were checked to ensure they were empty. The nestboxes were then monitored every three days or so from the beginning of April to check for the beginning of nest building (Briggs and Deeming, 2016). The nestboxes were occupied by blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) as well as pied flycatchers but there was always a sufficient supply of empty nestboxes available for the flycatchers. When new pied flycatcher nests were found inside nestboxes, they were alternately assigned to the experimental and control treatments in a systematic manner in order to control for seasonal variation in nest building behaviours (McGowan et al., 2004; Mainwaring and Hartley, 2008). There were 12 experimental and 12 control nests in 2016 and 16 experimental and 16 control nests in 2017, which meant that we had a total of 28 experimental nests and 28 control nests included in this study. After finding that nests had been initiated, we provided experimental pairs of pied flycatchers with fixed quantities of wool, feathers and deer hair – all of which are commonly available nest materials in their deciduous woodland habitats – on a prominent place on the floor within two-five metres of each of their nests during the remainder of the nest building period.

More specifically, we created a patch of bare earth measuring about 60 cm by 40 cm with a garden trowel, between two-five metres from the tree on which nestboxes were positioned and in the same orientation as the nestboxes to maximise the chances of the birds seeing the material when they were arriving at, or leaving, their nestboxes. We scattered 3.0 gs of roe deer (*Capreolus capreolus*) hair, which equates to about 1000 individual deer hairs, onto the patch of bare earth using hair that had been plucked from a dead roe deer carcass found dead approximately 10 km from the study site. The tufts of hair were marked at the ends with a black permanent marker pen so that a distinctive terminal band was present to allow the hair to be identifiable when the nests were dissected. The deer hair was flattened with the hand to press the hair into the ground to prevent them from being blown away.

Wool from sheep was collected from barbed wire fences and the individual fibres were separated to make it easier for the birds to select single or small groups of wool fibres rather than clumps of wool. This is important because the birds may have otherwise collected clumps of wool, rather than single strands, thereby increasing the amount of wool in nests and introducing bias. We laid 2.0 gs of wool on a broken ended small log in the scrapes, each of which measured 20 cm by 5 cm, which thereby allowed the wool to remain in place and yet still be available to the flycatchers in single fibres.

The feathers, meanwhile, were removed from a road-kill male pheasant (*Phasianus colchicus*) and a road-kill lesser black-backed gull (*Larus fuscus*) and were mixed together in a large plastic bag before being placed out in the woods for the flycatchers to collect. We laid 1.0 g of feathers in purpose-made green netting plastic bags so that feathers projected through the mesh and could easily be pulled out. The end of the bag was closed with wire and the bag pinned to the ground with metal wire so that the bag and hence the feathers remained in the patch of bare earth rather than being blown away in the wind. The completed scrape was left in place until the first eggs were laid and not replenished as routine monitoring showed that the materials were never used up. Control pairs were treated identically, although they were not provided with any nesting materials.

Table 1
Summary of General Linear Models examining outer nest material mass. The dependent variable was the ‘nest material weight’ (grams) and the explanatory variables were ‘treatment’ (experimental, control: factor), ‘year’ (2017, 2018: factor) and their interaction term. The materials we provided are shown with an asterisk.

Nest material	Factor	d.f.	F-value	P value
Moss	Treatment	1,55	0.0064	0.801
	Year	1,55	0.559	0.458
	Treatment x year	1,55	0.983	0.326
Lichen	Treatment	1,55	2.062	0.157
	Year	1,55	1.664	0.203
	Treatment x year	1,55	1.664	0. 203
Grass	Treatment	1,55	3.453	0.069
	Year	1,55	0.102	0.751
	Treatment x year	1,55	0.472	0.495
Leaves	Treatment	1,55	0.020	0.889
	Year	1,55	0.235	0.630
	Treatment x year	1,55	0.044	0.834
Twigs	Treatment	1,55	0.551	0.461
	Year	1,55	0.626	0.432
	Treatment x year	1,55	0.000	0.996
Fern	Treatment	1,55	2.103	0.153
	Year	1,55	0.067	0.797
	Treatment x year	1,55	0.180	0.673
Rush	Treatment	1,55	1.351	0.250
	Year	1,55	1.351	0.250
	Treatment x year	1,55	1.351	0.250
Root	Treatment	1,55	0.065	0.799
	Year	1,55	0.338	0.563
	Treatment x year	1,55	0.933	0.338
Bark	Treatment	1,55	0.010	0.922
	Year	1,55	0.147	0.703
	Treatment x year	1,55	0.840	0.364
Seeds	Treatment	1,55	1.600	0.211
	Year	1,55	0.070	0.792
	Treatment x year	1,55	1.225	0.273
Feathers*	Treatment	1,55	0.292	0.591
	Year	1,55	0.980	0.327
	Treatment x year	1,55	0.292	0.591
Hair*	Treatment	1,55	0.050	0.824
	Year	1,55	4.038	0.050
	Treatment x year	1,55	2.443	0.124
Wool*	Treatment	1,55	1.793	0.186
	Year	1,55	1.863	0.178
	Treatment x year	1,55	3.782	0.057
Artificial material	Treatment	1,55	0.097	0.757
	Year	1,55	0.024	0.877
	Treatment x year	1,55	2.420	0.126
Dust	Treatment	1,55	0.641	0.427
	Year	1,55	3.451	0.069
	Treatment x year	1,55	0.707	0.404

2.3. *Dissecting nests*

Nests were monitored throughout the remainder of the breeding attempt to quantify breeding parameters such as first egg dates, clutch sizes, brood sizes and fledging success. After the completion of the nesting attempt, nests were removed from the nestboxes and after immediately being placed in a sealed and labelled plastic bag, were placed in cardboard boxes and frozen for a period of 4–22 days at −20 °C to kill any invertebrates within the nests. The nests were then air-dried in separate plastic trays and stored in a cool, dry environment within a cardboard box in a garage until they were dissected (Briggs and Deeming, 2016).

Pied flycatcher nests have distinct outer nest and cup lining layers (Lundberg and Alatalo, 1992; Briggs and Deeming, 2016) and so we began by separating those outer nest and cup lining layers. Both layers were then dissected in order to quantify the mass of their composite materials, which are listed in Table 1. The mass of each material was quantified by weighing them on an electronic balance (Pesola PPS200) to the nearest 0.01 g, and deer hairs were individually counted and examined for the presence of a black band indicating it had been provided by us as part of the experiment. There was usually a very small amount of material left at the end which resembled debris rather than any particular material and was classified as ‘dust’ before being weighed (following Briggs and Deeming, 2016). All measurements were taken by one observer (KBB) to eliminate error due to inter-observer variability.

2.4. *Statistical analyses*

Our analyses were split into two parts to examine the outer nest and inner cup lining layers separately so as to reflect the two distinct components of pied flycatcher nests (Briggs and Deeming, 2016). We considered using compositional analyses to examine the composition of materials used to build nests but whilst it is normally a very useful approach, it relies heavily on the use of 'log-ratios' which is not recommended when the data set contains large numbers of zero values (Fry et al., 2000; Martín-Fernández et al., 2011) as ours does and so it is likely that this technique would have introduced bias to our study.

We therefore analysed variation in nest material mass using a general linear modelling (GLM) approach. The data were initially tested to determine whether they had a Gaussian error structure or not using Kolmogorov-Smirnov one sample tests before the data were analysed in the SPSS version 23 (SPSS, Chicago, IL, USA) statistical package. For each of the nest materials listed in Table 1, separate models were used to examine the influence of the experimental treatment and study year on the mass of those materials. For the outer nest layer, we ran GLM’s where the dependent variable was ‘material weight’ (grams) and the explanatory variables were ‘treatment’ (control, experimental: factor), ‘year’ (2016, 2017: factor) and their two-way interaction term. Each of the explanatory variables was assessed for significance when they were the last terms in the model in a rotational manner. As such all of the main terms, as well as their two-way interaction term, were initially entered into the models before the terms were sequentially rotated and dropped if they were non-significant until only those terms whose elimination would have significantly reduced the explanatory power of the models remained, thereby yielding the final minimal models. The probabilities for the explanatory factors (treatment and year) were thus calculated after removing the non-significant interactions from the models (Crawley, 1993).

We also used GLM’s to examine variation in nest building materials in the inner nest layer and the maximal models were simplified following the stepwise deletion approach described above. Throughout the study, mean values are presented ± 1 standard error and a critical P value of 0.05 is applied to denote significance.

3. Results

The mass of none of the nest materials that formed the outer nest layer varied in relation to either treatment or year (Table 1; Fig. 1a) although there was a non-significant trend towards deer hair and dust varying between years and for wool, the treatment x year interaction term also approached significance. Meanwhile, the mass of the nest materials that formed the inner cup lining layer did exhibit considerable variation (Table 2; Fig. 1b). The mass of deer hair incorporated into nest cups was significantly higher in experimental nests than in control nests (Table 2; Fig. 1b) and a P value of 0.054 indicates that there was a non-significant trend towards the amount of deer hair varying between years. There was, however, no variation in the mass of wool or feathers in relation to treatment but the mass of wool varied between years, being higher in 2016 than in 2017. Whilst the mass of bark and dust varied with year, both showed the opposite trend to wool as they were higher in 2017 than in 2016 (Table 2; Fig. 1b). Meanwhile, the mass of both ferns and roots varied with the experimental treatment, with both being higher in control nests than in experimental nests, although their masses did not vary between years (Table 2;

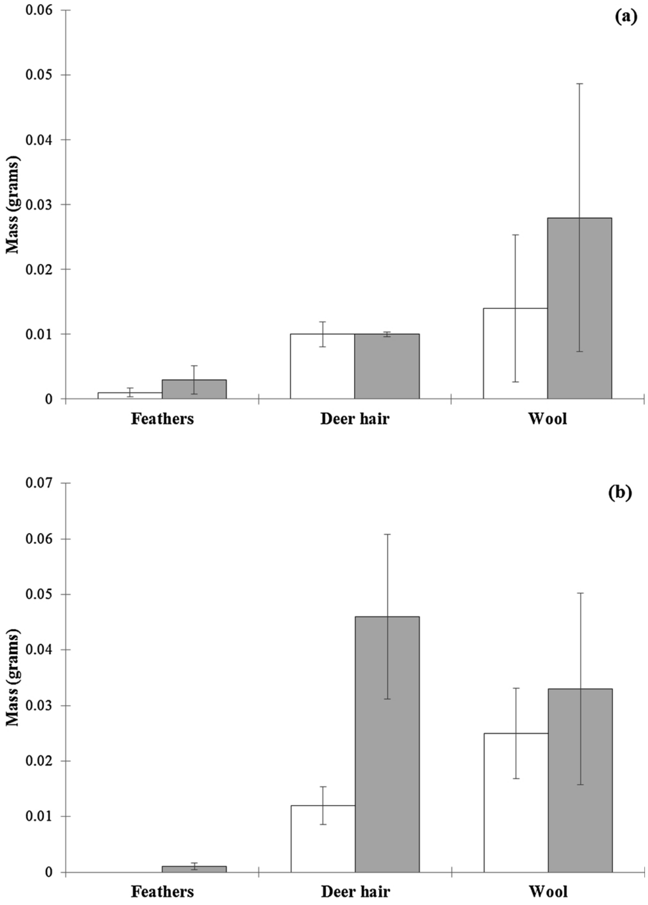

Fig. 1. The mean ± standard error mass of nest materials provided at experimental nests (grey bars) and control nests (white bars) for both (a) outer and (b) inner nest structures.

Fig. 1b).

Table 2

Summary of General Linear Models examining inner nest material mass. The dependent variable was the 'nest material weight' (grams) and the explanatory variables were 'treatment' (experimental, control: factor), 'year' (2017, 2018: factor) and their interaction term. The materials we provided are shown with an asterisk.

Nest material	Factor	d.f.	F-value	P value
Moss	Treatment	1,55	0.096	0.757
	Year	1,55	3.173	0.081
	Treatment x year	1,55	0.443	0.509
Lichen	Treatment	1,55	0.743	0.393
	Year	1,55	0.743	0.393
	Treatment x year	1,55	0.743	0.393
Grass	Treatment	1,55	0.639	0.428
	Year	1,55	2.466	0.122
	Treatment x year	1,55	0.206	0.652
Leaves	Treatment	1,55	0.018	0.894
	Year	1,55	2.775	0.102
	Treatment x year	1,55	0.871	0.355
Twigs	Treatment	1,55	0.351	0.250
	Year	1,55	0.351	0.250
	Treatment x year	1,55	0.351	0.250
Fern	**Treatment**	**1,55**	**0.022**	**0.022**
	Year	1,55	0.182	0.182
	Treatment x year	1,55	0.354	0.354
Rush	Treatment	1,55	0.011	0.917
	Year	1,55	0.011	0.917
	Treatment x year	1,55	2.157	0.148
Root	**Treatment**	**1,55**	**7.404**	**0.009**
	Year	1,55	0.103	0.749
	Treatment x year	1,55	0.044	0.834
Bark	Treatment	1,55	0.501	0.482
	Year	**1,55**	**5.826**	**0.019**
	Treatment x year	1,55	0.741	0.393
Seeds	Treatment	1,55	0.270	0.605
	Year	1,55	0.038	0.846
	Treatment x year	1,55	0.621	0.434
Feathers*	Treatment	1,55	2.902	0.094
	Year	1,55	0.116	0.735
	Treatment x year	1,55	0.116	0.735
Hair*	**Treatment**	**1,55**	**8.347**	**0.006**
	Year	1,55	3.871	0.054
	Treatment x year	1,55	2.382	0.129
Wool*	Treatment	1,55	0.337	0.564
	Year	**1,55**	**5.633**	**0.021**
	Treatment x year	1,55	0.908	0.345
Artificial material	Treatment	1,55	0.597	0.443
	Year	1,55	1.253	0.268
	Treatment x year	1,55	0.418	0.521
Dust	Treatment	1,55	0.535	0.468
	Year	**1,55**	**9.380**	**0.003**
	Treatment x year	1,55	0.804	0.374

4. Discussion

The main findings of this study were that when experimental pairs of pied flycatchers were provided with three kinds of nest materials close to their nests throughout the nest building period, the females who construct nests alone, built nests with inner cup lining layers that contained significantly more deer hair than control females, whilst the amount of wool and feathers did not differ between experimental and control nests. Although the materials in the outer nest layer did not differ between treatments, our study demonstrates that nest building females showed clear preferences for some materials over others and further shows that the composition of the pied flycatcher nests was unrelated to the local availability of apparently suitable nesting materials. Our experimental results therefore provide support for the hypothesis that pied flycatchers select nesting materials in a non-random manner from their surroundings rather than simply selecting those potential nesting materials that are most commonly and locally available to them.

Female pied flycatchers showed a clear preference for the deer hair that we experimentally provided whilst simultaneously avoiding the wool and feathers, which meant that the cup lining layer of their nests contained significantly more deer hair than nests built by control females. This contradicts a previous observational study of pied flycatchers in which it was anecdotally suggested that they are opportunist nest builders who collect whatever materials are close to the nest site (Stjernberg, 1974). Anecdotal evidence suggests, however, that territorial birds such as pied flycatchers tend to use the most appropriate nesting material within their territory. It is unclear why the flycatchers showed such a clear preference for the deer hair although we suggest that it performs an insulating function and thus keeps the embryos and nestlings within thermally acceptable limits (Hilton et al., 2004; DuRant et al., 2013). Alternatively, it may be possible the flycatchers avoided the wool because their nestlings may get their legs entangled in the wool and prevents them from fledging, as shown in blue tits (Stenning, 2018). The pied flycatchers may also have avoided the feathers because selecting them as nesting materials may introduce feather mites and other avian parasites and pathogens into the nest.

Observational evidence that potential nesting materials are not used in relation to their local availability comes from studies showing, for example, that co-existing Antarctic skuas (*Stercorarius* spp.) and kelp gulls (*Larus dominicanus*) used different materials to build their nests (Quintana and Travaini, 2000) and that hole-nesting passerines use aromatic green plant material despite it anecdotally considered to be locally scarce (Mennerat et al., 2009). However, both van Riper (1977) and Surgey et al. (2012) have shown that the use of nesting materials is opportunistic and it could well be that our experimental procedures mimicked the presence of a dead deer from which the flycatcher could collect hairs. It therefore seems unclear if nest materials are chosen in a non-random manner or opportunistically but our findings suggest that both possibilities can occur simultaneously (Deeming and Mainwaring, 2015).

The female flycatchers at experimental nests collected nest materials in an opportunistic fashion by taking the deer hair and yet simultaneously showed that such preferences are non-random by collecting either no, or only negligible amounts, of wool and feathers. The female flycatchers thus showed a clear avoidance of the wool and feathers. This agrees with studies showing that pied flycatcher nests in central Spain contained no wool or feathers (Moreno et al., 2009) but in north Wales, nests do contain feathers but not wool (KBB pers. obs.). Stjernberg (1974) is the only other recorder of pied flycatcher nest materials, in Finland, and recorded only one with a feather in the outer nest material, and no nests containing wool, but she reported that 46 per cent of nests had elk (*Alces alces*) hair in the cup lining layer. This level of selectivity suggests that the material composition of nests is unrelated to the risk of predation whilst collecting nesting materials (Lima, 2009) or the energetic costs of finding and transporting nesting materials (Mainwaring and Hartley, 2013) because if either of these scenarios were true then the flycatchers should have selected the materials we provided close to the nest. Although feathers are a widely used nesting material amongst birds that serve to provide insulation (Winkler, 1993; Hilton et al., 2004; Liljeström et al., 2009), repel ectoparasites (Windsor et al., 2013) or act as sexual signals (Veiga and Polo, 2005; Mainwaring and Hartley, 2009), it seems that as the flycatchers do not generally use feathers in their nests (Briggs and Deeming, 2016) then they did not recognise them as potential nesting materials.

The experimental provision of nesting materials close to the nests of the flycatchers changed the composition of the inner cup lining layer of their nests but there was no change in the composition of the outer nest layer, although there was a non-significant trend ($P = 0.050$) towards deer hair varying between years. The nests of pied flycatchers primarily consist of leaves, moss, lichens and grass (Lundberg and Alatalo, 1992) and so it may not be expected that the provision of wool, deer hair and feathers would alter the composition of the outer nest layers because they were unfamiliar with them. Alternatively, the outer nest layer serves primarily to provide a structural platform on which to lay eggs (Hansell, 2000) but may also serve to serve as a sexual signal. For example, the experimental change of nest size of blue tits (*Cyansistes caeruleus*), in which females build the nests alone, influenced male behaviour (Tomás et al., 2013). When the size of nests and the amount of green plant material were experimentally enlarged or reduced, male risk-taking behaviors were found to be significantly lower at those nests reduced in size and significantly higher at nests where green plants were added (Tomás et al., 2013). Females building larger nests therefore accrued fitness benefits via increased male investment and it may be surprising that the females did not collect the materials to increase the size of their nests, it is likely that as wool, deer hair and feathers do not provide much structural support that increased the size of nests, then they may have been avoided.

We have experimentally provided evidence for the widely held assumption that nest materials are not selected at random by birds, which means that they show strong preferences for some nest materials whilst actively avoiding others. Our findings also show that the nest material composition of pied flycatcher nests is not simply determined by the local availability of potential nest materials. To the best of our knowledge we have performed the first experiment to have provided wild birds with a variety of potential nest building materials (but see e.g. Muth and Healy, 2014; Bailey et al., 2014, 2015 for studies of captive birds) which means that several avenues of research are possible. It would be interesting to test the role of learning in such decisions because it may well be that, for example, birds raised in nests experimentally containing feathers subsequently collect lots of feathers when building their own nests during adulthood. It would, however, be important to consider that there could be confounding variables if pied flycatchers have been selected to avoid feathers as nesting materials due to the presence of parasites on feathers. Further, given that the presence of some nest materials influence the survival prospects of young (e.g. Soler et al., 2017), it would be interesting to examine how nest material composition of nests more generally influences both parental and offspring fitness, especially with regard to the collection of anthropogenic materials such as string and plastic that are increasingly being found in the nests of some bird species but is under-recorded at present.

Acknowledgments

We thank Rodney Everett, Alex Mather and Karl Oyston for permission to work in their woodlands; John Wilson, Jean Roberts, Paul Cammack and Sheila Cooper for their contribution to the ongoing pied flycatcher ringing project; and two anonymous reviewers for many useful comments.

References

Bailey, I.E., Morgan, K., Healy, S.D., 2014. Physical cognition: birds learn the structural efficacy of nest material. Proc. R. Soc. Lond. 281, 20133225.

Bailey, I.E., Backes, A., Walsh, P.T., Morgan, K.V., Meddle, S.L., Healy, S.D., 2015. Image analysis of weaverbird nests reveals signature weave patterns. Royal Soc. Open Sci. 2, 150074.

Betts, M.M., 1954. Experiments with an artificial nestling. Br. Birds 47, 229–231.

Briggs, K.B., Deeming, D.C., 2016. Use of materials in nest construction by Pied Flycatchers *Ficedula hypoleuca* reflects localised habitat and geographical location. Bird Study 63, 516–524.

Briggs, K.B., Mainwaring, M.C., 2017. Habitat geology influences intraspecific variation in the speckling patterns of blue tit *Cyanistes caeruleus* and great tit *Parus major* eggs. Acta Ornithol. 52, 11–20.

Collias, N.E., Collias, E.C., 1984. Nest Building and Bird Behaviour. Princeton University Press, Princeton.

Crawley, M.J., 1993. GLIM For Ecologists. Blackwell, London.

Deeming, D.C., Mainwaring, M.C., 2015. The functional properties of nests. In: Deeming, D.C., Reynolds, S.J. (Eds.), Nests, Eggs, and Incubation: New Ideas About Avian Reproduction. Oxford University Press, Oxford, pp. 29–49.

Dubiec, A., Góźdź, I., Mazgagski, T.D., 2013. Green plant material in avian nests. Avian Biol. Res. 6, 133–146.

DuRant, S.E., Hopkins, W.A., Hepp, G.R., Walters, J.R., 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. Biol. Rev. 88, 499–509.

Fry, J.M., Fry, T.R.L., McLaren, K.R., 2000. Compositional data analysis and zeros in micro data. Appl. Econ. 32, 953–959.

Hansell, M.H., 2000. Bird Nests and Construction Behaviour. Cambridge University Press, Cambridge.

Hansell, M.H., 2005. Animal Architecture. Oxford University Press, Oxford.

Healy, S.D., Morgan, K.V., Bailey, I.E., 2015. Nest construction behaviour. In: Deeming, D.C., Reynolds, S.J. (Eds.), Nests, eggs, and incubation: New ideas about avian reproduction. University Press, Oxford, Oxford, pp. 16–28.

Hilton, G.M., Hansell, M.H., Ruxton, G.D., Reid, J.M., Monaghan, P., 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. Auk 121, 777–787.

Lambrechts, M.M., Adriaensen, F., Ardia, D.R., Artemyev, A.V., Atiénzar, F., Bańbura, J., Barba, E., Bouvier, J.-C., Camproden, J., Cooper, C.B., Dawson, R.D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L.Z., Goodenough, A.E., Gosler, A.G., Grégoire, A., Griffith, S.C., Gustafsson, L., Johnson, L.S., Kania, W., Keišs, O., Llambias, P.E., Mainwaring, M.C., Mänd, R., Massa, B., Mazgajski, T.D., Møller, A.P., Moreno, J., Naef-Daenzer, B., Nilsson, J.-Å., Norte, A.C., Orell, M., Otter, K.A., Park, C.R., Perrins, C.M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytkönen, S., Shiao, M.-T., Silverin, B., Slagsvold, T., Smith, H.G., Sorace, A., Stenning, M.J., Stewart, I., Thompson, C.F., Tryjanowski, P., Török, J., van Noordwijk, A.J., Winkler, D.W., Ziane, N., 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithol. 45, 1–26.

Lambrechts, M.M., Charmantier, A., Demeyrier, V., Lucas, A., Perret, S., Abouladzé, M., Bonnet, M., Canonne, C., Faucon, V., Grosset, S., le Prado, G., Lidon, F., Noell, T., Pagano, P., Perret, V., Pouplard, S., Spitaliéry, R., Bernard, C., Perret, P., Blondel, J., Grégoire, A., 2017. Nest design in a changing world: great tit *Parus major* nests from a Mediterranean city environment as a case study. Urban Ecosyst. 20, 1181–1190.

Liljeström, M., Schiavini, A., Reboreda, J.C., 2009. Chilean swallows (*Tachycineta meyeni*) adjust the number of feathers added to the nest with time of breeding. J. Ornithol. 121, 783–788.

Lima, S.L., 2009. Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. Biol. Rev. 84, 485–513.

Lundberg, A., Alatalo, R.V., 1992. The Pied Flycatcher. T & AD Poyser, London.

Mainwaring, M.C., Hartley, I.R., 2008. Seasonal adjustments in nest cup lining in Blue Tits *Cyanistes caeruleus*. Ardea 96, 278–282.

Mainwaring, M.C., Hartley, I.R., 2009. Experimental evidence for state-dependent nest weight in the blue tit, *Cyanistes caeruleus*. Behav. Proc. 81, 144–146.

Mainwaring, M.C., Hartley, I.R., 2013. The energetic costs of nest building in birds. Avian Biol. Res. 6, 12–17.

Mainwaring, M.C., Hartley, I.R., Lambrechts, M.M., Deeming, D.C., 2014. The design and function of birds' nests. Ecol. Evol. 4, 3909–3938.

Mainwaring, M.C., Barber, I., Deeming, D.C., Pike, D.A., Roznik, E.A., Hartley, I.R., 2017. Climate change and nesting behaviour of vertebrates: a review of the ecological effects and potential for adaptive responses. Biol. Rev. 92, 1991–2002.

Mainwaring, M.C., Benskin, C.M.H., Hartley, I.R., 2008. The weight of female-built nests correlates with female but not male quality in the Blue Tit *Cyanistes caeruleus*. Acta Ornithol. 43, 43–48.

Martín-Fernández, J.A., Palarea-Albaladejo, J., Olea, R.A., 2011. Dealing with zeros. In: Pawlowsky-Glahn, V., Buccianti, A. (Eds.), Compositional Data Analysis: Theory and Applications. John Wiley & Sons, London, pp. 43–58.

McGowan, A., Sharp, S.P., Hatchwell, B.J., 2004. The structure and function of nests of long-tailed Tits *Aegithalos caudatus*. Funct. Ecol. 18, 578–583.

Mennerat, A., Perret, P., Lambrechts, M.M., 2009. Local individual preferences for nesting materials in a passerine bird. PLoS One 4, e5104.

Møller, A.P., Adriaensen, F., Artemyev, A., Bańbura, J., Barba, E., Biard, C., Blondel, J., Bouslama, Z., Bouvier, J.-C., Camprodon, J., Cecere, F., Chaine, A., Charmantier, A., Charter, M., Cichoń, M., Cusimano, C., Czeszewik, D., Doligez, B., Doutrelant, C., Dubiec, A., Eens, M., Eeva, T., Faivre, B., Ferns, P.N., Forsman, J.T., García-del-Ray, E., Goldshtein, A., Goodenough, A.E., Gosler, A.G., Góźdź, I., Grégoire, A., Gustafsson, L., Hartley, I.R., Heeb, P., Hinsley, S.A., Isenmann, P., Jacob, S., Järvinen, A., Juškaitis, R., Kania, W., Korpimäki, E., Krams, I., Laaksonen, T., Leclercq, B., Lehikoinen, E., Loukola, O., Lundberg, A., Mainwaring, M.C., Mänd, R., Massa, B., Mazgajski, T.D., Merino, S., Mitrus, C., Mönkkönen, M., Morales-Fernaz, J., Moreno, J., Morin, X., Nager, R.G., Nilsson, J.-Å., Nilsson, S.G., Norte, A.C., Orell, M., Perret, P., Perrins, C.M., Pimentel, C.S., Pinxten, R., Priedniece, I., Quidoz, M.-C., Remeš, V., Richner, H., Robles Díez, H., Russell, A., Rytkönen, S., Senar, J.C., Seppänen, J.T., Pascoal da Silva, L., Slagsvold, T., Solonen, T., Sorace, A., Stenning, M.J., Török, J., Tryjanowski, P., van Noordwijk, A.J., von Numers, M., Walankiewicz, W., Lambrechts, M.M., 2014. Clutch size variation in Western Palearctic secondary hole-nesting passerine birds in relation to nestbox design. Meth. Ecol. Evol. 4, 353–362.

Moreno, J., Merino, S., Lobato, E., Ruiz-de-Castañeda, R., Martínez-de la Puente, J., Del Cerro, S., Rivero-De Aguilar, J., 2009. Nest-dwelling ectoparasites of two sympatric hole-nesting passerines in relation to nest composition: an experimental study. Ecoscience 16, 418–427.

Muth, F., Healy, S.D., 2014. Zebra finches select nest material appropriate for a building task. Anim. Behav. 90, 237–244.

Peralta-Sanchez, J.M., Møller, A.P., Martin-Platero, A.M., Soler, J.J., 2010. Number and colour composition of nest lining feathers predict eggshell bacterial community in barn swallow nests: an experimental study. Funct. Ecol. 24, 426–433.

Polo, V., Veiga, J.P., 2006. Nest ornamentation by female spotless starlings in response to a male display: an experimental study. J. Anim. Ecol. 75, 942–947.

Quintana, R.D., Travaini, A., 2000. Characteristics of nest sites of skuas and kelp gull in the Antarctic peninsula. J. Field Ornithol. 71, 236–249.

Rodwell, J.S., 1991. British plant communities. Woodlands and Scrub, vol. 1 Cambridge University Press, Cambridge.

Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J.A., Hiraldo, F., 2011. Raptor nest decorations are a reliable threat against conspecifics. Science 331, 327–330.

Soler, J.J., Ruiz-Castellano, C., Figuerola, J., Martín-Vivaldi, M., Martínez-de la Puente, J., Ruiz-Rodríguez, M., Tomás, G., 2017. Telomere length and dynamics of spotless starling nestlings depend on nest-building materials used by parents. Anim. Behav. 126, 89–100.

Stenning, M.J., 2018. The Blue Tit. T & AD Poyser, London.

Stjernberg, M., 1974. Nest-building by the Pied Flycatcher *Ficedula hypoleuca*. Ornis Fenn. 5, 85–109.

Suárez-Rodríguez, M., López-Rull, I., Macías Garcia, C., 2013. Incorporation of cigarette butts into nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? Biol. Lett. 9, 20120931.

Surgey, J., du Feu, C.R., Deeming, D.C., 2012. Opportunistic use of a wool-like artificial material as lining of Tit (Paridae) nests. Condor 114, 385–392.

Tomás, G., Merino, S., Martínez-de la Puente, J., Moreno, J., Morales, J., Lobato, E., Rivero-De Aguilar, J., Del Cerro, S., 2012. Interacting effects of aromatic plants and female age on nest-dwelling ectoparasites and blood-sucking flies in avian nests. Behav. Proc. 90, 246–253.

Tomás, G., Merino, S., Martínez de la Puente, J., Moreno, J., Morales, J., Rivero de Aguilar, J., 2013. Nest size and aromatic plants in the nest as sexually selected female traits in blue tits. Behav. Ecol. 24, 926–934.

van Riper, C.I.I.I., 1977. The use of sheep wool in nest construction by Hawaiian birds. Auk 94, 646–651.

Veiga, J.P., Polo, V., 2005. Feathers at nests are potential female signals in the spotless starling. Biol. Lett. 1, 334–337.

Wang, Y., Chen, S., Jiang, P., Ding, P., 2008. Black-billed magpies (*Pica pica*) adjust nest characteristics to adapt to urbanization in Hangzhou, China. Can. J. Zool. 86, 676–684.

Windsor, R.L., Fegely, J.L., Ardia, D.R., 2013. The effects of nest size and insulation on thermal properties of tree swallow nests. J. Avian Biol. 44, 305–310.

Winkler, D.W., 1993. Use and importance of feathers as nest lining in tree swallows (*Tachycineta bicolor*). Auk 110, 29–36.