No cultural transmission of use of nest materials in titmice Paridae

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Bird nests often consist of stronger materials to maintain nest structure, and a softer layer of lining materials to reduce heat loss. We studied whether early learning affected the use of nest materials by cross-fostering between two tit species with similar breeding ecology, the blue tit *Cyanistes caeruleus* and the great tit *Parus major*, in a woodland area provided with nest boxes in Norway. In both species, only the female builds the nest. From previous studies, we know that early social learning affects a number of traits in these birds, including song repertoire, mate choice, foraging behaviour, and nest site choice. Nests of the two species are similar but blue tits use more feathers than great tits. This was confirmed in the present study, however, female blue tits raised by great tit foster parents, also supplied their nest with feathers, and female great tits raised by blue tits, used few feathers. The only treatment effect was that fewer feathers were found in nests of cross-fostered females in both species than in nests of controls. This may have been caused by time and energetic constraints during nest building because cross-fostered birds seemed to forage less efficiently than controls. The amount of hair was slightly greater in blue tits than in great tits, but it was not affected by the cross-fostering either. We conclude that no cultural transmission was found in the use of lining materials in the nest of the two species, perhaps because young birds hatch after their parents have stopped constructing the nest.

Keywords

cross-fostering; cultural transmission; *Cyanistes*; feathers; nest building; *Parus*; social learning

Bird nests may serve several functions, including protection of the content from adverse weather conditions and nest predation (Collias & Collias, 1984; Hansell, 2000). Materials may be added to hold and support the incubating bird and its eggs and chicks, to reduce heat loss, to signal quality to the mate and a threat to intruders, and perhaps to lower levels of bacteria (Mennerat et al., 2009; Mainwaring, 2017; Biddle, Deeming, & Goodman, 2018). The lining materials often consist of feathers and hair, both with excellent insulation properties depending on moisture in the nest (Hilton et al., 2004). However, nest building is costly in terms of time and effort spent collecting the materials and building the nest (Lens, Wauters, & Dhondt, 1994; Mainwaring, & Hartley, 2013), and such activities may expose the birds to predators (Slagsvold & Dale, 1996).

Although individuals may vary somewhat in materials used, the nests of a particular species are usually identifiable by some distinguishing traits (Goodfellow, 1977; Hansell, 2000; Healy, Walsh, & Hansell, 2008). Studies of captive birds indicate that nest building behaviour is largely innate (Hinde, 1958; Collias & Collias, 1964). For instance, domesticated canaries *Serinus canaria* raised in captivity without access to nest materials, built species specific nests (Hinde, 1958). Male village weaverbirds *Textor cullculatus* raised in the absence of any nest materials, still preferred the same green, flexible material to weave the nest as did wild birds (Collias & Collias, 1964). Hence, the absence of nest materials early in life may not necessarily influence subsequent nest building behaviour as an adult. Zebra finches *Taeniopygia guttata* raised in captivity in experimentally altered nests of brown, green or red colour, also showed an innate preference for nest materials of ´natural´ colours; brown materials were preferred over red (Sargent, 1965).

However, choice and handling of nest materials, as well as the quality of the nest, may also depend on experience obtained as a nestling and/or as an adult. In zebra finches, choice of materials was influenced by experience both as a nestling and as an adult

(Sargent, 1965; Muth & Healy, 2011). European starlings *Sturnus vulgaris* may select specific plants by using an olfactory pattern designed prior to birth, a mechanism probably influenced by early learning (Gwinner & Berger, 2008). Handling of nest materials in hybrids of two species of lovebirds *Agapornis* spp. seemed to have a strong genetic basis, however, experienced hybrids had a better building technique than first time breeders, suggesting that learning was also important (Dilger, 1962). In titmice Paridae, use of nest materials shows great variation in relation to environmental conditions, such as season, altitude and latitude, and ambient temperatures (Mainwaring, 2017), suggesting that the amounts of various nest materials are condition dependent and have low heritability (Järvinen, Kluen, & Brommer, 2017).

Cross-fostering experiments are powerful when studying whether or not birds acquire information on nest building from the rearing period by way of imprinting (Healy et al. 2008, O´Neill, Parker, & Griffith 2018). In an early study, South African weaverbirds *Textor* sp. were cross-fostered to canaries in captivity without access to normal nest materials and with no opportunity to watch adults of their own species. Nevertheless, they were still able to weave species specific nests as an adult (Marais, 1937). We studied the ecology and behaviour of blue tits *Cyanistes caeruleu*s and great tits *Parus major* in a woodland area in Norway provided with nest boxes. The two species are secondary-cavity nesters and have a similar breeding ecology. In both species, only the female builds the nest (Perrins, 1979). We cross-fostered offspring between the two species to study the significance of early social learning. Many traits were affected by the treatment, including song, mate choice, foraging, and choice of nest site, and this seemed to last for life (Slagsvold, Hansen, Johannessen, & Lifjeld, 2002; Johannessen, Slagsvold, & Hansen 2006; Hansen, Johannessen, & Slagsvold, 2008; Slagsvold & Wiebe, 2007; Slagsvold, Kleiven, Eriksen, & Johannessen, 2013). Here, we studied nest building of the two species, expecting that cross-fostering would also affect this trait through early social learning. The nests of the blue tits and great tits share similar materials, with a foundation of twigs, moss and grass, and then a cup of lining layer of hair, wool, fur, and feathers (Perrins, 1979; Britt & Deeming, 2011). We focused on the upper cup lining layer and the use of feathers and hair. Blue tits use more feathers than great tits (Perrins, 1979; Britt & Deeming, 2011) which enabled us to study effects of cross-fostering.

The study is interesting for several reasons. (1) To our knowledge, no previous study on the use of nest materials has been conducted where nestlings have been cross-fostered between two species in the wild. A study in the wild may be more reflective of natural availability of nest materials and natural nest-building stimuli than a study conducted in captivity. (2) Nestling blue tits and great tits fledge at a relatively advanced stage of development, usually when about 20 days old. Thus, they have a long time to learn features of the nest. (3) Both blue tits and great tits use feathers and hair as nest materials, and the difference between them is a matter of quantity rather than quality, where blue tits typically use more feathers than great tits (Fig. 1). In addition, collecting lining material may be costly, and we asked whether the cross-fostered birds brought fewer feathers and less hair to the nest than the controls. This was because in both species, cross-fostered birds seemed to forage less efficiently than controls, providing different sized prey items (Slagsvold & Wiebe, 2011; Wiebe & Slagsvold, 2015). We also asked whether the effect of cross-fostering differed between the two species. Cross-fostered great tits foraged higher above the ground than controls, whereas an opposite pattern was found in blue tits (Slagsvold & Wiebe, 2007). Perhaps tits combine feeding and collecting nest materials during excursions from the nest by bringing back some materials after feeding has finished. If so, for cross-fostered birds, it may have been more costly for great tits than blue tits, relative to their respective controls, to collect lining materials on the ground.

METHODS

Study Area and Study Species

The study was part of a long-term project on blue tits and great tits starting in 1995 and still in progress (Slagsvold et al., 2002; Slagsvold & Wiebe, 2007, 2018). The present fieldwork was conducted during 2008 - 2009 at Dæli near Oslo, Norway (59°56’N, 10°32’E), in a study area of 1.4 km^2 mainly covered by mixed deciduous and coniferous forest. In the study area, blue tits and great tits almost exclusively use our nest boxes for breeding. In both years, approximately 520 wooden nest boxes were attached to trees about 1.5 m above the ground. The distance between the entrance hole and the nest was only 5-9 cm allowing sufficient light to enter the nest boxes so that the nestlings could learn which nest materials were present. About 100 blue tit and 70 great tit pairs bred in the two years of study. In March for each year, the wooden nest boxes were cleaned and repaired and from early April on they were visited every 2-4 days to observe the contents and to identify the owners. Visits after nest building were less frequent and we recorded date of first egg laid (range 20 April-19 May; assuming that one egg was laid per day) and clutch size (range 4-14 eggs). We visited the nests again at the estimated time of hatching and ringed all nestlings when 10-16 days old, making it possible to identify local recruits. The nestlings were fitted with two colour rings in addition to the numbered metal ring, one for year of ringing and one for treatment. All nests were visited and disturbed the same number of times to control for disturbance. Unringed birds were captured by mist netting in autumn, or in the breeding season when the nestlings were at least 10 days old. We classified females as a yearling or older (49% were older).

Cross-fostering and Nest Materials

Cross-fostering has been performed yearly since 1995 during the incubation period and all host eggs were removed. When possible, to reduce the number of nests involved in the cross-fostering, clutches were switched between dyads of nests that were located close to each other and that had been incubated for a similar period of time. Controls were birds reared by parents of their own species mostly from nests with no swapping of content. We assumed that all immigrants (initially unringed birds) had been raised by conspecific parents and so the sample size for cross-fostered birds was smaller than for controls. Some materials may be added to the nest during egg-laying but few during incubation and rarely any after hatching (Haftorn, 1971). Video filming of seven blue tit nests in Norway confirmed that it is only the female that brings feathers and hairs to the nest (Roger Engvik and Kjell Mork Soot, pers. com.). Hence, when analysing use of nest materials, we focused on whether the focal females had been cross-fostered or not. Of the females with known origin of her mate, twenty-four (19 controls and 5 cross-fostered) were mated to a cross-fostered male.

Features of the nest material inside a nest box were recorded by two people who did not know whether the local female had been cross-fostered. The number of feathers (longer than 1 cm) visible in the nest cup and on the surface of the nest was counted. Nests with more than ten feathers were given the same, maximum score. The percent of the nest surface covered with hair (including wool) was categorized using 10% intervals. In 2008, we recorded the number of feathers, and the coverage of hair, during the egg-laying period (4-7 eggs laid), whereas in 2009 we recorded the variables at hatching. There was no annual effect in the occurrence of feathers or hairs between the two years (see below).

In titmice, the incidence is low for repeated use of particular lining materials by individuals in successive years (Surgey, du Feu, & Deeming, 2012) and thus we treated the data as independent. We could not transform the number of feathers or the coverage of hair for a normal distribution and so we used nonparametric Kruskal-Wallis and Mann-Whitney U tests. Statistical tests are two-tailed with an α-level of 0.05.

Ethical Note

The study complies with the current laws of Norway, and was approved by the Directorate for Nature Management in Norway (2008/3110, 2009/3137), and by the National Animal Research Authority in Norway (07/8921). Blue tits are smaller than great tits, and therefore, to prevent an extra cost of raising cross-fostered nestlings, we only let blue tit foster parents raise 4-6 great tit nestlings. Blue tit broods raised by great tit foster parents were never larger than control blue tit broods. Cross-fostering did not seem to influence survival of the offspring in the nest or after fledging (Slagsvold & Hansen, 2001; Slagsvold et al., 2002). To avoid disturbing the birds and destroying the nests, we only recorded the number of feathers, and the cover of hair, when viewing the nest from above.

RESULTS

Effects of Cross-fostering

For controls, there were more feathers in nests of blue tits than great tits (Fig. 2; Kruskal-Wallis test, N = 197, species: χ^2_1 = 76.9, P < 0.001, year: χ^2_1 = 1.08, P = 0.30, interaction: $\chi^2_1 = 0.94$, $P = 0.33$). The median number of feathers was nine for blue tits ($N = 102$) and only one for great tits ($N = 95$). Because there was no significant year effect, the data from the two years were combined below.

There were fewer feathers in nests of cross-fostered females than of controls (Fig. 2) but the interaction between species and treatment was not significant (Kruskal-Wallis test, $N = 231$, species: $\chi^2_1 = 58.7$, $P < 0.001$, treatment: $\chi^2_1 = 8.38$, $P = 0.004$, interaction: $\chi^2_1 = 0.59$, $P = 0.44$). Removing the interaction term showed strong effects for species and treatment (same test, $N = 231$, species: $\chi^2_1 = 100.5$, $P < 0.001$, treatment: $\chi^2_1 = 8.93$, $P = 0.003$). The median number of feathers was six for cross-fostered blue tits ($N = 15$) and none for cross-fostered great tits ($N = 19$). The negative effect of cross-fostering was particularly strong in great tits as shown when comparing values for cross-fostered birds and controls of the same species (Mann-Whitney U-test, blue tits: $z = -1.44$, $N_1 = 102$, $N_2 = 15$, $P = 0.15$; great tits: $z = -2.67$, $N_1 = 95$, $N_2 = 19$, $P = 0.008$). Cross-fostered blue tits had more feathers in their nest than control great tits (same test, $z = -3.42$, $N_1 = 15$, $N_2 = 95$, $P < 0.001$). With species and female treatment included in the model, there was no effect of female age (yearling or older; Kruskal-Wallis test, $N = 231$, $\chi^2_1 = 0.28$, $P = 0.60$), or whether or not the mate of the focal female had been cross-fostered (same test, $N = 223$, $\chi^2_1 = 0.004$, $P = 0.95$).

For controls, the cover of hairs did not differ between the two years of study (Kruskal-Wallis test, $N = 204$, species: $\chi^2_1 = 2.31$, $P = 0.13$, year: $\chi^2_1 = 3.58$, $P = 0.059$, interaction: $\chi^2_1 = 2.53$, $P = 0.11$). Therefore, the data from the two years were combined below. Then the cover of hairs in control nests was significantly greater in blue tits than in great tits (Fig. 3; Mann-Whitney U-test, $z = -2.52$, $N_1 = 108$, $N_2 = 96$, $P = 0.012$) with a median cover of 90% in blue tits and 70% in great tits.

For the cover of hairs, the interaction term between species and treatment was not significant (Kruskal-Wallis test, N = 236, species: χ^2_1= 2.23, P = 0.14, treatment: χ^2_1= 2.11, P = 0.15, interaction: χ^2_1 = 0.19, P = 0.66). When the interaction term was removed, there was a significant effect of species but not of treatment (same test, N = 236, species: χ^2_1= 6.84, P = 0.009, treatment: χ^2_1= 1.85, P = 0.17). The median cover of hairs for cross-fostered females was 75% for 14 blue tit nests and 60% for 18 great tit nests. With species and female treatment included in the model, there was no effect of female age (yearling or older; same test, N = 231, χ^2_1 = 0.80, P = 0.37), or whether or not the mate of the focal female had been cross-fostered (same test, N = 223, χ^2_1 = 0.30, P = 0.58).

DISCUSSION

Many more feathers and hairs were found in blue tit than in great tit nests but there was no significant interaction between species and treatment, and thus no evidence for cultural transmission from adult to offspring. Learning from parents may have more impact when an offspring can directly observe the behaviour of the parents. In tits, the young hatch after the nest is built and juveniles leave the parents before an opportunity to observe nest building, and usually disperse a great distance for their own breeding. If the parents attempt a second brood during the season, previous offspring might have a chance to observe their mother collecting nest materials, but in our study area, blue tits do not lay second clutches, and great tits very rarely do so. It may be difficult for offspring to observe the materials used in the nest in which they have been raised because many feathers are later covered and woven into the nest materials (Sanz & García-Navas, 2011), and the nest cup expands as the young grow rapidly and becomes trampled down when the chicks are feathered and close to fledging (Slagsvold, 1989).

Although early learning does not appear to affect nest construction, cross-fostering of the two tit species did show that it has a strong effect on subsequent foraging behaviour as an adult (Slagsvold & Wiebe, 2007). In this case, nestlings have direct experience with the prey items their parents give them, and juveniles which closely follow their parents during the post-fledging period, may learn where to find the items and how to handle them before ingestion. Tits may also learn foraging techniques by observing conspecifics in post-breeding flocks (Aplin et al., 2015). Perhaps young tits at the start of their first breeding season also have the opportunity to observe older females of both their biological and foster species collecting nest material. However, the results of the present study suggest they apparently did not use such social information. The time window for observing other birds building nests in spring is shorter than the time yearlings spend in flocks during the non-breeding season and, because of territoriality and cavity nesting, it may be difficult for inexperienced females to track the nest-building behaviour of others in the population. Optimal foraging and food type determine the survival of the birds and are thus of vital importance, whereas the inclusion of feathers in the nest may be less critical. Blue tits may visit nest sites of conspecifics during early spring, but such forays are more frequent in males than in females, males possibly seeking extrapair matings (Schlicht, Valcu, & Kempenaers, 2015).

There did not seem to be much social information from parent to offspring at the level of feathers vs. fur in the tits, which was in contrast to a study of their nest site choice. Cross-fostering affected the size of the nest box that individuals subsequently chose for their own breeding (Slagsvold et al., 2013), i.e., social learning from birds perceived as conspecifics was involved. The size of a nest cavity is permanent and perhaps easier to learn than presence of a few feathers in a nest. In blue tits, cross-fostering between conspecifics showed that the depth of an individual's nest within the cavity was not related to the nest depth of the foster mother (O´Neill et al., 2018), which may have a similar explanation; the depth of the nest materials is difficult for a nestling to assess.

Feathers in a nest may serve at least four, non-mutually exclusive functions: insulation, maintenance of nest structure, anti-microbial effect, and status signalling (Mainwaring, 2017; Ruiz-Castellano, Ruiz-Rodríguez, Thomás, & Soler, 2019). For instance, feathers and hairs may ensure that the nest is both elastic and warm. Blue tits place feathers not only in the nest cup but often all over the nest surface (Fig. 1) so the feathers appear to have functions additional to insulation and structural maintenance of the nest (Sanz & García-Navas, 2011). In the present study, the only effect of the treatment was that fewer feathers were found in nests of cross-fostered females than in control nests. When feeding nestlings as an adult, cross-fostered great tits provided a lower biomass of prey relative to conspecific controls than cross-fostered blue tits (Wiebe & Slagsvold, 2015). Collecting nest materials is costly for tits (Surgey et al., 2012; Mainwaring, 2017), and cross-fostered birds may have been more constrained when building a nest than conspecific controls, in particular the great tits. In blue tits, the heritability between mother and daughter is low both for use of feathers and nest depth (Järvinen et al., 2017; O´Neill et al., 2018). The use of lining materials may reflect factors linked to energy balance such as body reserves, local weather conditions, availability of nest materials, and time available for collecting (Hansell & Ruxton, 2002; Mennerat, Perret, & Lambrechts, 2009; Surgey et al., 2012; Mainwaring, 2017).

If the amount of lining material collected by a female is positively correlated with her foraging efficiency and body condition, it might signal her quality, influencing the male´s willingness to invest in the brood. In studies of blue tits in Spain, it was suggested that males deposited feathers in the nest to signal ownership, great competitive ability to intruders and willingness to invest (Sanz & García-Navas, 2011; García-Navas, Valera, &

Griggio, 2015). However, in our population, it is the female that collects feathers. We did not study the availability of feathers and hair in each territory but the male tit is more active than the female in establishing and defending the territory, and we found no effect of the origin of the male, which suggests that variation in feather availability did not confound the main conclusion. An experimental study showed that natural feather availability in woodlands is high (Hansell & Ruxton 2002).

We found that the amount of hair was not significantly affected by cross-fostering and both hair and feathers were probably collected on the ground. Cross-fostered blue tits were still able to collect many feathers and it may also have been possible for cross-fostered great tits to collect a few because they forage closer to the ground than blue tits (Slagsvold & Wiebe, 2007). We only recorded the number of feathers, and the percentage of the nest surface covered with hair. We recommend methods that are more quantitative in future studies, e.g. the total mass of hairs (see Loukola et al., 2020 for an example).

We conclude that no vertical social learning from adult to offspring was found in the use of lining materials in the nest of the two species, perhaps because young birds hatch after their parents have stopped constructing the nest.

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Figure legends

Figure 1. Nests built by the two study species. Blue tits (upper nest) use more feathers than great tits (lower nest). Photos by M. Aasen.

Figure 2. Frequency distribution of the number of feathers in nests of control (a; *N* = 102) and cross-fostered (b; *N* = 15) female blue tits, and the same for control (c, *N* = 95) and cross-fostered (d; *N* = 19) female great tits. Cross-fostered birds were reared by the other species.

Figure 3. Frequency distribution of the percentage of hair covering in nests of control (a; *N* = 108) and cross-fostered (b; *N* = 14) female blue tits, and the same for control (c; *N* = 96) and cross-fostered (d; *N* = 18) female great tits. Cross-fostered birds were reared by the other species.