

**Nest building behavior in birds:
Cross-fostered individuals resemble
their own species and not their foster
species**

Maria Aasen

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CEES



**Centre for Ecological and Evolutionary Synthesis
Department of Biology
University of Oslo, Norway**

Forord/preface

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Abstract

Variation in behavioral traits may be genetically or environmentally determined, or both. Previous studies on nest building behaviour in captive birds have proposed that nest building is mainly genetically determined. However, to settle this question, cross-fostering experiments in the wild has been recommended. The focus of the present study has been nest building behavior in blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) studied in a woodland near Oslo in Norway, where respectively, 95 and 79 nests of the two species were observed. Both build nests of mosses, lined with hair and wool. Blue tits also often apply feathers, which are only occasionally used by great tits. Some individuals of both species were interspecifically cross-fostered, i.e. blue tit nestlings were raised by great tit parents, and great tit nestlings were raised by blue tit parents. This provided the opportunity to study, in a natural environment, whether the interspecific variation in use of nest materials is primarily genetically or environmentally determined (due to learning from conspecifics, i.e. cultural transmission). The results show that, with regard to nest building, cross-fostered blue tits and great tits resemble members of their own species and not members of their foster species. This held true even when accounting for possible confounding variables such as laying date of first egg, clutch size, egg volume, and age. This implies that the variation in nest building behavior between these species is largely genetically determined. We suggest that nest building is a conservative trait that has evolved differently in blue tits and great tits.

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Introduction

The origin of bird nests can probably be traced back to the origin of the land egg in reptiles (Collias & Collias 1984), and the existence of nestlike structures in the Upper Triassic suggests that nest building, and possibly parental care, were developed by that time (Moratalla & Powell 1994). Today species of many animal groups build nests, however the most striking examples of diversity and complexity are found in spiders and mites (Arachnida), insects (Insecta), and birds (Aves; Hansell 2000). Hence, bird nests include the most advanced nests known among vertebrates (Collias & Collias 1984). Goodfellow (1977, p. 9) defined a bird's nest as 'a structure or excavation made by birds, or the modification of a structure or excavation already in existence, or any place in which eggs are laid and incubated until hatching'. This definition illustrates the great diversity within bird nests. The nest protects eggs and young from adverse weather, heat loss and nest predation (Goodfellow 1977; Hansell 2000). This is especially important in species rearing altricial young, i.e. young that are completely dependent upon parents after hatching (Goodfellow 1977). Whether caring for offspring is beneficial to parents, depends on relationships between parental expenditure and offspring fitness (Clutton-Brock 1991). Empirical studies indicate that nest building is costly (Slagsvold & Dale 1996; Mainwaring & Hartley 2009) and time consuming (Lens et al. 1994). These factors probably vary between species and individuals, but it is known that many birds, during one nest building event, make a thousand or more visits to gather and bring necessary materials to the nest (Collias 1964; Collias & Collias 1984). In addition, it is assumed that nest building in many birds reduce the survival of the builder, e.g. because the builder is more exposed to predators. This has been shown in pied flycatchers (*Ficedula hypoleuca*), where female disappearance peaked at the time of nest building (Slagsvold & Dale 1996).

There are several suggestions on how a bird knows what nest to build (shortly summarized by Healy et al. 2008). At the two extremes there are those who considered nest building behaviour as a wholly learned behaviour, and those who considered it as a classic example of an instinct (Goodfellow 1977; Collias & Collias 1984; Gould & Gould 2007). Learned behaviors are often said to be environmentally determined. However, because learning takes place within a brain whose properties have been shaped by gene-environment interactions, the genetic influence on development cannot be ignored (Alcock 2005). Furthermore, because environmental signals influence gene activity, no traits can be purely genetically determined (Alcock 2005). However, the variation in behavioural traits may be

mainly environmentally or genetically determined. Nest building behaviour was early studied by observing nests built by captive birds, raised without access to nest materials. Hinde (1958) showed that domesticated canaries (*Serinus canaria f. domestica*) nevertheless built species specific nests. Likewise, nest building behavior in mice (*Peromyscus* spp.) long reared in captivity, constructed nests identical to those of their wild ancestors (Dawson et al. 1988). These studies indicate that nest building behavior within birds and mammals is largely genetically determined.

Use of nest materials has been studied with regard to the material experienced as a nestling, and in particular with regard to the color of this material (Collias & Collias 1964; Sargent 1965). Collias and Collias (1964) studied male village weaverbirds (*Textor culiculatus*), that normally use fresh, green, flexible material to weave their nest. They found that young weaverbirds, whether or not reared in the absence of nest materials, selected green over other colors. Zebra finches (*Taeniopygia guttata*) raised in experimentally altered nests of brown, green or red color showed an innate preference for nest materials of “natural” colors, e.g. brown materials were preferred over red (Sargent 1965). In addition, choice of materials was influenced by experiences as an adult and nestling, where birds were more likely to choose nest materials alike those observed earlier in life.

Birds as blue tits (*Cyanistes caeruleus*) and starlings (*Sturnus vulgaris*) may add green plants rich in volatile compounds to the nest, suggested to serve as a barrier between nestlings and nest ectoparasites (Wimberger 1984; but see Fauth et al. 1991; Gwinner et al. 2000; Mennerat et al. 2008; Mennerat et al. 2009a). Starlings have been proposed to select these specific green plants by using an olfactory pattern designed prior to birth (Gwinner & Berger 2008). In addition, this pattern was probably influenced by early learning. Another approach to study nest building has been to observe hybrids between species that differ with regard to nest building. In mice, F₁ hybrids built burrows virtually identical to one of the parent species, indicating a strong genetic basis of nest building (Dawson et al. 1988). Likewise, Dilger (1962) suggested that handling of nest materials in hybrids of two species of lovebirds (*Agapornis* spp) had a strong genetic basis. Noteworthy, experienced hybrids had a better building technique than first time breeders, suggesting that also learning by experience was important in these small African parrots.

Given that experience is important during nest building, differences in age of the nest builders may result in intraspecific variation in nest quality. Birds with complex constructions may be especially prone to build better nest after practicing (Hansell 2000). Village weaverbirds are known for making complex and highly organized nests (Collias & Collias

1964). In nature, the first nest built by young males is more loosely and crudely constructed than nests built by experienced adult males, and experimental evidence have shown that nest building skills in this species improve with practice (Collias & Collias 1964). Likewise, Birkhead (1991) found that young magpies (*Pica pica*) more often build un-domed nests, when compared to adult birds (but see Baeyens 1981). However, in blue tits which build quite simple nests, age does not seem to influence nest weight (Tomas et al. 2006), and young female canaries build nests that appear as large and tidy as those built by experienced females (Hinde 1958). To sum up, most studies on nest building in captive birds indicate that nest building behavior is largely genetically determined. On the other hand, choice and handling of nest materials, as well as quality of the nests may also depend on experiences either as nestling or adult.

Because evidence on the genetic basis of any building behavior is rare (Collias & Collias 1984; Hansell 2000), more studies are required to settle whether variation in nest building is primarily genetically or environmentally determined. Young birds may, during early social interactions with their parents, e.g. learn how to recognize an appropriate mate. This is known as imprinting, and was first identified by Konrad Lorenz who described filial imprinting in ducklings (e.g. Barnard 2004; Alcock 2005). Recently, cross-fostering experiments in the wild have been recommended to determine whether birds acquire information during early development in a way that is akin to imprinting, or alternatively whether nests built by parents and offspring is similar due to genetics (Healy et al. 2008). Actually, such an experiment was performed by means of captive birds already in 1937 (Marais). South African weaverbirds, *Textor* sp. were cross-fostered to canaries (*Serinus canaria*) and reared without access to normal nest materials. During rearing, they could not observe adult weaverbirds. However, at breeding time the birds were able to weave species specific nests. This indicates a strong genetic determination of nest building behavior. Allowing nestlings to be raised by heterospecific foster species (i.e. cross-fostering) has as far as we know, never been performed in the purpose of studying nest building behavior in free living birds.

The aim of the present study is to see whether interspecific variation in nest building behavior is genetically determined or based on learning from conspecifics (cultural transmission) in a natural environment. This was studied in two closely related passerine birds, blue tits and great tits (*Parus major*). Individuals of the two species were cross fostered by switching eggs between nests so that blue tit nestlings were reared by great tit parents and great tit nestlings were reared by blue tit parents. This gave the opportunity to investigate

whether cross-fostered offspring were learning the nest building behaviour from their foster species. Earlier studies of these model species have investigated the influence of early learning on sexual imprinting (Slagsvold et al. 2002; Hansen et al. 2008), rival imprinting (Hansen & Slagsvold 2003), song structure (Johannessen et al. 2006) and foraging behavior (Slagsvold & Wiebe 2007), concluding that cultural transmission of behaviors are important in tits. The two species are secondary cavity nesters that commonly use artificial nest boxes. The female is the main builder of the nest (Haftorn 1971; Goodfellow 1977; Harrison 1985), and hence we have focused solely on females in the present study. Mosses are the most commonly used nest materials, however straws, dry grass and strips of bast may also be added to the nest. The nest cup consists of lining, of which both species may use wool and animal hair. In addition, blue tits frequently apply feathers, which are only occasionally used by great tits (Haftorn 1971; Harrison 1985).

Cross-fostering allows us to study whether variation in nest building behaviour is a result of social learning or is innate in these species. We came up with two main hypotheses: (i) variation in nest building is genetically determined, which yields the prediction that use of nest materials do not differ between cross-fostered birds and conspecific controls. Alternatively, (ii) variation in nest building behaviour is environmentally determined (due to cultural transmission during the nesting period), yielding the prediction that cross-fostered birds resemble members of their foster species more than members of their own species. An essential assumption in the present study was that there was enough light in the nest box so that the nestlings could learn which nest materials were used by the parents. This assumption was probably valid, due to a short distance between the entrance hole of the nest box and the nest itself (see below).

Cross-fostered birds may differ from controls in various ways that indirectly influence nest building behaviour. Consequently, to allow for confounding variables, we studied whether aspects of the nest correlated with various measures of female quality, i.e. laying date of first egg, clutch size, and egg volume. To take into account the possible effect of experience, female birds were divided into two age classes (yearlings and older).

Materials and Methods

Study area

The fieldwork was conducted from March - June 2008 at Dæli in Bærum municipality, Norway (60° N, 10 38° E). The study area is 1.6 km² and mainly covered by deciduous forest, although some areas of coniferous and mixed forest are also found here. Approximately 500 nest boxes are attached to tree trunks ca 1.5 m above ground level. The boxes were of two sizes, small (mean bottom area \pm SD: 97.6 \pm 4.8 cm²) and large (mean bottom area \pm SD: 166.0 \pm 15.8 cm²), with an entrance hole of 32 mm in diameter. To prevent nest predation from e.g. great spotted woodpeckers (*Dendrocopus major*) or cats (*Felis catus*), the entrance was surrounded by wire and wire or a spike secured the lid.

Study species

Every year about 120 pairs of blue tits and 70 pairs of great tits breed in the nest boxes in the study area. Of the remaining boxes, some are occupied by pied flycatchers, nuthatches (*Sitta europea*) and coal tits (*Periparus ater*). Blue tits and great tits are mainly monogamous and territorial in the breeding season. In southern parts of Norway, great tits start nest building around 10-15th of April and blue tits usually a bit earlier (Haftorn 1971). Both species build nests of mosses, and they generally add other materials as nest lining. Nest building lasts for 2 - 14 days, before the first egg is laid in late April or early May. Females usually produce one egg every day, and during this period the eggs are often covered with lining (Harrison 1985; Haftorn & Slagsvold 1995). The function of egg covering is still uncertain, but it seems more probable that it reduces the risk of nest predation than that it serves as protection against unfavorable climatic conditions (Haftorn & Slagsvold 1995). Some nest material can be added during egg laying and incubation, but rarely after hatching (Haftorn 1971). Both blue tits and great tits lay several white, reddish brown spotted eggs (blue tits: 8-12 eggs and great tits 8-9 eggs; Haftorn 1971) and the female alone is incubating for approximately 14 days. Both sexes feed the nestlings, which fledge around 22 days after hatching (Haftorn 1971).

Fieldwork

Since 1995 the study species have, under license from The Directorate for Nature Management and the National Animal Research Authority in Norway, been interspecifically cross-fostered; i.e. blue tit nestlings have been raised by great tit parents and vice versa. In the present study, eggs were exchanged during the incubation period and all eggs laid by the host were removed. Blue tits are smaller than great tits (adult body size of 12 cm and 15 cm

respectively; Haftorn 1971), therefore, to prevent an extra cost of raising cross-fostered nestlings, blue tit broods contained 4 - 6 great tit nestlings. Great tit broods with blue tit nestlings were never larger than control blue tit broods. In an initial study where great tits were reared by blue tits, the cross-fostering did not seem to influence survival of the offspring, neither in the nest nor after fledging (Slagsvold & Hansen 2001). Nestlings raised by conspecifics in the same study area, served as controls. All birds reared in this area were ringed with a unique combination of colored rings and a unique numbered metal-ring, making it possible to identify and correctly age the recruiting individuals. Immigrants (un-ringed birds) were given a metal ring and a common color ring for the year of capture. First year birds were given an aluminum ring on the left leg. Second year (or older) birds were given an aluminum ring on the right leg. We assumed that all immigrants had been raised by conspecific parents, thus they were considered as controls with regard to nest building. Below we define this group as control II, whereas birds that had been raised by conspecifics in this study area are termed control I. In this study, we will focus on female tits that have been cross-fostered by blue tits or great tits, together with control I and II females.

In early March nest boxes were cleaned and repaired. From late March on they were checked every other day to spot the first sign of nest building and to identify owners (female and male). Feathers visible on the surface of the nest, longer than 1 cm, were counted twice; once during egg laying, when the brood contained 4 - 7 eggs and once after hatching of the first nestling. Feathers inside and outside the nest cup were counted and summarized. For nests with numerous feathers, we only counted the first 10, and if more than 10 were observed, the number of feathers was termed >10. During egg laying (4 – 7 eggs laid), it was decided, in percent to the nearest ten, how much of the nest surface that was covered by hair (nest lining not including feathers) or moss. Other materials, such as wool, pieces of fur, grass and strips of bast, were recorded as present or not, but they were not further analyzed. Interior and exterior height of the nest were measured along the wall of the nest box (to the nearest mm), using a ruler. In analyses the mean value of the nest heights was used. Distance from the bottom of the nest box to the lower part of the entrance hole was measured (to the nearest mm), using a ruler. This measure, together with height of the nest, was calculated as a measure of distance from entrance hole to nest. Bottom area of the nest box was estimated from length and width (cm²). We observed laying date of first egg and clutch size for each nest. For three eggs, randomly chosen per clutch, egg volume was estimated from egg length (L) and breadth (B; measured by caliper to the nearest 0.1 mm) using the formula $0.51LB^2$

(Hoyt 1979). Nestlings were weighed to the nearest 0.1 g, using a 10 g Pesola spring balance on the first visit after hatching, and hatching date was estimated from a growth curve for each respective species (T. Slagsvold, unpublished data). Nestlings were ringed at day 10 posthatching of the first nestling.

Statistical analyses

Statistical analyses were performed using the statistical software environment R, version 2.8.1 (R Development Core Team 2006). A quantile-quantile plot against a normal distribution was used to test whether variables were normally distributed (Crawley 2007). Fisher's F test was used to determine whether the sample variances differed. This test is highly sensitive to outliers (Crawley 2007), which we took into account and defined as values more than 1.5 times the interquartile range ($Q3 - Q1$) above the third quartile or below the first quartile (Crawley 2007). Few samples contained outliers, and hence all data were included in the further analyses, where sample variances for most variables did not differ. A total of 174 nests (blue tit controls, $n = 90$; blue tit cross-fostered, $n = 5$; great tit controls, $n = 69$; great tit cross-fostered, $n = 10$) were observed, but due to some missing data, sample sizes in particular tests differ. For both species and all variables it was tested whether mean values of control I & II differed significantly using Wilcoxon rank-sum test or Student's t-test.

The statistical information on use of feathers as nest lining came in the form of counts, and to compare whether feathers were used as nest lining or not, counts were analyzed using a 2×2 matrix in a Pearson's chi-square test. This test cannot be used when expected frequencies are small (Crawley 2007); hence some analyses were performed using Fisher's exact test. The distribution of feathers was non-normal, both for feathers counted during egg laying and hatching. No transformation could make them normally distributed, therefore non-parametric tests were used in further analyzes. Use of feathers was compared; (i) for control blue tits and great tits; (ii) for controls and cross-fostered birds, and (iii) during egg laying and hatching. For the latter we tested whether the use of feathers in these periods correlated using Spearman's rank correlation. Ties in the data (repeats of the same measurements) made it difficult to calculate an exact p-value, however, according to Crawley (2007) this is seldom a real problem. For all graphical representations including feathers, ten and more than ten feathers were combined.

Due to a non-normal distribution of hair and moss, percentage values were arcsine square-root transformed (Zar 1999), however the variables were still not normally distributed. Wilcoxon rank-sum test was therefore used to compare sample means. We tested whether use

of feathers correlated with hair, moss, and nest height using Spearman's rank correlation. In addition, Wilcoxon rank-sum test was used to compare sample means of amount of moss within individuals of the same species, and treatment groups nesting in small or large nest boxes.

Nest height and distance from entrance hole to nest were normally distributed. Mean values of the two measured nest heights were calculated and used in the following analyses. Analysis of variance (ANOVA) was performed, applying backward stepwise model building to identify significant factors determining nest height. Height of nests was included as the response variable, and species (blue tit, great tit), treatment (control, cross-fostered) and size of nest box (small, large) as categorical explanatory variables. Akaike's information criterion (AIC) was used to select the best model. In addition, Student's t-test was used to compare sample means within individuals of the same species, and treatment groups nesting in small or large nest boxes. The same procedure was used with the measure of distance from entrance hole to nest.

In blue tits, laying date of first egg had a bimodal distribution (Appendix A) that was impossible to transform into a normal distribution, and hence, non-parametric tests were used to analyze these data. In great tits, the distribution was practically normal. For both species, clutch size was close to a normal distribution and egg volume was normally distributed. Age (yearlings or older, see below) was not normally distributed, and impossible to transform, hence non-parametric tests were used to analyze these data. Mean values were compared for control and cross-fostered individuals, and it was tested whether use of feathers, amount of hair and moss, and nest height correlated with laying date, clutch size, egg volume, and age.

Birds were classified in three age groups that were analyzed separately, and within these groups, birds were aged as yearlings (1Y) or older birds (2Y+). Age group one included recruits, ringed as nestlings, where we knew the correct age. Age group two included the former group and immigrants that have been trapped and ringed during autumn. Age group three included the two former groups and all un-ringed birds. Due to extensive trapping at many sites during the autumn, we assumed that older birds would have been trapped, and hence all un-ringed birds were assumed to be yearlings (1Y). By using Fisher's exact test we tested whether yearlings used feathers as frequently as older birds. Sample means for use of feathers, hair and moss, and nest height, for 1Y and 2Y+, were compared using Wilcoxon rank-sum test.

When analyzing the table of correlation coefficients on variables of nest and measures of female quality, the sequential Bonferroni technique was applied to control for the probability of incorrectly rejecting one or more true null hypothesis (Rice 1989).

Results

Control I & II compared

Control I & II did not differ significantly in use of feathers during egg laying and hatching, amount of hair, nest height, distance from entrance hole to nest, laying date of first egg, clutch size, or female age (tests not shown, $p > 0.07$). In blue tits, control I and II differed slightly for moss (Wilcoxon rank-sum test, $W = 353.5$, $n_1 = 5$, $n_2 = 79$, $p = 0.03$) and egg volume (Student's t-test, $t = -2.44$, $n_1 = 6$, $n_2 = 84$, $p = 0.05$). In the following, data from control I & II were combined in a single control group.

Feathers as nest lining during egg laying and hatching

During egg laying, 83 % ($n = 90$, where n refers to total sample size, which is the case for all sample sizes given after percentage values) of the blue tit controls used one or more feathers, whereas 26 % lined the nest with more than 10 feathers (Figure 2a; Appendix B). Median use of feathers was five (Table 1). During hatching, 94 % ($n = 79$) of blue tit controls used one or more feathers, where 43 % lined the nest with more than 10 feathers (Figure 2c; Appendix B). Median use of feathers was nine (Table 1). During egg laying, 15 % ($n = 66$) of great tit controls used feathers as nest lining (Figure 3a; Appendix B). Median use of feathers for this group was zero (Table 1). During hatching, 57 % ($n = 61$) of great tit controls used feathers as nest lining (Figure 3c; Appendix B). Median use of feathers was one (Table 1). Control blue tits differed significantly from control great tits both during egg laying (Pearson's chi-square test, $\chi^2_1 = 71.4$, $n_1 = 90$, $n_2 = 66$, $p < 0.001$) and hatching (Fisher's exact test, $n_1 = 79$, $n_2 = 61$, $p < 0.001$), supporting the assumption that blue tits use feathers more often than great tits (for illustration, see Figure 1).

During egg laying and hatching, 80 % ($n = 5$) of the cross-fostered blue tits used feathers as nest lining (Figure 2b and 1d; Appendix B). Median number of feathers was nine and six respectively (Table 1). During egg laying cross-fostered blue tits did not differ significantly from control blue tits (Table 1), but the former group differed significantly from the control great tits (Fisher's exact test, $n_1 = 5$, $n_2 = 66$, $p = 0.005$). During hatching cross-fostered blue tits neither differed significantly from control blue tits (Table 1) nor control great tits (Fisher's exact test, $n_1 = 5$, $n_2 = 66$, $p = 0.64$). During egg laying and hatching, 20 %

($n = 10$) of the cross-fostered great tits, used feathers as nest lining (Figure 3b and 3d; Appendix B). For both periods median number of feathers was zero (Table 1). During egg laying, cross-fostered great tits did not differ significantly from control great tits (Table 1), however they differed significantly from control blue tits (Fisher's exact test, $n_1 = 10$, $n_2 = 90$, $p < 0.001$). During hatching, cross-fostered great tits differed significantly from control great tits (Table 1). However, this was because they used fewer and not more feathers (Table 1), and they also differed from blue tit controls (Fisher's exact test, $n_1 = 10$, $n_2 = 90$, $p < 0.001$).



Figure 1. Examples of nests built by the two study species. Blue tit nest (top) lined with feathers and great tit nest (bottom) lined with hair and wool.

Table 1. Median number of feathers, and amount of hair and moss (%) in nests by blue tits and great tits. Test statistic given for comparisons between use of nest materials in control and cross-fostered birds. Hair and moss only observed during egg laying

Variable	Species	Period	Control	Cross-fostered	Test statistic	
			Median (n)	Median (n)	W	p
Number of feathers	Blue tit	Egg laying	5 (90)	9 (5)	-	1.00 ^a
	Blue tit	Hatching	11 (79)	6 (5)	-	0.32 ^a
	Great tit	Egg laying	0 (66)	0 (10)	-	0.65 ^a
	Great tit	Hatching	1 (61)	0 (10)	-	0.04 ^a
Hair (%)	Blue tit	Egg laying	90 (85)	15 (4)	289.5	0.01 ^b
	Great tit	Egg laying	70 (64)	70 (9)	310.5	0.71 ^b
Moss (%)	Blue tit	Egg laying	0 (85)	50 (4)	32.5	0.004 ^b
	Great tit	Egg laying	30 (64)	30 (9)	258.5	0.62 ^b

^a = Fisher's exact test ^b = Wilcoxon rank-sum test

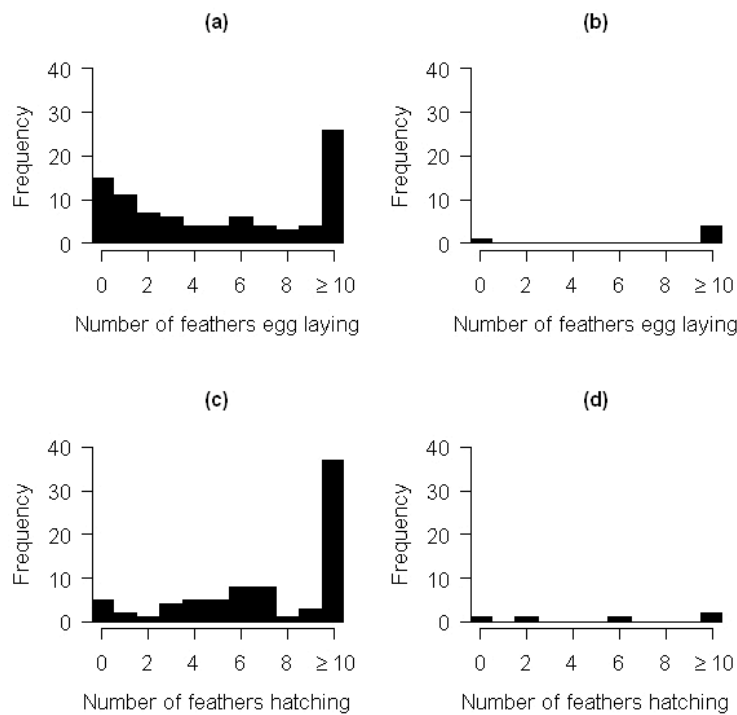


Figure 2. Blue tit use of feathers during egg laying and hatching for (a) controls, $n = 90$; (b) cross-fostered, $n = 5$; (c) controls, $n = 79$; and (d) cross fostered, $n = 5$. For median values, see Table 1.

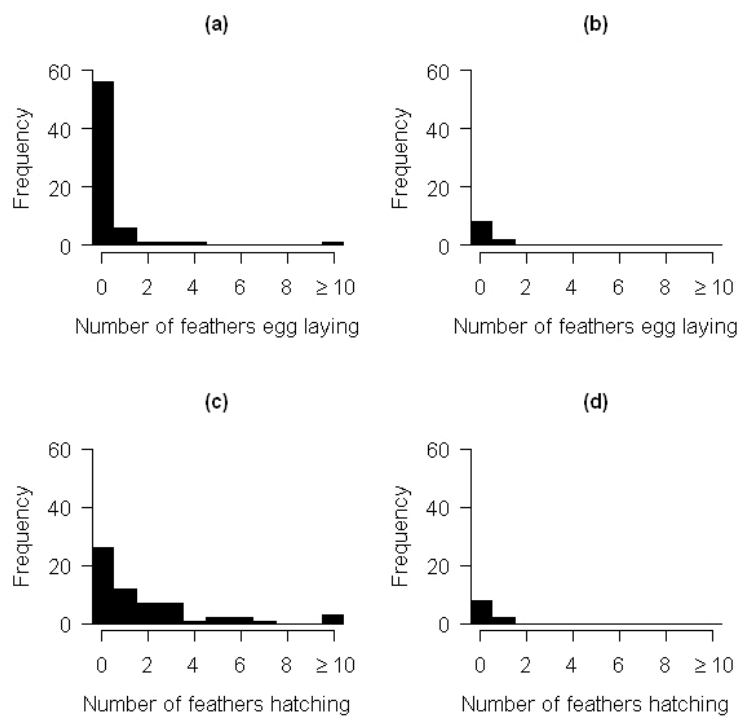


Figure 3. Great tit use of feathers during egg laying and hatching for (a) controls, $n = 66$; (b) cross-fostered, $n = 9$; (c) controls, $n = 61$; and (d) cross fostered, $n = 8$. For median values, see Table 1.

Blue tit controls used more feathers during hatching than during egg laying (Wilcoxon rank-sum test, $W = 2198.5$, $n = 79$, $p = 0.001$) and those that used many feathers during laying also did so during hatching (Figure 4a; Appendix C; Spearman's rank correlation, $r_s = 0.52$, $n = 79$, $p < 0.001$). For cross-fostered blue tits, use of feathers during egg laying and hatching did not differ significantly (Wilcoxon rank-sum test, $W = 16.5$, $n = 5$, $p = 0.41$) and the correlation coefficient between the two measures for individual birds was high, but not significant, probably due to a small sample size (Figure 4b; Spearman's rank correlation, $r_s = 0.73$, $n = 5$, $p = 0.17$). Great tit controls also increased use of feathers between egg laying and hatching (Wilcoxon rank-sum test, $W = 974.5$, $n = 59$, $p < 0.001$), however use of feathers during egg laying and hatching did not correlate (Figure 4c; Spearman's rank correlation, $r_s = 0.06$, $n = 59$, $p = 0.65$). For cross-fostered great tits, use of feathers during egg laying and hatching did not differ (Wilcoxon rank-sum test, $W = 50$, $n = 10$, $p = 1$) nor correlate (Figure 4d; Spearman's rank correlation, $r_s = -0.25$, $n = 10$, $p = 0.49$).

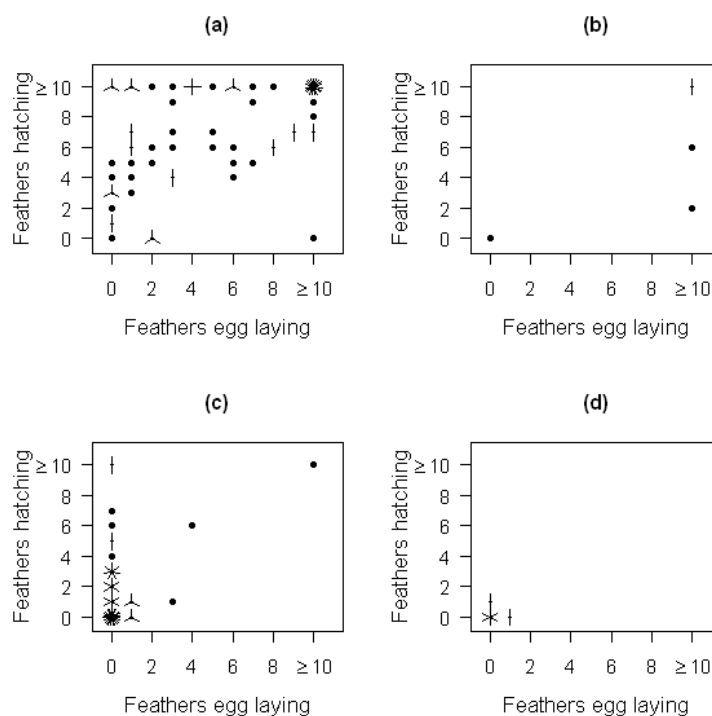


Figure 4. Number of feathers used by the same individuals during egg laying and hatching for (a) blue tit controls, $n = 79$; (b) blue tit cross-fostered, $n = 5$; (c) great tit controls, $n = 61$; and (d) great tit cross fostered, $n = 10$. Single points plotted as dots, whereas multiple points are plotted as ‘sunflowers’ with multiple leaves.

Amount of hair and moss

In blue tits 97 % (n = 89) and in great tits 100 % (n = 73) used hair as nest lining. Control blue tits had the greatest amount of hair on the nest surface (Figure 5; median = 90 %) and they used significantly more hair than great tit controls (Figure 5; median = 70 %; Wilcoxon rank-sum test, $W = 3322$, $n_1 = 85$, $n_2 = 64$, $p = 0.02$). Cross-fostered blue tits used less hair than control blue tits (Figure 5; Table 1; median = 15 %), however they also used less hair than control great tits (Wilcoxon rank-sum test, $W = 42$, $n_1 = 4$, $n_2 = 64$, $p = 0.02$). Cross-fostered great tits did not differ from great tit controls (Figure 5; Table 1; median = 70%) nor blue tit controls (Wilcoxon rank-sum test, $W = 506$, $n_1 = 10$, $n_2 = 85$, $p = 0.09$). Blue tit controls showed a negative correlation between use of feathers and use of hair (Figure 6a; Spearman's rank correlation, $r_s = -0.51$, $n = 85$, $p < 0.001$), i.e. those that used many feathers used less hair. This was also found in great tit controls (Figure 6b; Spearman's rank correlation, $r_s = -0.27$, $n = 64$, $p = 0.04$).

In blue tits 47 % (n = 89) and in great tits 22 % (n = 73) had a nest completely covered with lining, meaning that no moss was visible on the nest surface. Control blue tits had the lowest amount of moss visible on the nest surface (median = 0 %) and they built nests with significantly less moss than great tit controls (median = 30 %; Wilcoxon rank-sum test, $W = 1656.6$, $n_1 = 85$, $n_2 = 64$, $p < 0.001$). Nests of cross-fostered blue tits (median = 50 %) had significantly more moss than those of control blue tits (Table 1), but did not differ significantly from control great tits (Wilcoxon rank-sum test, $W = 184$, $n_1 = 4$, $n_2 = 64$, $p = 0.14$). The median value for cross-fostered great tits was the same as in great tit controls (median = 30 %; Wilcoxon rank-sum test, $W = 258.5$, $n_1 = 9$, $n_2 = 64$, $p = 0.62$). Hence also cross-fostered individuals differed from blue tit controls (Wilcoxon rank-sum test, $W = 175$, $p = 0.004$). In blue tit controls there was a positive correlation between amount of moss in the nest and use of feathers during egg laying (Appendix C; Spearman's rank correlation, $r_s = 0.26$, $n = 85$, $p = 0.02$). This was also so for great tit controls (Appendix C; Spearman's rank correlation, $r_s = 0.31$, $n = 64$, $p = 0.01$). Use of hair and moss was highly negatively correlated in blue tit controls (Appendix C; Spearman's rank correlation, $r_s = -0.80$, $n = 64$, $p < 0.001$) and great tit controls (Appendix C; Spearman's rank correlation, $r_s = -0.97$, $n = 64$, $p < 0.001$). In controls of both species, the proportion of moss did not differ between nests in small and large nest boxes (Appendix D). However, cross-fostered great tits used significantly more moss in small than in large nest boxes (Appendix D). For cross-fostered blue tits, too few data were available to conduct a meaningful test.

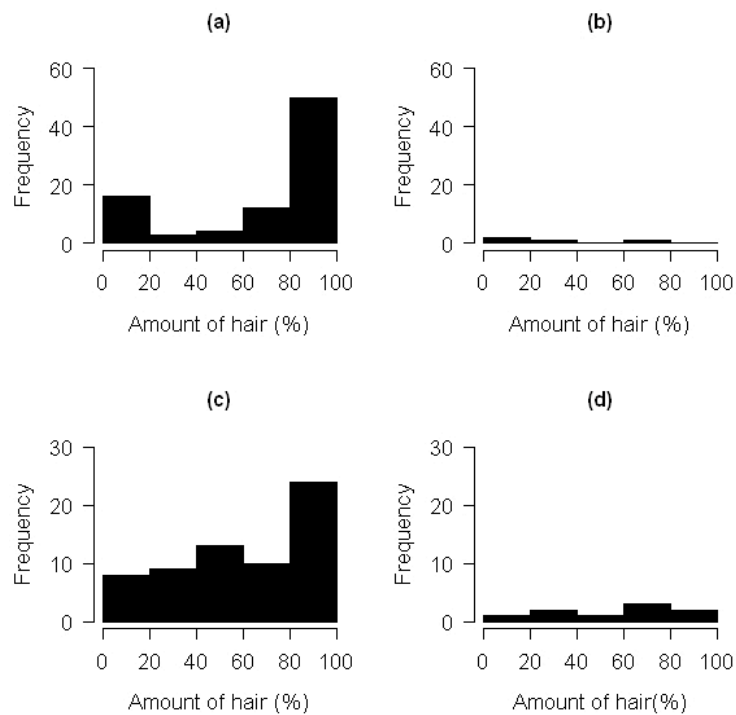


Figure 5. Frequency of individuals in relation to amount of hair on the nest surface for (a) blue tit controls, $n = 85$; (b) blue tit cross-fostered, $n = 4$; (c) great tit controls, $n = 64$; and (d) great tit cross-fostered, $n = 9$.

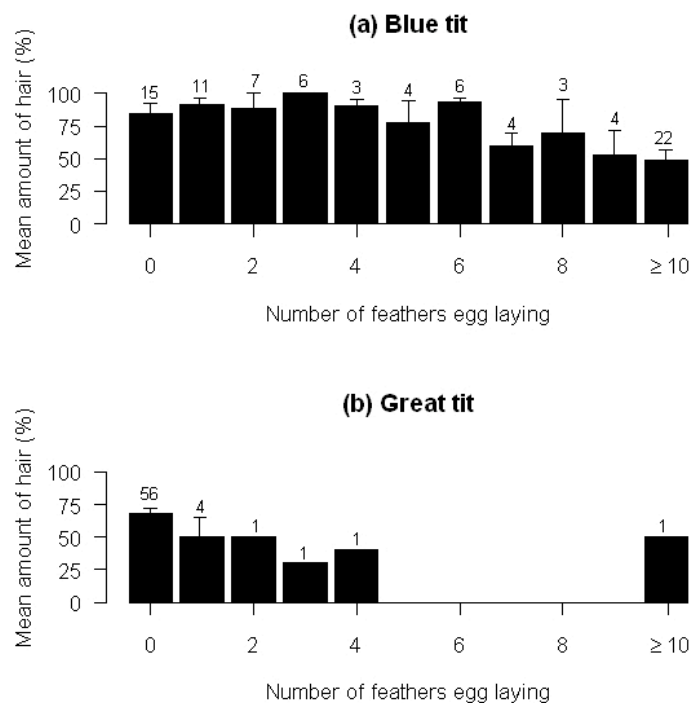


Figure 6. Mean amount of hair (% , + 1 SE) in relation to number of feathers during egg laying for (a) blue tit controls, $n = 85$; and (b) great tit controls, $n = 64$. Numbers of nests are shown above bars.

Nest height and distance from entrance hole to nest

ANOVA showed that nest height was significantly associated with species and size of nest box. Control blue tits built higher nests than control great tits, and nests built in small nest boxes were lower than nests built in large nest boxes (Figure 7; Appendix D; blue tit control small: 6.44 ± 1.04 cm, blue tit control large: 7.88 ± 2.09 cm, great tit control small: 6.33 ± 1.65 cm, great tit control large: 7.58 ± 1.47 cm). In small nest boxes, cross-fostered individuals built higher nests than controls (Figure 7; Appendix D; blue tit cross-fostered small: 6.83 ± 1.21 cm; great tit cross-fostered small: 6.49 ± 1.27 cm), and in large nest boxes cross-fostered individuals built lower nests than controls (Figure 7; Appendix D; blue tit cross-fostered large (n = 1): 6.85 cm; great tit cross-fostered large: 6.70 ± 1.57 cm). However, nest height was not significantly associated with treatment (i.e. control or cross-fostered).

ANOVA showed that distance from entrance hole to nest was significantly associated with species. In controls nests of blue tits had a shorter distance from the entrance hole to the nest than nests of great tits (Appendix D; blue tit control small: 7.15 ± 1.44 cm, blue tit control large: 6.86 ± 2.23 cm, great tit control small 7.92 ± 2.47 cm, great tit control large: 7.70 ± 2.31 cm). Distance from entrance hole to nest was not significantly associated with treatment and size of nest box.

When analyzing nests of birds breeding in small and large nest boxes separately, nest height did not correlate with laying date of first egg, clutch size, egg volume, or age (tests not shown, $p > 0.07$). In great tit controls nesting in large nest boxes, there was a negative correlation between nest height and number of feathers counted during egg laying (Spearman's rank correlation, $r_s = -0.46$, $n = 51$, $p < 0.001$), i.e. higher nests contained less feathers. Otherwise nest height did not correlate with any aspects of the nest (tests not shown, $p > 0.06$). This was also the case when pooling individuals nesting in small and large nest boxes (Appendix C; tests not shown, $p > 0.06$).

Measures of female quality

When analyzing nest materials and measures of female quality (for mean values and results of t-tests, see Appendix E and Appendix F), use of feathers during egg laying and hatching, and nest height did not correlate with laying date of first egg and clutch size (tests not shown, $p > 0.09$). For control and cross-fostered blue tits and control great tits, laying date and clutch size did not correlate with hair and moss. In cross-fostered great tits, there was a positive correlation between amount of hair and moss and laying date, where individuals laying the first egg later in the season used less hair than those laying early (Figure 8a and b; Spearman's

rank correlation $r_s = 0.70$, $n = 10$, $p = 0.036$). Hence later in the season, a larger portion of the nest surface was covered with moss (Spearman's rank correlation $r_s = 0.70$, $n = 10$, $p = 0.036$). In cross-fostered great tits it was also found a correlation between proportion of hair and moss and clutch size, where individuals laying several eggs had more hair as nest lining (Figure 8c and d; Spearman's rank correlation $r_s = 0.79$, $n = 10$, $p = 0.01$) and hence less moss (Spearman's rank correlation $r_s = 0.79$, $n = 10$, $p = 0.01$).

In blue tit controls, use of feathers during egg laying was negatively correlated with egg volume (Figure 9a; Spearman's rank correlation $r_s = -0.23$, $n = 88$, $p = 0.03$), i.e. those that used several feathers had smaller egg volume. However, for all other treatment groups, there was no such correlation (tests not shown, $p > 0.22$). Feathers during hatching, amount of hair and moss, and nest height did not correlate with egg volume (tests not shown, $p > 0.06$).

However, when p-values of statistical significance were corrected using the sequential Bonferroni technique (Rice 1989), measures of nests did not correlate with laying date of first egg, clutch size, or egg volume (Appendix G).

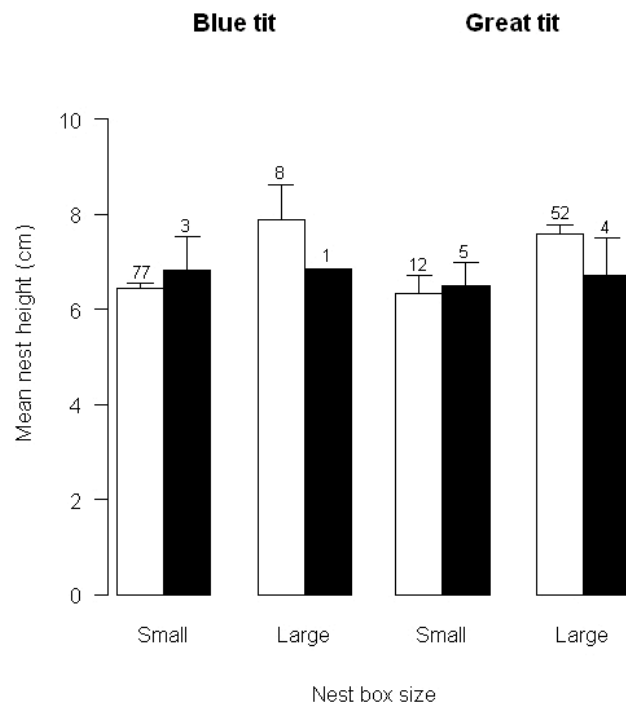


Figure 7. Mean nest height (cm + SE) for small and large nest boxes for blue tits and great tits. Open bar = control, solid bar = cross-fostered. Numbers of nests are shown above bars.

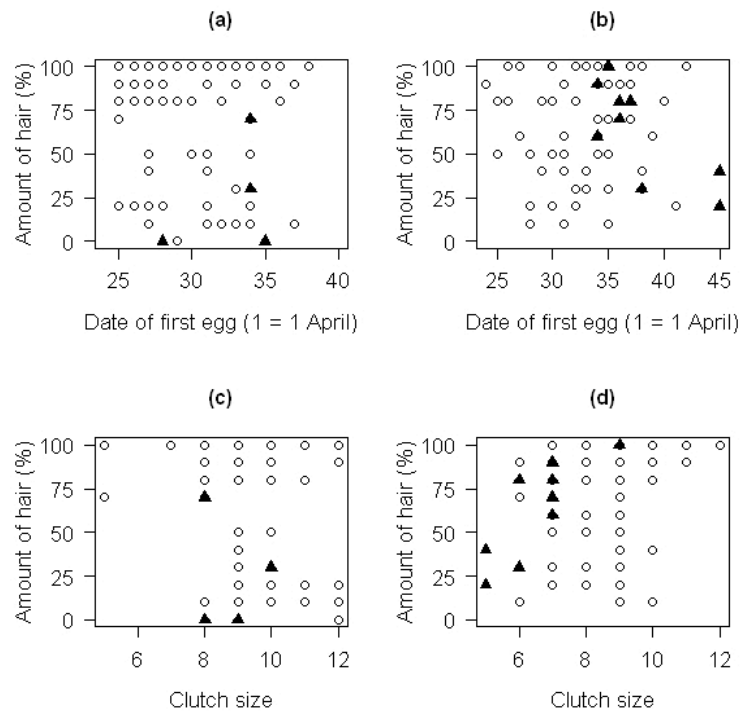


Figure 8. Amount of hair (%) in the nest plotted against laying date of first egg and clutch size in (a) blue tits; (b) great tits; (c) blue tits; and (d) great tits. White circles = control birds, black triangles = cross-fostered birds.

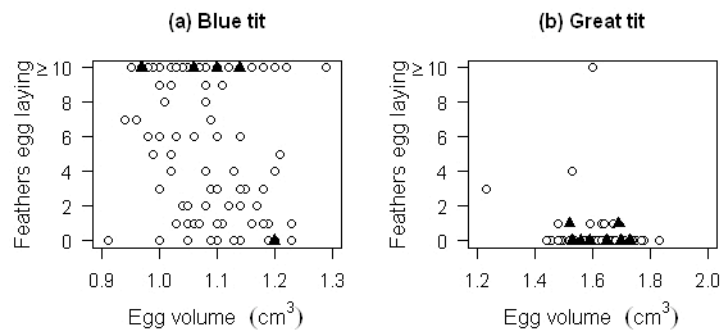


Figure 9. Number of feathers during egg laying plotted against egg volume (cm^3) for (a) blue tits, $n = 93$; and (b) great tits, $n = 75$. White circles = control birds, black triangles = cross-fostered birds

Age

In controls of both species, use of feathers did not differ significantly between older birds and yearlings (age group one; Fisher's exact test, blue tits: $n_1 = 3$, $n_2 = 3$, $p = 1$ and great tits: $n_1 = 3$, $n_2 = 9$, $p = 1$). This was also the case when analyzing birds in age group two (Fisher's exact test, blue tits: $n_1 = 33$, $n_2 = 29$, $p = 0.74$, and great tits: $n_1 = 9$, $n_2 = 3$, $p = 1$) and three (Fisher's exact test, blue tits: $n_1 = 33$, $n_2 = 56$, $p = 1$, and great tits: $n_1 = 33$, $n_2 = 33$, $p = 1$). Likewise, in cross-fostered birds of both species, use of feathers did not differ significantly between older

birds and yearlings (Fisher's exact test, blue tits: $n_1 = 3$, $n_2 = 2$, $p = 1$, and great tits: $n_1 = 5$, $n_2 = 5$, $p = 0.44$).

For blue tit and great tit controls, sample means for yearlings and older birds (age group one) did not differ in use of feathers, hair and moss, or nest height (tests not shown, $p > 0.06$). This was also the case when analyzing age group two and three. Due to low sample sizes, means of yearlings and older birds were not compared in cross-fostered birds.

In general variables of the nest did not correlate with age (tests not shown, $p > 0.10$). However, in cross-fostered blue tits yearlings used more feathers than older birds (Spearman's rank correlation, $r_s = -0.97$, $n_1 = 2$, $n_2 = 3$, $p = 0.005$). When p-values of statistical significance were corrected using the sequential Bonferroni technique (Rice 1989), age in cross-fostered blue tits was still negatively correlated with feathers used during hatching (Appendix G).

Discussion

There has been a long standing debate on whether nest building behavior is environmentally or primarily genetically determined. To our knowledge, we are the first to study use of nest materials by cross-fostering free living birds, with the aim of finding out whether nest building is influenced by the social rearing conditions as a nestling. Our results suggest that variation in nest building behavior is genetically determined, as with regard to nest building, cross-fostered blue tits and great tits resemble members of their own species and not members of their foster species.

Differences between control birds of the species in use of nest materials formed the background for testing the significance of nest building. Consistent with earlier literature (Haftorn 1971; Harrison 1985), we found that control blue tits lined the nest with more feathers than control great tits. Blue tits also used significantly more hair as nest lining than great tits, and hence less moss was visible on the nest surface. When taking size of nest box into account, blue tits built higher nests than great tits. Results from these analyses, i.e. of differences between the species in use of nest materials, formed the background for testing the significance of cross-fostering.

An essential assumption for the present study was that there was enough light in the nest box, so that nestlings could visually observe what nest materials surrounded them in the nest. This assumption seems valid because nests were so close to the entrance (mean \pm SE: 7.4 ± 1.88 cm), that even humans could observe the nest materials through the entrance hole. Apparently there is enough light in the cavity for parent birds to distinguish between nestlings according to the color of their gapes (e.g. Gotmark & Olsson 1997).

Effect of cross-fostering

In both species, most aspects of nests (use of feathers, amount of hair and moss, and nest height) did not differ between controls and cross-fostered birds, although there were some exceptions; compared to controls, cross-fostered blue tits used less hair as nest lining, however they also used less hair than great tit controls. Hence, nests of cross-fostered blue tits had more moss than those of blue tit controls. However, in amount of moss, they did not differ from great tit controls. During hatching, cross-fostered great tits had fewer feathers in their nest than controls. However, sample size of cross-fostered birds was low. These results indicate that cross-fostered blue tits and great tits in general built nests like members of their own species, and not like members of the foster species.

As mentioned, cross-fostered birds may differ from controls in various ways that may indirectly influence nest building behaviour. Consequently, to allow for confounding variables, we studied whether aspects of the nest correlated with various measures of female quality (i.e. laying date of first egg, clutch size, egg volume) and female age. In blue tits, controls and cross-fostered birds did not differ in any of these variables. In great tits, cross-fostered individuals laid later and smaller clutches compared to controls.

Use of feathers as nest lining has generally been thought to provide insulation for eggs and nestlings (e.g. Møller 1991; Hilton et al. 2004; Pinowski et al. 2006). This property may be particularly important during the incubation period and brooding of small nestlings (Møller 1987), because it may influence the cost of incubation (White & Kinney 1974; Lombardo et al. 1995), and nestling growth rate (Møller 1991; Lombardo et al. 1995). The former has been shown to have a clear effect on female fitness, mainly through reduced female survival (Visser & Lessells 2001). In addition, it has been suggested that nest lining serves as a barrier between the nestlings and the nest ectoparasites (Møller 1984; Winkler 1993), e.g. Winkler (1993) found a lower incidence of parasites in feathered nests (but see Lombardo et al. 1995) and thus suggested that feathers may act to reduce ectoparasites. Mertens (1977) showed that great tit broods ran a risk of hyperthermia during the breeding season. This risk was suggested to explain why swallows (*Hirundo rustica*) remove nest lining late in the breeding cycle (Møller 1987). The risk of hyperthermia for nestlings may therefore be greater late in the breeding season, due to higher temperature. Due to this, and given that there are costs of nest building (Collias & Collias 1984; Slagsvold & Dale 1996; Hansell 2000), one may assume that females laying the first egg late in the breeding season, require nests lined with less feathers than females laying early in the season. Our study shows intraspecific variation in

amount of nest lining (feathers and hair). However, when p-values of statistical significance were corrected using the sequential Bonferroni technique (Rice 1989), laying date of first egg, did not correlate with measures of nests. Likewise, use of feathers in nests of tree swallows (*Tachycineta bicolor*) did not decrease during breeding season (Lombardo 1994).

Different aspects of nests may be associated with measures of female quality, as clutch size, and egg volume. Previously, female quality has especially been studied with regard to nest size (Slagsvold & Dale 1996; Alabrundzinska et al. 2003; Tomas et al. 2006; Alvarez & Barba 2008; Mainwaring et al. 2008), and some studies empirically support that parental condition influence investment in nest construction (Tomas et al. 2006; Mainwaring et al. 2008). On the other hand, Slagsvold and Dale (1996), found that amount of nest materials used by handicapped females, with some flight feathers removed, did not differ from controls (three species of tits studied). Further, Tomas et al. (2006) found that in blue tits, nest size does not correlate with clutch size (but see Alabrundzinska et al. 2003). Likewise, when p-values of statistical significance were corrected, we found that nest height, and other variables of nest did not correlate with clutch size and egg volume.

During hatching, number of feathers used by cross-fostered blue tits correlated with age, where older birds used fewer feathers than yearlings. This result even held when p-values were corrected, however, a greater sample size is needed to verify this finding. Generally, and in contrast to Collias and Collias (1964, see introduction), we found that nests built by yearlings did not differ from those built by older birds. E.g. number of feathers as nest lining, and height of nest did not differ between these age groups. Similarly, young captive canaries build nests of as high quality as older birds (Hinde 1958), and in blue tits nest size did not correlate with age (Tomas et al. 2006). Hence, as suggested by Hansell (2000), experience may be more important in species building complex nests (as weavers), compared to those building simple nests. However, in tree swallows, building nests of dry grass, with a nest cup lined with feathers, older birds used more feathers as nest lining than yearlings (Lombardo 1994). There has been observed severe competition for feathers in this species, and Lombardo (1994) has suggested that skill gained through experience is an important component in feather gathering ability. In contrast to blue tits, tree swallows typically do not retrieve feathers from the ground (c.f. Lombardo 1994). Feathers are probably more easily available on the ground than in the air, and hence the competition for feathers may be less severe in blue tits. This is in accordance with Hansell and Ruxton (2002), who suggested that a large number of feathers was available naturally in the wild, and that in some species collecting

feathers may be easy and cheap. However in this conclusion, the risk of adult predation when collecting feathers was not taken into account (c.f. Slagsvold & Dale 1996). In summary, our results indicate that the observed nest building behaviour in cross-fostered birds probably was not confounded by measures of female quality or age. We therefore suggest that the interspecific variation in nest building behaviour between blue tits and great tits is genetically determined, and that it does not improve with experience (i.e. age) of the builder.

Our results are consistent with earlier studies of nest building in captive birds (Marais 1937; Hinde 1958; Dilger 1962; Collias & Collias 1964; Sargent 1965; Collias & Collias 1973; Gwinner & Berger 2008). Domesticated canaries (*Serinus canaria f. domestica*; Hinde 1958) and weaverbirds (Marais 1937), reared without access to normal nest materials, built species specific nests when they later were given suitable nest materials. In free living blue tits it has recently been found that the aromatic plant composition of nests resulted from individual preferences (Mennerat et al. 2009b). Whether this preference was vertically transmitted from mother to daughter remains to be investigated in more detail, however females did not add plants to the nest in a composition similar to that added in the area experienced as a nestling. In contrast to our study, handling of nest materials and selection of nest materials have in some species been shown to be influenced by experiences as nestling and adult (Dilger 1962; Sargent 1965; Gwinner & Berger 2008).

In the present study, blue tit controls lined the nest with more feathers than great tit controls. This may be explained by two reasons. First, across species, smaller birds tend more often to use feathers than larger birds (Møller 1984). This is in accordance with our finding that blue tits, which as mentioned are smaller than great tits (adult body size of 12 cm and 15 cm respectively; Haftorn 1971) use the most feathers. Second, in European passerines, early breeding species tend more often to have feathers as nest lining than late breeders (Møller 1984). This is in accordance with our finding that blue tits breed earlier in the season, compared to great tits, and hence may experience lower temperatures during the incubation period and hatching of the nestlings. Like great tits, coal tits (*Periparus ater*) build nests lined with hair and wool (Haftorn 1971). This is supported by six observed coal tit nests in the current study. Five nests were without feathers, and one nest contained two feathers. The probability of observing two or less feathers in a nest of a blue tit is 36.7% ($33 \div 90 \times 100$; $p = 0.37$). Provided that use of feathers is the same for coal tits and blue tits, the probability of observing six coal tit nests with two or less feathers is: $P = p^6 = 0.37^6 = 0.003$. Because coal tits are even smaller than blue tits (adult body size of 11 cm), and breed earlier in the season

(Haftorn 1971), but still do not use a significant amount of feathers, body size and breeding time may not be the entire explanation for lack of use of feathers in great tits.

An independent phylogenetic analysis can shed light on possible evolutionary pathways of use of nest materials. A phylogenetic tree is a hypothesis about evolutionary relationships among species, often based on morphological or molecular data (Futuyma 2005). As for morphological and molecular data, behaviors shared by species close together in a phylogenetic tree, are likely to be shared through recent common ancestry. Based on comparisons of nucleotide sequences of the mitochondrial cytochrome-*b* gene, coal tits, blue tits and great tits were classified in different genera, where coal tits and great tits shared a common ancestor with each other more recently than with blue tits (Gill et al. 2005). Use of hair as nest lining seems to be conserved from branch to branch in the tree, despite changes in other features. This indicates constraints on evolutionary change (c.f. Barnard 2004). We thus suggest that use of nest materials is a conservative trait, which due to phylogeny differs among these species. This is consistent with our present finding that variation in use of nest materials is genetically determined. However, further analysis of nest building in several related species is necessary to determine evolution of use of nest materials within the bird family Paridae.

Given that nest building require some kind of ‘complex’ cognition, Healy et al. (2008) suggested that it could be used as a tool for understanding complex cognition in birds and other vertebrates. However, the present study, suggesting that variation in nest building is genetically determined, supports the view that at least some part of nest building behavior is simple, i.e. it does not require cognitive complexity. This is consistent with the suggestion that it is possible to build both simple and sophisticated structures by only using a limited repertoire of stereotyped movements (Hansell 2000). However, because all construction behaviors do not necessary requires a similar level of cognitive complexity (Hansell & Ruxton 2007), this study does not exclude that nest building in some species may share complex cognitive requirements.

Concluding remarks and future research

To sum up, the present study on use of nest materials showed no evidence for nest building behavior being learned by the foster-species during the nesting period. Instead, the results imply that the interspecific variation in nest building behavior between blue tits and great tits is mainly genetically determined. This held true even when accounting for possible confounding variables such as laying date of first egg, clutch size, egg volume, and age. That

nests build by yearlings did not differ from nests built by older birds, indicate that nest building behaviour in these species did not improve with experience (i.e. age) of the builder. Consistent with these results, we suggest that nest building is a conservative trait that has evolved differently in these two species.

Suggestions for further studies should be to include data collected during the field-season 2009. This gives the opportunity to study the same female for several years, and then see whether e.g. use of feathers is consistent for years. It also gives the opportunity to study nest building in offspring of females measured in 2008, and in such a way compare nest building in mothers and daughters.

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Appendices

Appendix A

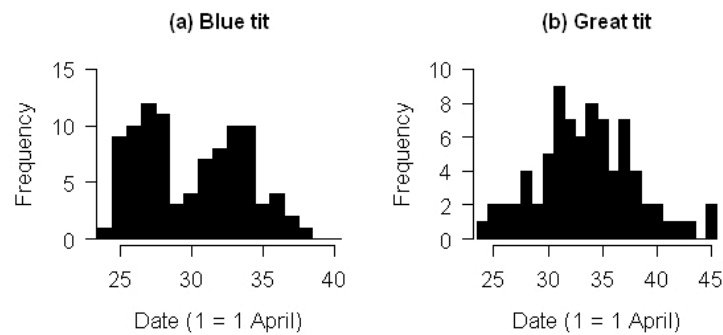


Figure A1. Laying date of first egg for (a) blue tits, $n = 95$; and (b) great tits, $n = 79$.

Appendix B

Table B1. Number of individuals using feathers as nest lining or not

Species	Treatment	Period	Feathers present		Total number of nests
			Yes	No	
Blue tit	Control	Egg laying	75	15	90
	Control	Hatching	74	5	79
	Cross-fostered	Egg laying	4	1	5
	Cross-fostered	Hatching	4	1	5
Great tit	Control	Egg laying	10	56	66
	Control	Hatching	35	26	61
	Cross-fostered	Egg laying	2	8	10
	Cross-fostered	Hatching	2	8	10

Appendix C

Table C1. Results of correlation analyses between variables of nest building. C = control, and CF = cross-fostered. Feathers counted during E = egg laying, and H = hatching. Mosses and hair only observed during egg laying

Variable	Species	Feathers (H)		Hair (%)		Moss (%)		Nest height (cm)	
		C	CF	C	CF	C	CF	C	CF
Feathers (E)	Blue tit	***	-	***	-	*	-	-	-
	Great tit	-	-	-	-	*	-	**	-
Feathers (H)	Blue tit			*	-	-	-	-	-
	Great tit			+	-	+	-	-	-
Hair (%)	Blue tit					***	-	-	-
	Great tit					***	***	+	-
Moss (%)	Blue tit							-	-
	Great tit							+	-

Significant codes: - $p > 0.10$ + $p < 0.10$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

Appendix D

Table D1. Mean proportion of mosses (%), nest height (cm), and distance from entrance hole to nest (cm) in nests of blue tits and great tits according to treatment and size of nest box. Test statistics are given for tests testing the hypotheses that sample means do not differ between small and large nest boxes

Variable	Species	Treatment	Size of nest box						Tests statistic	
			Small			Large			W/t	p
			Mean	SD	n	Mean	SD	n		
Moss (%)	Blue tit	Control	15	24.04	77	13	20.53	8	309 ^a	0.99
		Cross-fostered	67	35.12	3	30	-	1	-	-
	Great tit	Control	24	19.75	12	35	29.34	52	257 ^a	0.34
		Cross-fostered	54	24.08	5	15	12.91	4	18.5 ^a	0.05
Nest height (cm)	Blue tit	Control	6.44	1.04	77	7.88	2.09	8	-1.92 ^b	0.09
		Cross-fostered	6.83	1.21	3	6.85	-	1	-	-
	Great tit	Control	6.33	1.65	12	7.58	1.47	52	-2.42 ^b	0.03
		Cross-fostered	6.49	1.27	5	6.70	1.57	4	-0.22 ^b	0.84
Distance entrance hole to nest (cm)	Blue tit	Control	7.15	1.44	76	6.86	2.23	8	0.35 ^b	0.73
		Cross-fostered	6.73	0.58	3	7.05	-	1	-	-
	Great tit	Control	7.92	2.47	12	7.70	2.31	52	0.28 ^b	0.78
		Cross-fostered	8.13	0.68	5	9.15	0.73	4	-2.14 ^b	0.07

^a = Wilcoxon rank-sum test and ^b = Student t-test.

Appendix E

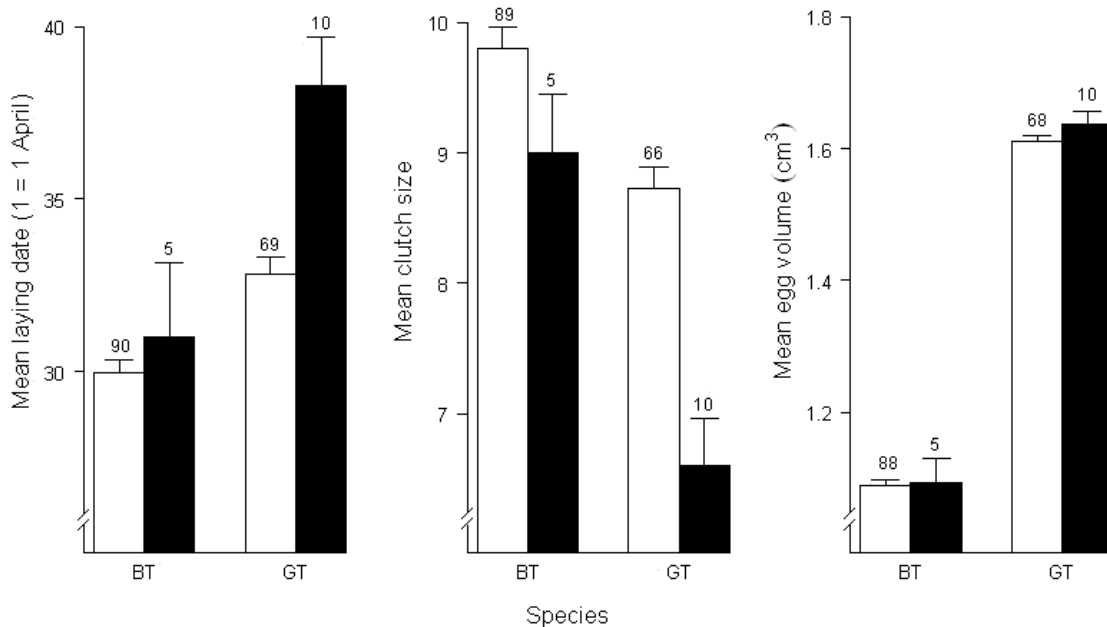


Figure E1. Laying date of first egg (1 = 1 April), clutch size, and egg volume (mean + SE cm³) plotted for blue tits (BT) and great tits (GT). Open bar = control, solid bar = cross-fostered. Sample size are shown above bars. For mean values and results of t-tests testing the hypothesis that sample means do not differ between control and cross-fostered birds, see Appendix F.

Appendix F**Table F1.** Measures of female quality in control and cross-fostered blue tits and great tits. Test statistics are given for tests testing the hypotheses that sample means do not differ between control and cross-fostered birds

Variable	Species	Control			Cross-fostered			Test statistic	
		Mean	SD	n	Mean	SD	n	t	p
Laying date (1 = 1 April)	Blue tit	30	-	90	34	-	5	178	0.44 ^a
	Great tit	33	4.08	69	36.5	4.37	10	-3.74	0.003
Clutch size	Blue tit	10	1.48	89	9	1	5	1.68	0.15
	Great tit	9	1.32	66	7	1.17	10	5.25	< 0.001
Egg volume (cm ³)	Blue tit	1.08	0.08	88	1.10	0.09	5	-0.13	0.90
	Great tit	1.62	0.10	68	1.67	0.08	10	-0.96	0.35

^a Median values and W given for Wilcoxon rank-sum test.

Appendix G**Table G1.** Results of correlation analyses between variables of nest building and measures of female quality. C = control, and CF = cross-fostered. Feather counted during E = egg laying, and H = hatching^a

Variable	Species	Laying date		Clutch size		Egg volume		Age	
		C	CF	C	CF	C	CF	C	CF
Feathers (E)	Blue tit	-	-	-	-	*	-	-	-
	Great tit	-	-	-	-	-	-	-	-
Feathers (H)	Blue tit	-	+	-	-	-	-	-	**
	Great tit	-	-	-	-	-	-	-	-
Hair (%)	Blue tit	-	-	-	-	-	-	-	-
	Great tit	-	*	-	*	-	-	-	-
Moss (%)	Blue tit	-	-	-	-	-	-	-	-
	Great tit	-	*	-	*	-	-	-	-
Nest height (cm)	Blue tit	-	-	-	-	-	-	-	-
	Great tit	-	-	-	-	+	-	-	-

Significant codes: - p > 0.10 + p < 0.10 * p < 0.05 ** p < 0.01

^aWhen taking the sequential Bonferroni technique (Rice 1989) into account, none of the correlations were significant for the whole table. When analyzing each variable separately, the negative correlation between feathers and age in cross-fostered blue tits was still significant.

