ORIGINAL ARTICLE

Nest ornaments and feather composition form an extended phenotype syndrome in a wild bird

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Abstract

Many species throughout the animal kingdom construct nests for reproduction. A nest is an extended phenotype—a non-bodily attribute—of the individual building it. In some bird species, including our study population of blue tits (*Cyanistes caeruleus*), conspicuous feathers or other material are placed on top of the nest. These so-called nest ornaments do not contribute to nest insulation, but are hypothesised to have a signalling function. Here, we apply the concept of behavioural syndromes, with focus on between-individual variation (repeatability) and between-individual correlations, to the study of avian nest construction. We find that nest ornamentation is a moderately repeatable trait in female blue tits, which suggests it is an extended phenotype of the female. Furthermore, the tendency to ornament the nest covaries across females with another aspect of her extended phenotype, the composition of the nest lining material, and these two traits thus form an extended phenotype syndrome. Assuming the correlation is reflected on a genetic level, it implies that nest ornamentation and composition of the nest lining do not evolve in isolation; one aspect may be an evolutionary by-product of selection on the other aspect and their overall flexibility to respond to change is reduced.

Significance statement

The avian nest is an extended phenotype (a non-bodily attribute) of its builder with potentially multiple functions in terms of insulation and signalling. In particular, many bird species' nests contain nest ornaments, feathers or other materials that are placed on top of the nest and that stand out from the nest material due to their colour and/or size. We quantified between-individual variation (repeatability) of nest ornamentation behaviour in a wild population of blue tits and between-individual covariation (syndrome) of nest ornamentation to other features of nest construction. We find that nest ornamentation is a repeatable trait limited to females in our study population. The tendency to ornament the nest covaries across females with another aspect of her extended nest phenotype, the composition of the nest lining material. These correlated traits thus form an extended phenotype syndrome. It hence becomes crucial to recognise that a study of a single aspect of nest construction in isolation captures only a part of the complexity, as one aspect may have evolved as a correlated response of selection on the other aspect. Moreover, such a syndrome implies limited flexibility in the range of adaptive response.

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Introduction

Behavioural syndromes—independent behaviours that are correlated on a between-individual level (Sih et al. 2004)—are interesting because they describe how behavioural variation, including less-than-optimal behaviour, persists in animal populations. A tendency to behave in a specific manner that is selected for within one context or under certain circumstances may be maladaptive when carried over to another context or when the circumstances change (Sih et al. 2004, 2012). Individuals of several species show such tendencies, i.e. behavioural consistency that is quantified as repeatability, also in nest construction. For example, preferences for nesting

materials that are displayed across breeding seasons have been found in pied flycatchers (*Ficedula hypoleuca*: Briggs and Mainwaring 2019), blue tits (*Cyanistes caeruleus*: Mennerat et al. 2009; Järvinen et al. 2017a) and common starlings (*Sturnus vulgaris*: Gwinner and Berger 2008).

The primary function of bird nests is to serve as receptacles for eggs and young. Nest construction is thus among the most fundamental behaviours that determine reproductive success in birds (Hansell 2000; Mainwaring et al. 2014). Bird nests display within-species variation in size, structure, function and material content (e.g. Deeming et al. 2012; Tomás et al. 2013; Rubalcaba et al. 2017; Biddle et al. 2018). Bird nests count as extended phenotypes, which is the part of a phenotype that is expressed outside of the individual and includes all the effects it has in the environment (Dawkins 1982; Schaedelin and Taborsky 2009). By constructing nests, animals extend their control over the environment and manipulate it to create suitable conditions for reproduction. Nest building is energetically costly, exposes the builder to predators and requires trade-offs in terms of time budget (Collias and Collias 1984; Mainwaring and Hartley 2009). Nests as extended phenotypes thus convey information on individual fitness and reproductive investment and may function in signalling (Schaedelin and Taborsky 2009). Nest materials, especially those of limited availability, may be used as a signal that is directed towards mates or intraspecific competitors. For example, white plastics placed in black kite (*Milvus migrans*) nests resulted in fewer intruding competitors in the territory (Sergio et al. 2011). Apparently, the competitors regarded the plastic material as an honest indicator of the nest owner's fitness and competitive ability (Sergio et al. 2011). Individuals of several other bird species are also known to place unusual or conspicuous material on top of the nest. Some previous studies have referred to such components as nest ornaments (Sanz and García-Navas 2011; García-Navas et al. 2013) for their putative role in sexual signalling (Sanz and García-Navas 2011; Sergio et al. 2011; García-Navas et al. 2013; Mainwaring et al. 2016).

Between-individual—and in particular additive genetic—variation in nest building implies a population has the capacity to adapt its reproductive behaviour when faced with environmental change. What is unknown at present is whether different aspects of the nest as an extended phenotype covary between individuals, and hence form an extended phenotype syndrome. Extended phenotype syndrome, the term we present here, is a behavioural syndrome as studied through the extended phenotypes (the nest characteristics), as a proxy for nest construction behaviour. Investigating a behavioural syndrome in nest construction requires direct observation of individuals displaying construction behaviour. Instead, correlations between measurements of nest characteristics consider the nest characteristics, the outcome of nest construction behaviour. Indeed, multiple nest characteristics, with potentially different functions, may covary. Such covariation is an important consideration from an evolutionary aspect, because it determines whether nest characteristics are able to evolve in isolation. If one nest characteristic is genetically linked with other nest characteristics, its evolution would be constrained as any one nest characteristic would be expected to also show a correlated response to selection on other nest characteristics (Lynch and Walsh 1998; Dingemanse and Dochtermann 2013). If nests indeed form an extended phenotype syndrome, it would necessitate studies of an integrative nature, jointly considering multiple aspects of nest construction and their fitness consequences.

In blue tits, our model species, females are known to build the nest alone (Cramp and Perrins 1993), although Sanz and García-Navas (2011) found that some blue tit males provided feathers as nest ornaments in a Spanish population of blue tits. In blue tits, nest ornaments stand out from the nest material within the cavity or nest box. Nest ornaments are often feathers, but may also be flower petals, other fresh plant matter, artificial material like pieces of plastic or dyed wool, or pieces of skin of small mammals. The items are placed on top of other nest material, on the nest rim and not in direct contact with the nest cup, and thus play no role in nest insulation. A follow-up study in the same blue tit population tested the effect of experimentally supplemented and removed feathers (García-Navas et al. 2013): males removed the supplemented feathers, supposedly because they assumed them to signal of a cuckolding attempt by extra-pair males. Another experiment carried out in a different population of blue tits also found that the supplemented feathers were removed but only during nest construction and were mostly retained during the incubation period. The study did not determine which sex was responsible for the removal (Mainwaring et al. 2016).

In our study population of blue tits in Finland, nests vary in size (Järvinen et al. 2017b) and the material used in the nest lining (Järvinen et al. 2017a). The individuals differ in the proportion of feathers used in the nest lining material. This preference is both repeatable and modestly (albeit not statistically significantly) heritable (Järvinen et al. 2017a). Here, we study nest ornamentation as a potentially sex-specific behavioural trait and look at individual consistency of this behaviour across breeding seasons in both males and females. We expect to find between-female variation in the number of nest ornaments because the nest construction traits that we have studied thus far (the nest size and material composition) have been limited to females in our population (Järvinen et al. 2017a). However, if nest ornaments indeed are contributed by males in our population (cf. Sanz and García-Navas 2011), we predict also (or possibly only) between-male variation in the number of nest ornaments. Additionally, we are interested in whether the number of nest ornaments forms a behavioural syndrome with other nest characteristics, the height of the nest and the composition of the nest lining material. We have previously

established that these nest characteristics are individual traits in our study population (Järvinen et al. 2017a). By combining this knowledge with the fact that behavioural traits often co-vary and thereby form behavioural syndromes, we hypothesise that individual-specific nest traits also covary and thus form an extended phenotype syndrome.

Material and methods

Study site

We used long-term data recorded on a population of blue tits breeding in nest boxes in Tammisaari, southwest Finland (60° 01′ N, 23° 31′ E). The data used in this study was collected between 2006 and 2018, during which time the site consisted of 319–470 nest boxes located in patches of mixed boreal forest in between areas of farmland. The nest boxes ($W \times H \times D = 125$ mm $\times 200$ mm $\times 81$ mm, bottom thickness = 22 mm; bottom surface area, 125 mm $\times 81$ mm $= 101$ cm^2; bottom-to-hole distance = 170 mm) were made of untreated spruce and had an entrance hole with a diameter of 26 mm.

Study species

The blue tit is a socially monogamous, secondary hole-nesting passerine. It readily builds a nest in a nest box if available. Female blue tits choose the nesting site and build the nest that typically consists of a base layer of moss and dry grass, and a lining of hair, fur, wool and feathers (Britt and Deeming 2011; Deeming and Mainwaring 2015). Other common nest components include bark, wool, pine needles and fresh plant matter. Small mammal fur, flower petals and human-made materials such as wool insulation are also occasionally incorporated.

Description of a nest ornament

Nest ornaments in the form of feathers were primarily defined by their location in the nest: they were located on top of the nest and on the rim and not in the nest cup, and they stood out of the bulk of the nest based on colour (as perceived by human eye under natural light) and/or size (Fig. 1). We focused on feathers because these were the typical ornaments observed in the nests. To differentiate between feather ornamentation and a general preference for feathers as nest material, we also considered non-feather ornaments, which were defined as any nest components that fit the above-described criteria for nest ornaments but were not feathers but, e.g., small mammal fur or colourful wool (described in detail and illustrated in the Online Resource).

Data collection

Every breeding season starting from late April, the nest boxes were checked once a week until the eggs hatched. We estimated the laying date of an incomplete clutch by back-calculating with the assumption that one egg was produced daily. We calculated the expected hatching date based on the date of clutch completion and assumed an incubation period of 12 days (Kluen et al. 2011). We began to check the nest every afternoon on the day of the expected hatching and continued until the first egg hatched (day 0).

In 2018, we photographed each nest during 4 weeks of construction (starting from the last week of April). Due to asynchrony in nest building, each nest was photographed between one and four times (once: 7 nests, twice: 26 nests, three times: 38 nests and four times: 26 nests). The nests were photographed directly from above and were not removed from the nest box. In 2006–2018, the nests were photographed 2 days (day 2) after hatching. The height of the nest material was measured (2008–2018, except in 2011) and the proportions of different nest materials were scored also on day 2. The nest height was measured as the distance between the floor of the nest box and the top of the nest in all four corners of the nest with a knitting needle fitted with a millimetre paper (2006–2012) or electronic calliper (2013–2018). The average of these values was used as the measure of nest height. The nests were removed from the nest box and the proportions of different nest materials were estimated by eye. The base layer of the nest was separated from the nest cup. The base layer typically consists of moss. The nest cup lining typically contains ungulate hair (of moose *Alces alces* or white-tailed deer *Odocoileus virginianus*), combined with grass and/or strips of bark and/or feathers. Blue tits use feathers from a variety of species. The proportion of feathers in the nest lining is calculated as the proportion of feathers in the nest after excluding moss (i.e. the base layer), and this proportion was arcsine-square-root transformed to approximate a Gaussian distribution (Järvinen et al. 2017a, b).

We used both the photographs taken during the construction period in 2018 and those taken after hatching in 2006–2018 (excluding 2007 when only the nest cup was photographed) to record nest ornaments according to the criteria described in 2.3. To reduce inter-observer variability, PJ scored all the photographs. To minimise subjectivity, two other researchers (JB and K. Schreven) followed the criteria and scored a subset of the photographs. The scores were unanimous with those of PJ.

Adults were caught when providing care for their offspring. Adults were ringed (if unringed) with a metal ring to allow lifelong individual identification and aged as either yearling (hatched the previous breeding season) or older on the basis of the colour of the coverts of their primary feathers.

Fig. 1 Photographs of nests with feather ornaments in the study population of blue tits. The feather ornaments are marked with yellow arrows and the nest cups with dashed white circles. These nests belong to different females and were constructed within different nest boxes (i.e. breeding sites) and in different years
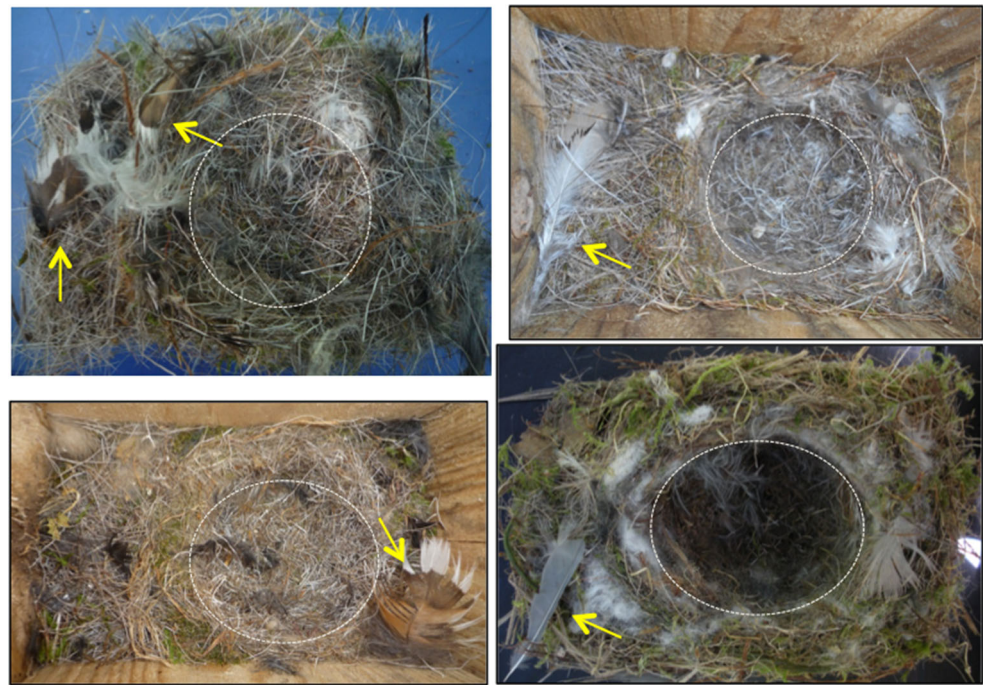
Our previous results indicate that the nest features post-hatching are a female trait (Järvinen et al. 2017a). However, if males provided the nest ornaments, these should optimally be introduced before or during the egg laying period. Considering the nest ornaments' putative function in sexual signalling, before females finished laying eggs would be the time males could influence female reproductive investment and to increase the number of eggs they lay. Females, on the other hand, should signal to males around hatching time to elicit an increase in male parental care at the beginning of a period when it is most needed (Soler et al. 2007). Because our long-term data consist of nest measurements taken after hatching, we had to determine whether the nest ornament status after hatching corresponds to that of the pre-egg laying to the incubation period. Thus, in 2018, we studied the association between the scores of nest ornaments each week of the construction period and those of post-hatching. This data (see results) showed we could rely on the long-term post-hatching nest data to represent nest ornament status throughout the breeding season.

To minimise observer bias, collection of data on nest construction and nest ornamentation was blind with respect to the identity and traits of the parents.

Statistical analysis

All the statistical analyses were conducted in R (R Core Team 2019). Uncertainty of an estimate was provided as ± the standard error of an estimate unless indicated otherwise.

Repeatability

We aimed to determine whether nest ornamentation behaviour showed consistency specific to males or females in our study population. We used the number of nest ornaments (0–5) counted when the eldest nestlings were 2 days old as response variable in a Poisson generalised linear mixed model (GLMM) with a log link, which was conducted with ASReml-R (v4.1.0.90, Butler 2018). We included age (1 vs. ≥ 2 years) of the adult female and male as factorial fixed effects, because experience and learning can influence the choice of nest material (Muth and Healy 2011, 2014; Sergio et al. 2011; Bailey et al. 2014). Variation across years, nest boxes, females and males were estimated by including these variables as random effects. The adjusted repeatability (i.e. the repeatability conditional upon the fixed effects in the model; Nakagawa and Shielzeth 2010) of the Poisson regression on the latent scale was computed as the ratio of the between-individual variance over the sum of all variance components. The adjusted repeatability on the data scale was computed following formulas given by de Villemereuil et al. (2016). In general, transformation from the latent scale to the data scale includes additional variation induced by the Poisson distribution and results in lowered repeatability (Nakagawa and Shielzeth 2010).

Multivariate models

Nest height and the proportion of feathers in the nest lining are repeatable and heritable female traits in our study population (Järvinen et al. 2017a). Here we analysed the covariance of

nest ornaments, the proportion of feathers in the nest lining and height of the nest material in a multivariate mixed model. The number of nest ornaments was modelled as a Poisson distributed variable. Following Järvinen et al. (2017a), nest height and the arcsin-square-root of the proportion of feathers in the nest cup lining was modelled as Gaussian distributed variable. The multivariate mixed models were conducted using ASReml-R 4. Correlations were calculated based on the estimates provided by these models.

Association between ornaments during construction and after hatching

We measured the correlation between the scores of nest ornaments during each week of the construction period and those of post-hatching in 2018 by calculating Goodman-Kruskal gamma values with the R package 'MESS' (v0.5.5, Ekstrøm 2019).

Data availability

The dataset generated and analysed during the current study along with the R code used to perform the analyses are available in the Zenodo repository, doi: https://doi.org/10.5281/zenodo.4021911.

Results

Nest ornamentation

In total, 996 nests were scored for nest ornaments when the eldest nestlings were 2 days old. Overall, 24% (244/996) of the nests contained one or several feather ornaments (0 = 752, 1 = 171, 2 = 50, 3 = 16, 4 = 5 and 5 = 2). Feathers were the main type of nest ornament used (Online Resource). There were 671 females and 587 males whose nests were scored in either one ($n_F = 457$, $n_M = 387$) or several breeding seasons (females: $n_2 = 135$, $n_3 = 54$, $n_4 = 20$, $n_5 = 3$, $n_6 = 2$; males: $n_2 = 134$, $n_3 = 46$, $n_4 = 13$, $n_5 = 6$, $n_6 = 1$).

Pre- and post-hatching ornaments were positively correlated. The highest correlations were found between the nest ornament status the first week of nest construction and after the eggs hatched ($\gamma = 0.68$, CI = 0.41–0.94, $p = 0.003$; Fig. 2). We therefore conclude that counts of the ornaments made when the nestlings were 2 days old are representative of ornamentation at early nest building.

Repeatability of nest ornamentation

Nest ornamentation was repeatable in females with a latent-scale estimate of 0.25 ± 0.2 (observed scale repeatability 3%). In contrast, nest ornamentation was not repeatable in males
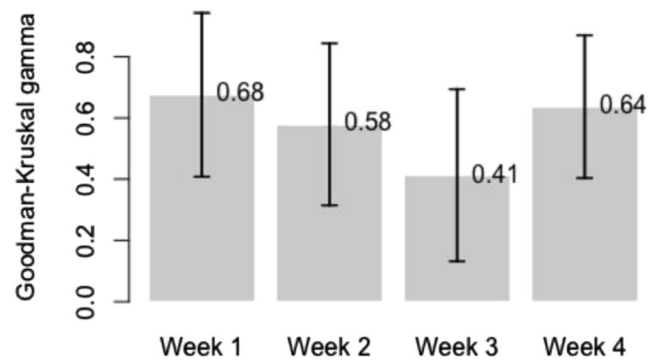

Fig. 2 Goodman-Kruskal gamma correlations of the number of nest ornaments between day 2 after hatching and each week of nest construction. The bars represent 95% confidence intervals. All correlations are statistically significant (weeks 1, 2 and 4: $p < 0.03$; week 3: $p = 0.01$)

($R_{latent} = 0.04 \pm 0.19$, $R_{observed} = 0.005$; Table 1). Females older than 1 year incorporated more nest ornaments (Table 1): the integration of the fixed effect coefficient of the Poisson regression over the random effects (de Villemereuil et al. 2016) shows that yearling females are expected to have 0.6 ornamental feathers and females older than 1 year are expected to have 0.88 ornamental feathers. Qualitatively the same findings were obtained when analysing feather and non-feather nest ornaments combined (Online Resource).

Correlation between nest ornamentation and proportion of feathers in the nest lining

Given that there was no repeatability for males for nest ornamentation, we did not consider multivariate models for males. On a between-female level, the number of feather nest ornaments was correlated with the proportion of feathers in the nest lining ($r = 0.42 \pm 0.16$). The between-female correlations

Table 1 Factors affecting the number of feather nest ornaments analysed using a Poisson GLMM with a log link ($N = 881$). The number of feather nest ornaments was used as a response variable and year, nest box, male and female identities as random explanatory variables. Age of the female (1 vs. ≥ 2 years) was included as a factorial fixed effect. Repeatability (R) was calculated for males and females

Random variable	Estimate (± SE)	Z	$P > z$	R (± SE)
Year	0.04 (± 0.04)	1.09	0.14	
Nest box	0.16 (± 0.12)	1.31	0.10	
Male	0.07 (± 0.17)	0.45	0.33	0.04 (± 0.19)
Female	0.43 (± 0.18)	2.39	0.009**	0.25 (± 0.20)

Fixed variable	Estimate (± SE)			
Age:				
Intercept (1 year)	− 1.36 (± 0.12)			
≥ 2 years	0.38 (± 0.13)			

Significance values: **$p < 0.01$

of nest height with the number of feather ornaments and of nest feather content with nest height were low and not significant (Table 2). On the level of the nest box, the different characteristics of the nest did not significantly covary (Table 2). Qualitatively the same findings were obtained when analysing feather and non-feather ornaments combined (Online Resource).

Discussion

Behavioural syndromes are suites of correlated behaviours that show individual consistency. Here, we extend the concept of behavioural syndromes to involve extended phenotypes, which are the attributes of an individual that are expressed on its environment (Dawkins 1982). We have previously shown that the propensity to use feathers in the nest lining (quantified as the proportion of feathers in the nest) is a repeatable and modestly heritable behaviour that is limited to females (Järvinen et al. 2017a). Here, we find that the proportion of feathers in the nest is positively correlated with another repeatable nest feathering trait: nest ornamentation. About 25% of the variation in the number of nest ornaments is due to between-female differences in their latent propensity to ornament their nest. Although nest ornamentation and nest construction with feathers are correlated behaviours, they are not identical, given the correlation falls below unity ($r = 0.42$). Instead, nest ornaments, together with the proportion of feathers in the nest, form an extended phenotype syndrome in females in our study population of blue tits.

Nest ornaments are typically feathers that stand out from the rest of the nest material due to their size or colour and placement. They are placed on top of the nest and apart from the nest cup, which reduces their potential

to function in insulation. Feather nest ornaments have been observed in a few species. In spotless starlings (*Sturnus unicolor*), males carry green plants to the nest, which females reciprocate by providing ornamental feathers (Polo and Veiga 2006). These feathers are positioned non-randomly on the side that provides the maximum amount of UV reflection (Veiga and Polo 2005). In blue tits, Sanz and García-Navas (2011) observed males bringing feathers to the nest. A subsequent study by García-Navas et al. (2013) provided experimental evidence of this male ornamentation behaviour in the same population. Our results on the between-individual consistency in ornamentation only present in females provide no support for male ornamentation behaviour in our population. It should be noted, however, that our analyses focus on repeatability (i.e. consistency across breeding seasons) in our scoring of nest ornamentation and construction of nests, and not on direct observations of individuals conducting the behaviour. Hence, it remains possible that males bring feathers for ornamentation of the nest in our study population, but they do so inconsistently from one breeding season to the next. Importantly, however, repeatability in behaviour is a crucial ingredient from an evolutionary perspective. This is because repeatability is the upper estimate for heritability (Falconer and Mackay 1996). If nest ornamentation evolves in the context of signalling from one parent to another, it must inherit from one generation to the next (i.e. be heritable), as it is otherwise evolutionary transient. From that perspective, our finding of an absence of male repeatability for nest ornamentation reveals an absence of evolutionary potential for males using nest ornamentation as a signal. Clearly, for this conclusion to gain generality, demonstrating repeatability of nest ornamentation in females only in other blue tit populations and in other species where females build nests is needed.

Table 2 Covariance of the number of feather ornaments, proportion of nest feather content and nest height analysed with a multivariate mixed model ($N = 1126$). Age (1 vs. ≥ 2 years) and year were included as a factorial fixed effects. Female identity and nest box identity were used as random variables. The number of feather ornaments (ornament) was modelled as Poisson distributed variable (with dispersion set as 1). Nest height and the (arcsin-square-root transformed) proportion of feathers (feather%) were modelled as Gaussian distributed variables. Significance of the covariance ($P > z$) differing from zero was computed on the basis of the Z test of the estimate over its standard error. Correlations (r) were calculated on the female level only

Random variable	Covariance	Estimate ($\pm$ SE)	Z	$P > z$	r ($\pm$ SE)
Nest box	feather%:ornament	-0.00054 (± 0.010)	0.054	0.43	
	nest height:feather%	0.033 (± 0.11)	0.30	0.32	
	nest height:ornament	-0.62 (± 0.88)	-0.70	0.22	
Female	feather%:ornament	0.040 (± 0.017)	2.38	0.009**	0.42 (± 0.16)
	nest height:feather%	-0.057 (± 0.19)	-0.30	0.46	-0.032 (± 0.11)
	nest height:ornament	0.73 (± 1.5)	0.50	0.16	0.065 (± 0.13)

Significance values: **$p < 0.01$

This study, as with any study conducted in a wild population, suffers from the drawback that environmental conditions, which we did not include in the statistical analyses, can be confounded with between-individual variation and therefore inflate its estimate. With regard to nest building, a prime environmental condition could be the availability of different nest materials, in particular feathers may in our case have limited availability, although Hansell and Ruxton (2002) found that feathers are not in short supply in woodlands. Our analyses correct for variation between years and variation between breeding sites (nest boxes), although none of these explains a significant proportion of variance in nest ornamentation (Table 1). We do not know, however, whether allowing for variation between nest sites adequately corrects for spatial heterogeneity in the study area. In particular, the spatial scale females collect nest material may extend over multiple nest sites (Mennerat et al. 2009, but see Surgey et al. 2012).

We have in this study applied the concept of behavioural syndromes, with its focus on individual consistency and between-individual correlations, to the study of avian nest building. Our findings suggest that ornamentation of the nest is an extended phenotype of the female only. The tendency to ornament the nest covaries across females with another aspect of her extended phenotype, the composition of the nest lining material. Whenever multiple behaviours form a syndrome, it becomes crucial to recognise that a study of a single behaviour in isolation captures only a part of the complexity. For example, nest ornamentation may be a correlated behaviour to the functionally and adaptively more important aspect of which material is used to construct the nest lining (or vice versa). Furthermore, other behavioural traits may covary with the nest construction traits. For example, nest ornamentation could be correlated with the individual's level of activity or 'boldness', where the individuals that foraged more actively or over a greater range might incorporate more ornaments into the nest. Our findings thus indicate that research avenues where nest construction is viewed as part of behavioural syndromes may shed further light on the fascinating behavioural complexity of nests.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

Ethical approval   Birds were caught and handled by personnel with a ringing license. All experiments complied with the Finnish law on animal experiments and were approved by the animal experiment committee of Southern Finland. Bird handling was done with the highest possible care.

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