

Research



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Animal behaviour

Low heritability of nest construction in a wild bird

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In birds and other taxa, nest construction varies considerably between and within populations. Such variation is hypothesized to have an adaptive (i.e. genetic) basis, but estimates of heritability in nest construction are largely lacking. Here, we demonstrate with data collected over 10 years from 1010 nests built by blue tits in nest-boxes that nest size (height of nest material) and nest composition (proportion of feathers in the nest) are repeatable but only weakly (12–13%) heritable female traits. These findings imply that nest construction may evolve but only if subjected to strong and consistent selection pressures.

1. Introduction

Organisms of various taxa including insects, spiders, crustaceans, fish, birds and mammals construct nests [1]. While built mainly for reproduction, nest construction varies across and within populations of the same species. Several hypotheses have been explored to explain this variation in birds, including, e.g. thermoregulation, nest characteristics as extended phenotypes, predator and brood parasite avoidance, anti-parasite and -bacteria strategies and individual preference [2]. Most of these hypotheses interpret observed variation as adaptation, and thus assume—implicitly or explicitly—potential forces of selection acting on additive genetic variation in nest construction. It remains poorly explored, however, whether variation in nest construction is indeed heritable or only non-genetic adjustments in response to environmental conditions [3,4]. Few avian studies have quantified repeatability, the upper value of heritability [5], of nest construction [6–10]. These studies looked at repeatability within a single season, with one exception [6]. The only evidence, to our knowledge, of heritable nest properties has been found in the barn swallow (*Hirundo rustica*), where various parameters of nest size (volume, thickness and material) were shown to be highly heritable (h^2 of 0.33–0.68) by using parent–offspring regression [4].

Here, we calculate repeatability and heritability of nest size and nest composition in a wild pedigreed population of blue tits (*Cyanistes caeruleus*). Working on data from 1010 nests constructed by marked individuals over 10 years, we use the so-called animal model [11] to estimate the heritability of nest size and the proportion of feathers in nests. Because the animal model uses resemblance across all relatives in the pedigree to estimate additive genetic variance, it is less sensitive to bias caused by cultural inheritance than parent–offspring resemblance [12]. In addition, the animal model allows for correcting for variation in characteristics across nest sites, which we show to be important.

2. Material and methods

We recorded the height and composition of blue tit nests on first broods (less than 10% of females with a first brood produce a second brood) constructed between 2008 and

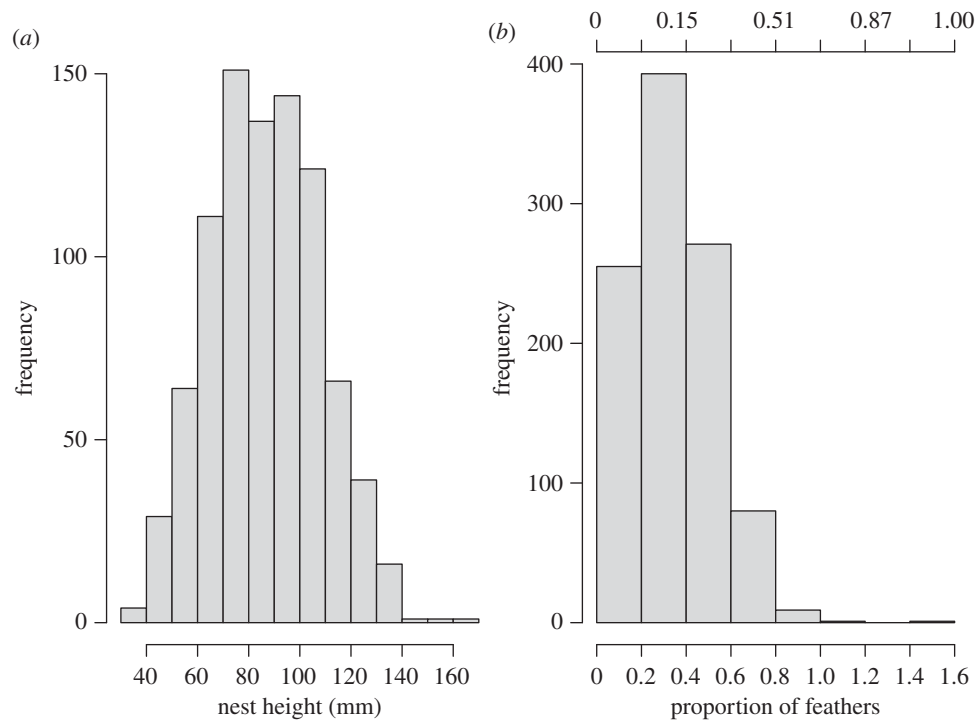


Figure 1. Frequency distribution of (a) nest height in 888 nests, and (b) arcsin-square root transformed proportion of feathers in 1010 blue tit nests. The proportion of feathers was arcsin-square root transformed prior to analysis and this frequency distribution is plotted with the untransformed proportions indicated on the scale above the plot. Thus, the proportion of feathers in most nests was between 3.9% and 15%.

2017 in a population breeding in nest-boxes in southwest Finland (60°01' N, 23°31' E). Nest height and composition were measured when nestlings were 2 days old. The year 2011 was an exception: nest composition was scored when nestlings were 5–9 days old, while nest height was not recorded. Nest height was the average distance from the bottom of the box to the top of the nest measured with a sliding calliper in each corner, and is positively linearly related to volume as the nest-boxes were of equal size (details in [13]). Feathers are often used as nesting material and have been found to provide insulation [14], function as signals (e.g. [15]), reduce nest bacteria [16] and possibly reduce ectoparasites [17]. We assessed the proportion of feathers from all nest material, excluding moss, as an estimate of the proportion of feathers in the nest lining, where moss is rarely used. The nest was removed from the nest-box to visually estimate the proportion (out of 100%) of different materials and returned immediately after (within 5 min).

To analyse nest construction traits, we used a linear mixed model that uses pedigree-derived estimates of relatedness to estimate additive genetic (co)variance, the so-called animal model [11,18]. The pruned pedigree (electronic supplementary material, figure S1) consisted of 429 animals; for 10 of these parents were not known, for 417 the dam was identified and for 403 the sire was identified. The maximum pedigree depth was nine generations, and for 880 animals parentage was unknown. Social males were assumed to be sires in the pedigree and hence, because of extra-pair paternity (on average 13% [19]), some of the paternal links in the pedigree are erroneous. These errors are unlikely to alter the estimates of additive genetic variance as we find that only female blue tits express nest construction traits.

The proportion of feathers in the nest was arcsin-square root transformed to approximate a Gaussian distribution. We considered age (not known or not captured, 1, greater than or equal to 2 years) of the female and male as factorial fixed effects. Our starting model further included year and observer identity as random effects. We constructed a sequential set of four additional models testing for the significance of the inclusion of the random effects (see the electronic supplementary material [20]) testing significance of each additional term with a likelihood ratio test (LRT). Because

nesting sites may differ in quality and environmental conditions, we first tested for between-nest-box variation in nest characteristics by entering identity of the nest-box as a random effect. Second, we considered nest construction (height and composition) as a female trait and tested for female identity as a random effect. Third, we tested for between-male variation in nest composition by including male identity as a random effect. Fourth, we partitioned between-female variation into variation due to permanent environment versus additive genetic effects. Permanent environment effects are a combination of various (non-heritable) effects, which are conserved across the repeated records of the individuals and include, for example, maternal and early-life effects [11].

3. Results

Nest height was measured in 888 nests, and nest composition in 1010 nests. Both nest characteristics showed considerable between-nest variation (figure 1). There were 648 females and 557 males, whose nest composition was scored either in one breeding season ($n_F = 421$, $n_M = 353$) or in multiple years (females: $n_2 = 147$, $n_3 = 51$, $n_4 = 22$, $n_5 = 3$, $n_6 = 3$; males: $n_2 = 131$, $n_3 = 47$, $n_4 = 19$, $n_5 = 5$, $n_6 = 1$, $n_7 = 1$). The proportion of feathers varied between 0 (20%, 198/1010 nests) and 1 (1 nest), but most nests contained some feathers (mean 14%, figure 1).

(a) Nest height

Ages of female (Wald $\chi^2 = 4.3$, $p = 0.12$) and male ($\chi^2 = 1.9$, $p = 0.60$) parents did not affect nest height. Spatial (between-nest-box) variation was clear ($p < 0.001$; electronic supplementary material, table S1; table 1). Model comparison revealed that nest size was highly repeatable in females ($p < 0.001$; electronic supplementary material, table S1). Between-male variance in nest size was not significant ($p = 0.15$; electronic supplementary material, table S1). Further

Table 1. Variances in nest construction parameters partitioned. Fixed effects are reported in the text. The proportion of feathers was arcsin-square root transformed prior to analysis (cf. figure 1). Variances (V) are reported for the female's additive genetic (A, FEM) and permanent environmental (PE, FEM) levels, as well as for between nest-box (BOX), between year (Y), between observer (OBS) and residual (RES) levels. The proportion of each variance component over the sum of all variance components is reported with its standard error (s.e.), where the proportion of V_A is the heritability h^2 printed in bold. Heritability is statistically non-significant for both models (p -values are denoted by asterisks and reported below the table). The results of the supported reduced models, where $V_{A,FEM}$ and $V_{PE,FEM}$ are combined, are reported as repeatability R with their s.e. The other variance components included in these reduced models are printed in bold and are included and are approximately the same as reported here (electronic supplementary material, table S1).

| | estimate | s.e. | proportion \pm s.e. | R \pm s.e. |
|---|----------|------|-------------------------------------|------------------|
| <i>nest size</i> | | | | 0.40 \pm 0.050 |
| V_{YEAR} | 67.1 | 36.5 | 0.14 \pm 0.064 | |
| V_{OBS} | 22.4 | 14.3 | 0.045 \pm 0.028 | |
| V_{BOX} | 59.7 | 14.4 | 0.12 \pm 0.029 | |
| $V_{A,FEM}$ | 57.8 | 57.5 | 0.12 \pm 0.12* | |
| $V_{PE,FEM}$ | 138.8 | 59.3 | 0.28 \pm 0.12 | |
| V_{RES} | 152.1 | 15.8 | 0.31 \pm 0.042 | |
| <i>proportion of feathers (variance estimate and s.e. $\times 10^3$)</i> | | | | 0.23 \pm 0.049 |
| V_{YEAR} | 0.30 | 0.41 | 0.0065 \pm 0.0088 | |
| V_{OBS} | 3.2 | 1.8 | 0.069 \pm 0.035 | |
| V_{BOX} | 2.3 | 1.3 | 0.051 \pm 0.028 | |
| $V_{A,FEM}$ | 6.2 | 4.7 | 0.13 \pm 0.10** | |
| $V_{PE,FEM}$ | 4.3 | 4.9 | 0.094 \pm 0.11 | |
| V_{RES} | 29.7 | 2.4 | 0.65 \pm 0.057 | |

* $p = 0.15$, ** $p = 0.07$.

partitioning of between-female variance into variation due to additive genetic effect (heritability) and permanent environmental effects was statistically non-significant ($p = 0.15$; electronic supplementary material, table S1), with the point estimate indicating that 12% of variation in nest size was heritable (table 1).

(b) Nest composition

Ages of female (Wald $\chi^2_3 = 4.9$, $p = 0.18$) and male ($\chi^2_3 = 3.9$, $p = 0.26$) parents did not affect nest composition (i.e. the proportion of feathers in the nest). Spatial variation between nest-boxes was significant ($p = 0.005$; electronic supplementary material, table S1). Nest composition was repeatable in females ($p < 0.001$; exemplified by images in electronic supplementary material, figure S2) but not in males ($p = 0.5$; electronic supplementary material, table S1), and showed evidence of heritability in females ($p = 0.07$; electronic supplementary material, table S1) with a point estimate of 13% (table 1).

4. Discussion

We found that female blue tits display repeatable nest size and nest composition across years. These traits show evidence of modest heritability of 12% and 13%, respectively, although these estimates are statistically non-significant. This finding stands in strong contrast to the only published study of heritability in avian nest construction to date, which suggests high heritability (greater than 60%) of size (outer volume) and material in barn swallow nests [4]. The main difference between that and the current study is that here we estimate

heritability using kin resemblance in nest characteristics across the entire pedigree. Compared to parent–offspring regression, this method is largely insensitive to cultural resemblance (individual replicating its natal nest) and thus allows more precise estimates of heritability [11,12]. Furthermore, we find that spatial variation across nesting sites is an important factor to control for as it explains a significant part of the variation in nest characteristics.

Female blue tits construct the nest [2], but at least in a Mediterranean population, males decorate it with feathers [21]. These observations imply that males may differ from each other in terms of nest composition. However, we find neither between-male variation in the proportion of feathers nor in the size of the nest in our study population. Hence, our analyses show that nest construction is a sex-limited trait in blue tits. This has important ramifications for adaptation because sex-limitation halves the potential of traits to respond to selection [18]. We conclude that while nest construction has adaptive potential, which should enable birds to respond to novel or divergent selection pressures arising either from natural or sexual selection, heritability of nest construction is modest and likely requires strong and consistent selection for adaptation to occur. Evolutionary quantitative genetic analyses, like our study, are not restricted to avian species but are likely to be instrumental in providing insight into the behaviour of other nest-building vertebrates, such as fish [22]. Our findings thus add to a much-needed foundation, upon which investigations into selective costs and benefits of nest construction can be built.

Ethics. 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 (PH694A). Bird handling was done with the highest possible care.

Data accessibility. Data on nest characteristics measured and covariates used in the model as well as the pedigree: Dryad (<http://dx.doi.org/10.5061/dryad.c561m>) [23]. R script detailing the analyses conducted here on these data are provided in the electronic supplementary material, S1.

Authors' contributions. J.E.B. and E.K. designed the study. All authors collected data in the field. J.E.B. and P.J. wrote the first draft, which was

commented upon and improved by all authors. All authors agree to be held accountable for the content of this paper and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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