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Letter

The correlates of intraspecific variation in nest height and nest building duration in the Eurasian blue tit *Cyanistes caeruleus*

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Birds build nests primarily as a receptacle to lay their eggs in, but they can also provide secondary benefits including structural support, camouflage and adjustment of the microclimate surrounding the eggs and offspring. The factors underlying intraspecific variation in nest characteristics are poorly understood. In this study, we aim to identify the environmental factors that predict nest height variation and the duration of nest building in blue tits *Cyanistes caeruleus*, evaluating latitude, elevation, temperature and the timing of egg-laying as predictors of nest height, while also taking into account female and male parental identity. Using 713 nest height observations collected over a period of five years along a 220 km transect in Scotland, we found that if the annual mean timing of egg-laying was earlier, nests were taller. However, there was no correlation between nest height and elevation, latitude, the minimum temperature in the 14 days pre-egg-laying or the phenology of birds within a year. Female parental identity accounted for a large amount of variation in nest height, suggesting that individual behaviour has an influence on nest structure. We also found that nest building duration was shorter when egg laying occurred earlier in the year, and that across all observations taller nests took longer to build. Overall, our results show that blue tits are able to alter their nest characteristics based on environmental gradients like latitude (in the case of building duration) and the annual mean phenological variation of egg laying, and that birds build relatively taller nests faster.

Keywords: egg-laying, elevation, hole-nesting bird, latitude, nest structure, phenology

Introduction

Nest construction behaviour is widespread across the animal kingdom (Moratalla and Powell 1996), including among birds, where nest characteristics can be highly diverse (Hansell 2000). Historically, nests have been considered to be merely receptacles containing eggs, however there is mounting evidence that nests are specifically designed to improve reproductive success. For example, Lombardo et al. (1995) found that fewer chicks fledge from nests which contain fewer feathers, and Podkova and



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Surmacki (2017) found that nests in cavities with lower levels of illumination tend to be taller, in order to increase the eggs' exposure to light, which increases embryonic metabolic rates (Cooper et al. 2011). The materials used and the structure of the nest allows for adjustment of the microclimate (Lombardo et al. 1995, Hilton et al. 2004, Podkova and Surmacki 2017, de Zwaan and Martin 2018) and defensive camouflage (Westmoreland and Kiltie 2007), as well as providing structural support to the eggs and potentially decreasing the risk of ectoparasitism (Quiroga et al. 2012, Tomás et al. 2012), predation (Møller 1987, Lovell et al. 2013) and bacterial infection (Gwinner and Berger 2005, Mennerat et al. 2009, Peralta-Sanchez et al. 2010, Álvarez et al. 2013, Loukola et al. 2020).

Previous studies in cavity nesting passerines considered the energetic costs of nest building and incubation to be negligible compared to the cost of chick rearing (Hansell 2000, Moreno et al. 2008). However, experimental manipulation of the costs of nest building has shown that birds which spend a shorter period of time building nests increased their provisioning rate (Moreno et al. 2010), had lower stress levels (Moreno et al. 2008) and laid larger clutches (Lambrechts et al. 2012). Nest weight also correlates with female, but not male, quality in the blue tit *Cyanistes caeruleus* (Mainwaring et al. 2008), a species in which females exclusively build the nests (Perrins 1980). Therefore, across passerines, nest building and structure have the potential to both reflect and influence the fitness of the builder. Evaluating the reasons for intraspecific variation in nest characteristics in cavity nesting species is important due to the many studies on avian life history which make use of nest-box nesting birds (Tomás et al. 2006). While nest boxes allow for cavity size to be standardised, structural aspects of the nest, such as height, weight and composition are not controlled for but may impact reproductive success (Moreno et al. 2008, 2010, Lambrechts et al. 2012). For example, the specific composition of nests is known to differ with changes in the environment (Heenan et al. 2015, de Zwaan and Martin 2018), with direct repercussions for reproductive fitness (Pérez et al. 2008, Tomás et al. 2013, Gładalski et al. 2016).

Several hypotheses are used to explain intraspecific variation in nest characteristics, and we shall focus on two of these. Firstly, the individual quality hypothesis states that nest characteristics directly reflect the quality of the builder, thus higher quality individuals will build higher quality nests (Soler et al. 1998, Mainwaring et al. 2008) and this has been demonstrated in cavity-nesting (Tomás et al. 2006, Mainwaring et al. 2008) as well as open nesting passerines (Moreno et al. 1994, Soler et al. 1998). Sanz and García-Navas (2011) found that male blue tits who provide feathers to these nests tend to have greater provisioning rates to the offspring, whereas females respond to the male behaviour by increasing clutch size. There is also evidence that larger nests and nests which are constructed faster may correlate with better parental quality (Mainwaring and Hartley 2009). A recent study on nest characteristics in blue tits found that the identity of the builder accounts for a large component ($R^2 = 0.62$)

of the intraspecific variation in nest height (O'Neill et al. 2018). However, this study estimated nest height based on estimating the proportion of the nest box filled and further research with nest heights or volumes measured precisely is required to confirm the importance of builder identity.

Secondly, the thermoregulatory hypothesis states that the main benefit of bird nests is to reduce heat loss and protect against temperature fluctuations during periods of incubation when the female is off the nest and during offspring provisioning (Tomás et al. 2006). As the eggs of many avian species must be maintained between 34 and 36°C for chicks to develop, the nest may play a role in protecting the eggs from temperature fluctuations during incubation (White and Kinney 1974). Limiting egg heat loss would also aid the brooding adult during incubation, reducing energetic costs. Although the nest cup lining is likely to be the primary insulator (Mainwaring and Hartley 2008), the nest base may also provide some thermal benefits (Kaliński et al. 2014). Furthermore, nest sites may be selected to be more thermally favourable (Ardia et al. 2006, Maziarz and Wesolowski 2013), and certain behaviours during incubation, like egg covering, are likely to aid in maintaining a steady nest microclimate (Loukola et al. 2020). Several studies have found that nest insulation materials and nest mass and height correlate with environmental factors like elevation, latitude and spring temperature over time and space (McGowan et al. 2004, Mainwaring and Hartley 2008, Mainwaring et al. 2012, 2014, Álvarez et al. 2013), while others have found no relationship between nest structure and these same variables (Suárez et al. 2005, Tomás et al. 2006, Schöll and Hille 2014). Nests built comparatively later in the year also contain fewer insulating hairs and feathers (McGowan et al. 2004, Harničárová and Adamík 2016). Furthermore, advancing nesting phenology allows birds to track their thermal niche, potentially reducing average temperatures during nesting by over 1°C (Socular et al. 2017). Spatial studies across large latitudinal gradients further elaborate our understanding of how geographic variation influences nest building (Mainwaring et al. 2012, Heenan et al. 2015), but a study encompassing many sites consistently monitored over a period of several years, with site-specific environmental and parental data, is of value in further teasing apart the environmental correlates of nest structure. Where nest height is studied across multiple years and locations we can arrive at various predictions regarding the relationship between timing and nest height. For instance, when the annual mean timing is earlier birds may build taller nests if they perceive the risk of cold snaps as being greater earlier in the year and we might expect to see a similar relationship within a site and year with the earliest birds building the tallest nests. If, however nest height is determined by absolute timing – perhaps via photoperiod – then we would expect to see the effect of timing on nest height to be similar whether we look across years, across sites or within site-years. Alternatively, if nest building at a site or year is timed to try to keep incubation temperature constant (Socular et al. 2017), we would expect to see no effect across years or sites. It is also possible that later breeding individuals within a site-year

might build lower nests to shorten the period of nest-building and advance their relative phenology.

The duration of nest building may also vary intraspecifically and impact the structure of the nest. Mainwaring and Hartley (2008) found that as the season progresses, the length of blue tits' nest-building period decreases and provided three potential reasons behind the decline in building duration. Firstly, they suggest that nest material may be in limited supply, although this is perhaps unlikely (Hansell and Ruxton 2002, McGowan et al. 2004). Secondly, increasing ambient temperatures and lower risks of cold snaps may reduce the need for insulation, thus decreasing the amount of nest material required. Lastly, they suggest building time may decrease as a mechanism for the birds to catch-up with environmental phenology and better match their offspring demand to food peak phenology (Mainwaring and Hartley 2008). In turn, the nests of later breeders within a year would then be expected to be smaller, as less time is spent collecting materials, and fewer materials are expected to be required to maintain a proper microclimate for the offspring (Mainwaring et al. 2012). Building time may also reflect the quality of the nest-building parent, with faster constructed nests correlating with higher parental quality (Mainwaring and Hartley 2009).

In this study, we aim to understand how spring phenology and biogeographic variables like elevation and latitude affect the nest characteristics of the blue tit. Being widespread, common and willing to occupy nest boxes allows the study of large sample sizes across biogeographic gradients and the standardisation of cavity-size. We use five years of blue tit nest building data collected along a 220 km transect in Scotland (Shutt et al. 2018), from identical nest boxes located at forty-four different sites, totalling over seven hundred nest height and nest building duration samples. We use this data to clarify the relationship between the environment and nest characteristics and examine whether birds can adjust nest height and building duration and make environment-dependent decisions about nest building. Specifically, we ask whether nest height changes with the timing of egg-laying (annual mean and within year deviation), elevation, latitude and temperature, and whether the duration of nest building changes with the timing of egg-laying across years, nest height, elevation, latitude and temperature.

Methods

Study system

Nest data were collected along a 220 km transect spanning from Edinburgh (55.98°N–3.40°E) to Dornoch (57.89°N–4.08°E) in Scotland from 2014 to 2018. Six to eight nest boxes (front-opening Schwegler 1B with 26 mm entrance holes located 141 mm above the outer bottom of the nest box and a 120 mm internal diameter) were placed at 44 different sites along this transect; 40 sites were installed for the period 2014–2016 (Shutt et al. 2018) with a further four

added in 2017. Pre-2017 all but one site had six nest boxes, and post-2017 the number of nest boxes was increased to eight at most sites. Nest boxes were placed at approximately 40 m intervals, ca 1.5 m off the ground and facing away from the prevailing south–west wind. Nest box location was determined using a handheld GPS and site elevation was obtained from the Google Maps elevation API, with elevations ranging from 10 to 433 m a.s.l. (Shutt et al. 2018).

Each site was visited every two days from mid-March (2014–2015) or early April (2016–2018) until the breeding season had finished (early- to mid-June). We decided to use nest height (mm) as a proxy for the complete nest structure as it is possible to measure height before the nest is altered by the presence of offspring. Furthermore, taller nest heights correlate with increased thermal insulation (Alabrudzińska et al. 2003), humidity (Wesołowski et al. 2002) and light (Podkowa and Surmacki 2017), all of which are beneficial to the offspring. Although the nest lining is likely to play a larger role in thermal insulation, the moss base which contributes to the height may also confer thermal benefits (Mainwaring and Hartley 2009). Nest height was measured at each visit from the first visit in which nesting material was found in a nest box (either the first or second day of nest building) until the first egg was laid, and the dates of commencement of both nest building and egg-laying were recorded in ordinal dates. Nest height was recorded using a ruler placed at the outside of the nest box to the topmost point of the nest, discounting straggly parts (Fig. 1). In 2014, nest height was measured from the inside of the nest box, but this was changed to the current method to improve between-recorder accuracy as the bottom of the nest box is more repeatedly determinable than

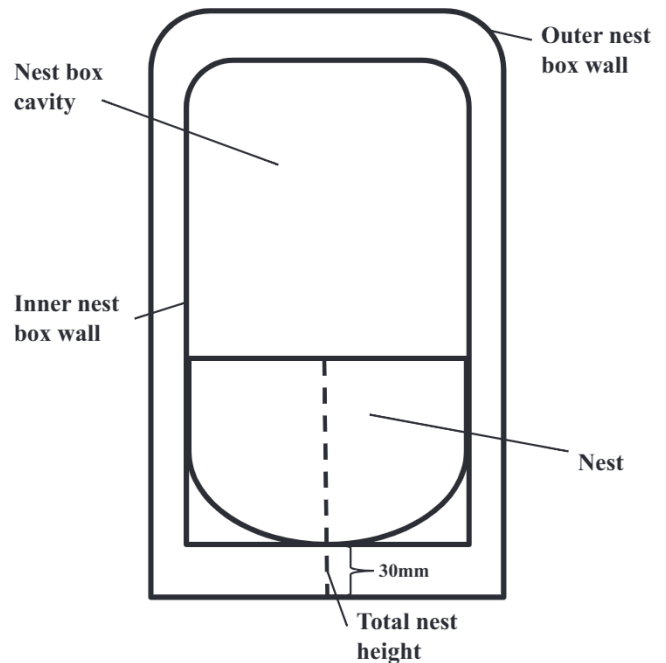


Figure 1. Illustration of nest box height measurements. The dotted line indicates the height which was measured (in mm).

the top of the inside. To correct for this difference in technique, the average height of the lower ledge of the nest box (30 mm) was added to the 2014 height measurements. We chose this particular method of measuring nest height based on anecdotal evidence that stray strands of nesting material hanging down through the gap to the front of the nest box made it difficult to determine the exact bottom of the nest without disturbing it. As we wanted to limit disruption to the nest, we chose to measure to the exact bottom of the nest box instead. We anecdotally found this to be more appropriate for repeatable between-observer measurements.

The ordinal date of the first egg laid in every nest box was recorded based on whether one or two eggs were present, assuming a one-egg-per-day lay-rate (Perrins 1980). Adult birds were caught and individually identified by a metal ring when the chicks were over 10 days old. The percentage of adults caught increased from 2014 to 2018, from 63.5% of adults caught in 2014 to 85.5% caught in 2018, with the mean identification rate across all years being 73.8%. Temperature data was available for each site from two iButton dataloggers (Maxim: DS1922L) accurate to a resolution of 0.0625°C and placed at opposite ends of each site from mid-February, recording every hour. They were placed in water-tight cylinders on the north side of trees, with a hole at the bottom to allow ambient air circulation (Bell 2014, Shutt et al. 2019).

Statistical analyses

All analyses were carried out in R (<www.r-project.org>). To establish the causes of variation in nest height, we used a linear mixed-effects model (LMM), using the packages `lme4` (Bates et al. 2015) and `lmerTest` (Kuznetsova et al. 2017). We included three fixed effect predictors that captured various aspects of breeding phenology: the annual mean first egg date across all sites to control for early versus late seasons (year mean FED), the annual mean phenological deviation of each site from the study-wide annual mean first egg date to capture spatial variation in phenology between sites (site-year deviation FED), and the deviation of each nest box from the site-year mean to capture between-individual variation in phenology within a site and year (relative FED) (van de Pol and Wright 2009). In addition, we included mean site latitude, mean site elevation and the mean site minimum temperature in the 14 days before the first egg was laid as fixed effects. Year, female parent identity, male parent identity, nest box location, site and recorder were treated as random effects. Parental identity was included as individuals may survive from year to year and may even return to the same site or nest box in different years. Where a parental identity was unknown it was assigned a unique identifier, so that nest height observations with missing parental information could be retained in the model. The temperature variable was selected after model comparison of the mean and minimum temperatures in the seven- and fourteen-days pre-egg-laying via Akaike information criteria (AIC) (Burnham and Anderson 2004). These two potential time periods were selected based on anecdotal observations of

bird activity pre-nest building, previous research which shows that the temperature pre-FED can influence nest structure, and AIC testing (Britt and Deeming 2011). This led to different temperature variables being retained for the nest height and nest building duration models.

The variables described above were chosen to best answer our question of how environmental and individual characteristics may be associated with nest height. Year mean FED determines whether breeding began early or late across all sites, whereas the site-year deviation FED determines whether breeding began early or late at that site compared to the other sites in that year. The relative FED then determines whether the breeding phenology for that nest was late or early compared to the other nests at that site. These variables are included to determine if and how phenology impacts on nest building. Latitude and elevation measurements were site-specific, as variation in elevation and latitude between nest boxes at the same site was negligible. We mean-centred all continuous variables to ease interpretation of the results (Schielzeth 2010).

In addition to the fixed effects, we also included several random terms to capture structure in the data. Female and male identity were included as random effects because there were birds which nested in the focal nest boxes across multiple years. These variables also allow us to determine (and control for) whether individual female birds build similar nests across years, and whether the presence of certain male partners influences the structure of the nest the female builds. The nest box term accounts for variation in the microhabitat surrounding the nest, as well as variation between the nest boxes themselves, while the site term encompasses variation in the broader habitat and conditions. The year term was included to account for variation in the different breeding seasons.

To determine what factors relate to variation in nest building duration, we used a second LMM that included individual nest deviation from the global mean FED (henceforth 'individual FED'), site latitude, site elevation, nest height and the mean site temperature in the seven days before the first egg was laid as fixed effects, and year, nest box, female parent identity and nest height recorder as random effects. We used individual FED across all years in this model, as our more specific phenology variables used in our first model led to this second model becoming over-saturated and rank deficient. Nest building duration was calculated as the date at which the final nest height ± 3 mm was reached minus the date of first recorded nest building. The final nest height ± 3 mm was used as the birds tend to alter the shape of the nest (usually by flattening it out at the front) before laying eggs, without adding more material, as well as to account for any potential measurement error.

Results

The nest heights ranged from 48 mm to 128 mm, with an average height of 83.94 mm \pm 0.42 mm standard error

(heights include 30 mm comprising the base of the nest box). The smallest nest was therefore only 18 mm high, and while an outlier, it was not excluded as eggs were laid and chicks successfully hatched. Mean annual first egg dates ranged from day 117.8 in 2014 to day 126.2 in 2016. In years where breeding commenced earlier, nests were larger, with nest height predicted to increase from a mean of 82.24 mm in the year with latest annual mean FED to 87.82 mm in the earliest (LMM, slope = -0.736 ± 0.154 , $p < 0.001$) (Table 1, Fig. 2A), while the timing of egg-laying between and within sites are not related to nest height (LMM, slope = -0.006 ± 0.010 , $p = 0.952$; slope = -0.051 ± 0.090 , $p = 0.569$, respectively) (Fig. 2B–C). Although the effects of elevation (LMM, slope = 0.010 ± 0.006 , $p = 0.0914$) (Fig. 2D) and latitude (LMM, slope = 1.469 ± 0.940 , $p = 0.119$) are non-significant, there is a weak trend for larger nests at higher elevations and more northerly sites (Fig. 2E). There is no relationship between the minimum temperature pre-egg-laying and nest height (LMM, slope = -0.241 ± 0.231 , $p = 0.297$).

Based on the random terms we see that the nest height varied substantially among different females, as well as between nest boxes (Table 1, Fig. 3). However, there was very little variation among males, sites, years or nest height recorders (Fig. 3). The estimate of among-female variance in nest height is consistent with 95% of females building nests that vary in the range of ± 15.06 mm.

Nest building duration ranged from 1 day to 43 days, with an average duration of 10.6 ± 7.4 days. When the first egg date was earlier, birds spent less time building their nests than when it was later (Table 2, Fig. 4A) (LMM, slope = 0.096 ± 0.047 , $p = 0.039$), consistent with a 4.32 day increase in average nest-building duration between day 100 and day 145 (the minimum and maximum FEDs in the model). Furthermore, nests which took more time to build were taller (LMM, slope = 0.178 ± 0.0099 , $p < 0.001$) (Fig. 4B). There is no relationship between nest building duration and elevation (LMM, slope = 0.002 ± 0.003 , $p = 0.517$) (Fig. 4C), but

at higher latitudes, nest building took longer than at lower latitudes (LMM, slope = 1.531 ± 0.508 , $p < 0.01$) (Fig. 4D). There was no relationship between the mean temperature in the seven days pre-egg-laying and nest building duration (LMM, slope = 0.044 ± 0.151 , $p = 0.768$) (Fig. 4E). The variance of the random effects suggests that nest building duration varied between different females, as well as between years (Table 2, Fig. 5). However, there was very little variation between nest boxes or nest height recorders (Fig. 5).

Discussion

We found evidence that both the duration of nest building and the final nest height are correlated with annual differences in egg-laying phenology and the builder's identity, and nest building duration is also influenced by latitude. When egg-laying commences earlier, nests are built higher. Furthermore, nests with earlier FEDs tend to be built faster. However, within and between years, taller nests take longer to build, contrary to our predictions and previous findings (Mainwaring and Hartley 2008), as we expected later breeders to spend less time building in order to catch up with the caterpillar peak. It is possible that it is a plastic response of the female parent to build taller nests if breeding commences earlier, guarding against possible cold spells during the incubation period, and that these nests are built faster due to a reduced amount of time before egg-laying commences.

Female identity explained a large proportion of the variation in nest height as well as nest building duration, supporting recent findings in different populations of blue tits that individual females are consistent in their own nest construction, but that differences exist between individuals (Järvinen et al. 2017a, O'Neill et al. 2018). It is thus possible that the nest is a component of the extended phenotype of the builder and reflects the quality or personality of the individual (O'Neill et al. 2018). There was also a large amount of variation in nest height between different nest boxes, and a similar effect of nest box identity on nest height was found by O'Neill et al. (2018). Nest building duration also differed between the different years studied, possibly as an effect of spring phenology or due to inter-year differences in temperature or rainfalls.

We found no relationship between nest height and the minimum temperature in the fourteen days pre-egg-laying, or nest building duration and the mean temperature in the seven days pre-egg-laying, possibly because when birds breed earlier in warmer years (Shutt et al. 2019) they may reduce the thermal insulation during the nesting phase. However, this result could also be evidence that the nest height plays a minimal role in nest insulation, compared to the nest cup lining, which we did not analyse in this study. We did find some evidence that nests at higher elevations and latitudes may be larger, which may be due to temperature, although this trend was non-significant. It is possible that nest size trends do exist but are more apparent on larger geographical scales, as another study over a larger latitudinal scale (7°) did find

Table 1. Effects on nest height. Slopes (coefficient) are shown with their associated standard errors (SE) from the full LMM. FED = first egg date. The significant slope is given in bold ($p < 0.001$).

Fixed term	Coefficient \pm SE
Intercept	84.22 \pm 0.721
Year mean FED	-0.736 \pm 0.154
Site-year deviation FED	-0.006 \pm 0.099
Relative FED	-0.051 \pm 0.090
Elevation	0.011 \pm 0.006
Latitude	1.469 \pm 0.940
Minimum temperature	-0.241 \pm 0.231
Random term	Variance (estimate)
Female ID	58.90 (41.15–75.57)
Male ID	0.45 (0.00–9.753)
Nest box	20.25 (10.32–31.64)
Site	0.00 (0.00–4.92)
Nest height recorder	1.68 (0.00–9.35)
Year	0.00 (0.00–2.08)
Residual	41.20 (28.72–55.92)

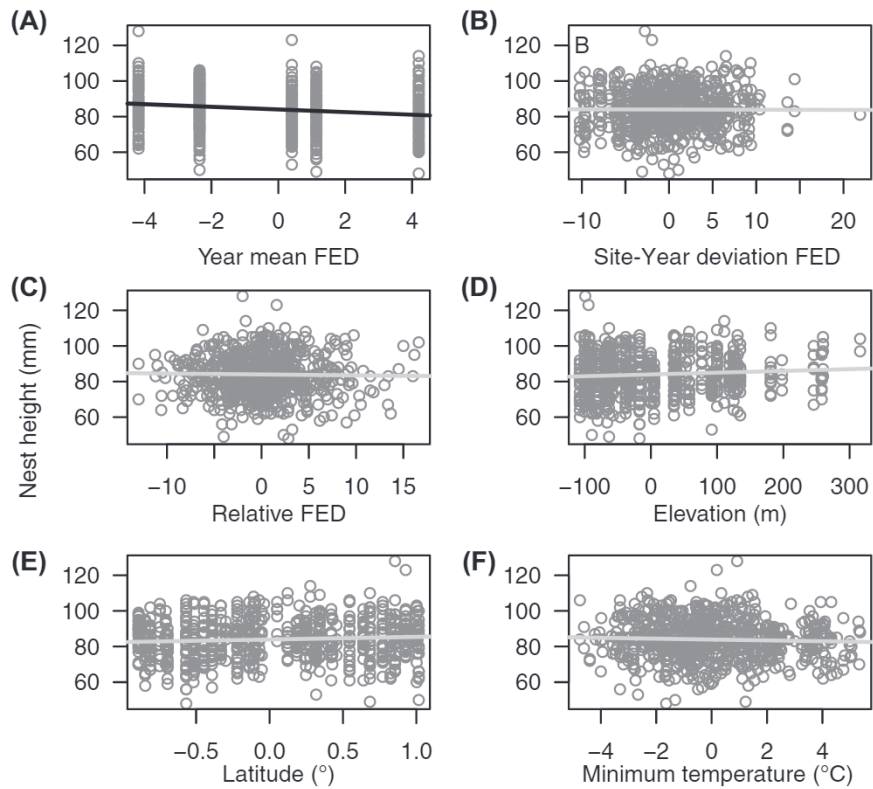


Figure 2. Relationships between nest height and (A) year mean FED, (B) site deviation FED, (C) nest box FED, (D) elevation, (E) latitude, (F) minimum temperature in the 14 days pre-egg-laying. Black lines show significant LMM slopes, whereas grey lines show non-significant trends. All continuous variables were mean centred.

that birds at lower latitudes built nests with lower insulatory capabilities, although they adjusted this through changes in wall thickness rather than height (Mainwaring et al. 2014). Previous research in our study system has found that blue tits delay egg-laying at higher elevations (Shutt et al. 2019), thus

the birds may be phenologically tracking the thermal niche without alterations to the nest structure (McGowan et al. 2004, Järvinen et al. 2017b). Furthermore, we found that birds nesting at higher latitudes take longer to build their nests, independent of nest height, possibly to ensure that the nest is capable of insulating the eggs against colder temperatures at the higher latitudes, or to adjust for differences in photoperiod. Potentially, the quality of insulating materials increases at higher latitudes, rather than the total material mass or height, but finding enough of such materials (like

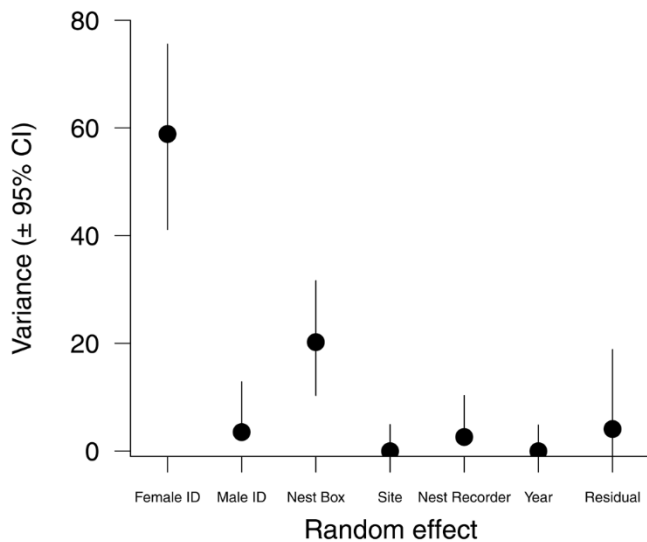


Figure 3. Nest height variance accounted for by random effects. 95% CIs were calculated using likelihood profiles.

Table 2. Effects on nest building duration. Slopes (coefficient) are shown with their associated standard errors (SE) from the full LMM. The significant slopes are given in bold ($p < 0.05$).

Fixed term	Coefficient \pm SE
Intercept	11.05 \pm 1.096
Individual FED	0.096 \pm 0.047
Nest height	0.178 \pm 0.099
Elevation	0.002 \pm 0.003
Latitude	1.531 \pm 0.508
Minimum temperature	0.044 \pm 0.151
Random term	Variance (estimate)
Female ID	4.56 (0.50–9.21)
Nest box	0.00 (0.00–2.49)
Nest height recorder	0.76 (0.00–3.61)
Year	5.14 (0.79–21.46)
Residual	43.59 (37.19–51.65)

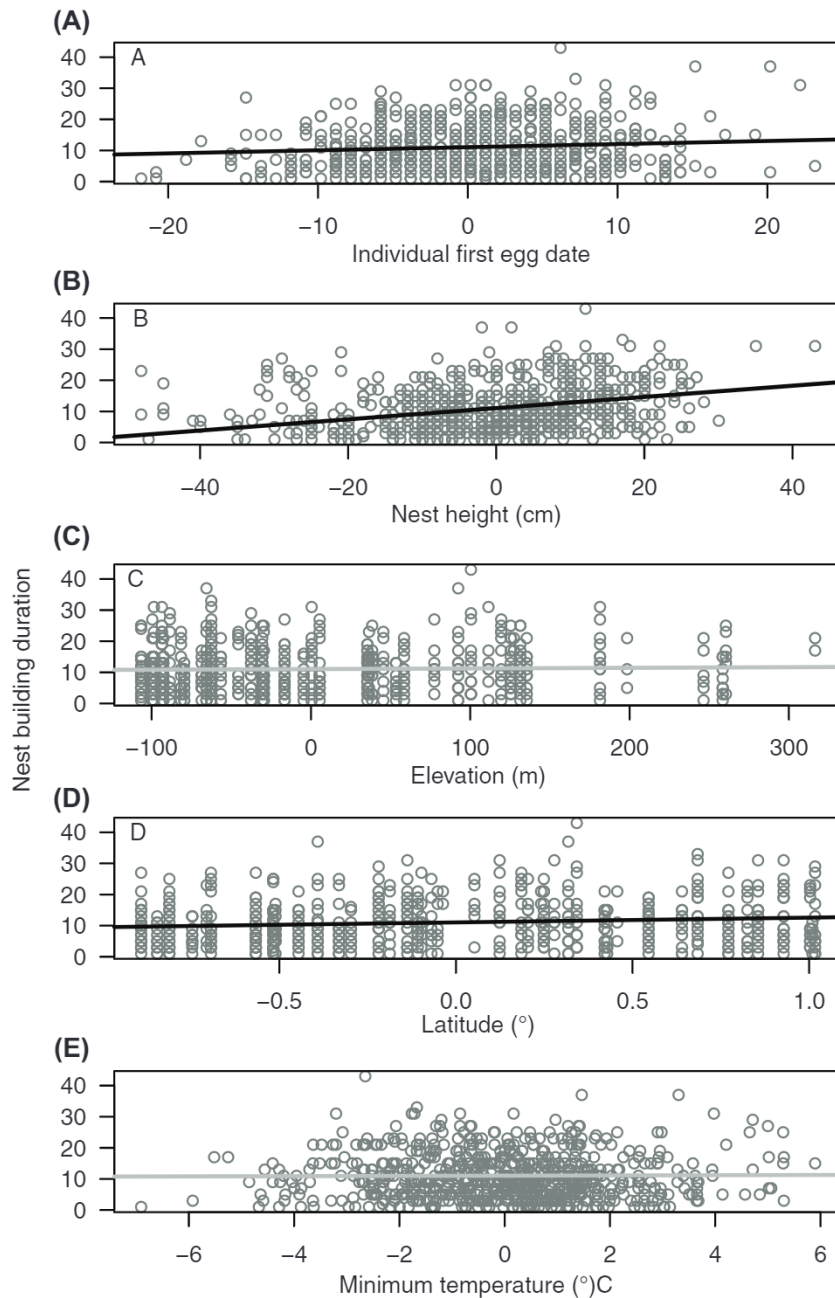


Figure 4. Relationships between nest building duration (in days) and (A) individual first egg date, (B) nest height, (C) elevation, (D) latitude, (E) minimum temperature in the seven days pre-egg-laying. Black lines show significant LMM slopes, whereas grey lines show non-significant trends. All continuous variables were mean centred.

feathers and hair) may take longer thus increasing building duration (Mainwaring and Hartley 2008, Harničárová and Adamík 2016). It is possible that there is also an effect of latitude on nest height, but that the effect size is small such that it only becomes apparent over larger distances (Mainwaring et al. 2012).

There was no effect of the site-year deviation FED, nor the relative FED, on nest height. Previous studies in both blue tits and other species have also found no effect of first egg-laying date on nest structure (Lambrechts et al. 2016,

Järvinen et al. 2017b, O'Neill et al. 2018), although nest characteristics are known to vary seasonally (McGowan et al. 2004, Mainwaring and Hartley 2008). However, as we did find an effect of the year mean FED, it appears that the timing of egg-laying does influence nest height across a much larger scale than previously researched, though we caution that this correlation is based on five years only.

Temperature is known to decrease with increasing latitude and elevation but none of these factors are correlated with nest height in our study. Given that the same variables have

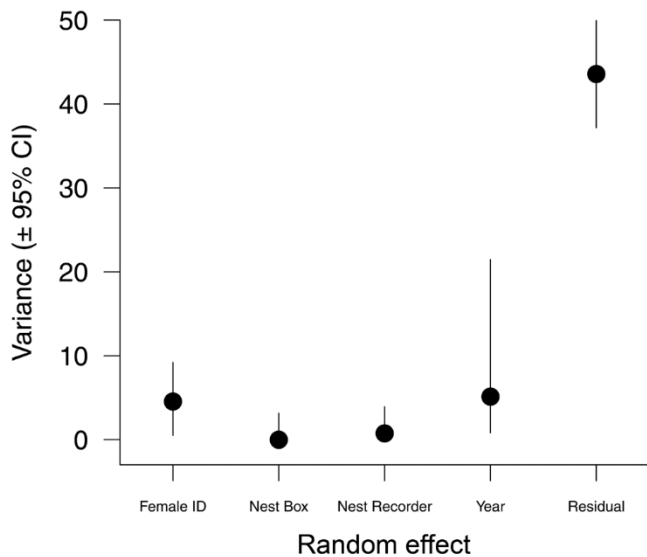


Figure 5. Nest building duration variance accounted for by random effects. 95% CIs were calculated using likelihood profiles.

been shown to be correlated in previous studies in both blue tits and other cavity nesting passerines (Mainwaring et al. 2012, 2014, Schöll and Hille 2014) this suggests that there is either no universal pattern in the relationship between environmental factors and nest characteristics (at least not in cavity nesting passerines), or that the geographical extent of our study was insufficient to capture the trends previously described. An alternative suggestion is that the birds' phenology tracks spring temperature so that conditions are quite constant in space and time, and therefore there is no need to build bigger nests, or to build faster. Lastly, as elevation did not appear to influence the nest height or building duration, it may be possible that the building period is affected more by photoperiod, specifically the duration of night and twilight periods, than temperature alone.

The individual quality hypothesis and the thermoregulation hypothesis may work in conjunction, for example by an increased parental investment into reproduction when thermoregulatory needs are greatest (García-López de Hierro et al. 2013, Mainwaring et al. 2014). We have found evidence that much of the variation in both nest height and nest building duration is influenced by the female parent, but not the male parent. This is perhaps not surprising, as blue tit males do not assist in building the nest (Perrins 1980), but it does suggest that the individual's quality may not be the driving factor for changes in nest height. Feather-carrying by male blue tits has however been shown to cause the female partner to increase the clutch size post-mating, while males from ornamented nests also increased their provisioning rate to the offspring (Sanz and García-Navas 2011). The individual quality hypothesis may thus be more applicable to nest composition, rather than structure, where it may play a smaller role.

We have shown in this study that there is an effect of the year mean FED on nest height. This implies that, although large-scale environmental factors may not impact nest

structure, blue tits are likely able to plastically alter their nest height based on spring phenology. A future study evaluating whether there is an effect of nest characteristics such as height on offspring and parental fitness will be beneficial in establishing whether future changes in climate will impact the species at the population level. In order to establish whether nest height and the phenology mediated plasticity in nest height is adaptive experimental manipulations of nest height and insulation properties in the field are required. Järvinen et al. (2017b) found that manipulating nest height did not affect either offspring or female parental condition, thus suggesting that nest height does not directly influence fitness. However, the manipulations to nest height were done several days after hatching. Future research where nest height is manipulated during or before incubation may show different effects, as there is evidence that birds prefer to build larger nests, possibly to provide a thermodynamic benefit (Mainwaring and Hartley 2009, Mainwaring 2017) which may only be influential during the incubation phase. However, such manipulations may increase the rate of nest abandonment, which should be taken into consideration.

In conclusion, we demonstrate that the annual mean timing of egg-laying influences nest height in multiple populations of blue tits and provide evidence that female parental identity influences the intraspecific variation in nest height. Furthermore, we show that nest building duration increases with increased FED, nest height and latitude.

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Author contributions

Dagmar der Weduwen: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Investigation (supporting); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Katharine Keogan:** Investigation (equal); Project administration (equal); Supervision (equal); Writing – review and editing (supporting). **Jelmer Samplonius:** Investigation (equal); Project administration (equal); Supervision (equal); Writing – review and editing (supporting). **Albert Phillimore:** Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Validation (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Jack Shutt:**

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Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.b5mkkwhcb>> (der Weduwen et al. 2020).

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