BioOne DIGITAL LIBRARY

Great Tits Parus Major Adjust Nest Size to Weather Experienced Prior to Start of Nest Building

Authors: Mazgajski, Tomasz D., Gołębiewska, Aneta, and Chylarecki, Przemysław

Source: Acta Ornithologica, 59(1) : 35-52

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/00016454AO2024.59.1.004

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

ACTA ORNITHOLOGICA
Vol. 59 (2024) No. 1

Great Tits *Parus major* adjust nest size to weather experienced prior to start of nest building

Tomasz D. Mazgajski*, Aneta Gołębiewska & Przemysław Chylarecki

Museum and Institute of Zoology, Polish Academy of Sciences, Twarda 51/55, 00–818 Warszawa POLAND
*Corresponding author, email: tmazgajski@miiz.waw.pl

Mazgajski T. D., Gołębiewska A., Chylarecki P. 2024. Great Tits *Parus major* adjust nest size to weather experienced prior to start of nest building. Acta Ornithol. 59: 35–51. DOI 10.3161/00016454AO2024.59.1.004

Abstract. Intraspecific variation in nest size received considerable attention in the last two decades. A number of studies of small passerines found that nests built at lower ambient temperatures were larger than those built at higher temperatures. As larger nests, although costly, provide a better thermal environment for eggs and small nestlings, this has been interpreted as adaptive phenotypic plasticity. Yet, a comparable number of studies failed to confirm the relationship between temperature and nest size. We used data from a nest box population of Great Tits *Parus major* breeding in central Poland to test the possible effect of temperature on nest size built by females with multiple nests measured during a 3-year study. Using the sliding window approach, we identified the exact time window for which the given weather variable best explained the variation in the nest trait, in addition to that already explained by study year, clutch type (first or second) and female identity. For each nest trait and weather variable, we tested all possible time windows over a 30-day period prior to the first egg laying date (FED). We found that for the studied Great Tit population time windows of sensitivity of nest traits to temperature opened 19–24 days before FED and closed 6–15 days before FED. Maximum daily temperature was consistently a better predictor of nest size characteristics than either minimum daily temperature or mean daily temperature. For precipitation, the only significant sensitivity window opened 27 days before FED and closed 3 days before FED. Thus, temperature sensitivity time windows opened 5–10 days before the start of nest building and lasted no longer than halfway through the building period. Temperature effects were only detectable after accounting for the strong effects of female identity on nest size. The failure to observe temperature effects on nest size in some previous studies may be explained by considering temperatures during nest building rather than some time earlier, or by ignoring persistent female effects on nest size in the analyses.

Key words: cavity nesters, phenology, nest building, nest size, nest traits, tits, female effect, sliding windows, climwin

Received — Mar. 2024, accepted — Aug. 2024

INTRODUCTION

The timing of reproduction plays a central role in models of birds' breeding effort optimisation, as the decision of when to start breeding has multiple consequences for individual fitness (Daan & Tinbergen 2007, Verhulst & Nilsson 2008, Williams 2012). In general, parent birds should synchronise their reproduction with the seasonal peak of food availability, which is typically late spring in many ecosystems (Daan et al. 1989). More specifically, females should time egg laying in such a way that hatching overlaps with the period of highest food availability, when the energy requirements of rapidly growing nestlings are the greatest. Thus, proper brood timing requires the female to make a correct decision several weeks in advance about when exactly to start laying eggs. This is even more challenging as the timing of seasonal peaks in food availability varies from year to year, often quite considerably, depending on local weather conditions. For example, the peak of larval biomass, a key food resource for breeding tits, can vary by about 30 days between earliest and latest springs (Both & Visser 2005, Charmantier et al. 2008). Consequently, Marsh Tits *Poecile palustris* lay eggs 26 days earlier in the warmest springs than in the coldest springs (Wesołowski 2023), while Great Tits *Parus major* show a difference of about 25 days between the earliest and latest seasons (Charmantier et al. 2008, Glądalski et al. 2016).

Clearly, birds about to start egg laying in early spring must rely on some environmental cues (Chmura et al. 2019) to adjust the exact date of

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

laying the first egg to the expected time period of increased food availability a few weeks later. A considerable body of research exists showing that while the photoperiod acts as a proximate constraint, spring phenology (indexed, e.g., by tree bud burst or insect availability), precipitation and ambient temperature can all act (or interact) as primary cues for the timing of breeding, enabling birds to successfully adjust laying dates to eventually track the inter-annual variation of resource pulses (Charmantier et al. 2008, Thomas et al. 2010, Williams 2012, Phillimore et al. 2016). Ambient temperature was found as the main cue used by birds breeding in temperate climates, while the effect of precipitation was stronger among birds breeding in tropical climates (Cohen et al. 2018). For many bird species, at the population level, warm springs have been shown to advance laying dates, while cold springs delayed the onset of laying (Dunn & Winkler 2010, Dunn 2019, McLean et al. 2022). However, the extent of these adjustments may sometimes be imperfect in relation to associated shifts in the timing of peak food supplies (the mismatch hypothesis; Both 2010).

Most research on the adaptive value of reproductive timing revolves around the egg laying date as the key decisive event that effectively determines the timing of other reproduction stages. Indeed, once the female has laid the first egg in a clutch, and especially has started to incubate, her possibilities of shifting the timing of other reproductive stages — in particular hatching date or the date of the brood's maximum energy demands — are severely limited (but see Cresswell & McCleery 2003). However, it is not actually the laying date that sets the clock here. For many birds species, including the vast majority of passerines, the decision of when to lay the first egg is preceded by the decision of when to start nest building. Tits and other small hole-nesting passerines usually take some 10–15 days to build a nest (Smith et al. 2013), which is at least twice as long as the duration of egg formation started by the rapid follicle growth phase (4–5 days for the Great Tit; Kluyver 1951, 1952, von Haartman 1990). This means that the key decision about reproductive timing is linked to the onset of nest building. The distinction is not as trivial as it may seem, as the date of starting nest building need not be tightly linked to the date of starting egg laying (Wesołowski 2013). Marsh Tits that start nest building on the same day may differ in egg-laying date by some 10–20 days (Wesołowski 2013).

In sharp contrast to the timing of egg laying, our knowledge of the factors influencing the timing of nest building is rather limited. We can only speculate that similar cues to those used for egg laying may be involved. Indeed, ambient temperature was found to influence the onset of nest building in tit species (Wesołowski 2013, Shutt et al. 2019), although bud burst was not (Shutt et al. 2019). However, the timing of nest building is important not only because of the time constraints involved in laying eggs at the "right" time. The data accumulated over recent years indicate that nest characteristics can be treated as an extended phenotype of the nest builders, mostly females (Hansell 2000, 2005; Woods et al. 2021; see review in Deeming 2023). Nest characteristics have been found to be repeatable across females (Jarvinen et al. 2017, O'Neill et al. 2018, der Weduwen et al. 2021) and to have high selective value by enhancing breeding success (e.g., Powell & Rangen 2000, Alabrudzińska et al. 2003, Alvarez & Barba 2008, Jelinek et al. 2016, Lambrechts et al. 2017). In general, larger nests provide better thermal conditions during incubation and chick rearing (Campbell et al. 2018, Lambrechts & Caro 2022). Consistent with this, birds of the same species breeding in harsher climates build larger nests than birds nesting in milder climates (e.g., Rohwer & Low 2010, Crossman et al. 2011, Perez et al. 2020).

However, building larger nests is costly in terms of time, energy and exposure to predators (Hansell 2000, Antonov 2004, Moreno et al. 2008, Mainwaring & Hartley 2013, Wysocki et al. 2015), suggesting that the actual size of the nest should reflect some sort of optimisation. Larger nests, which provide better thermal conditions during the later stages of reproduction, take longer to build (Wysocki et al. 2015, der Weduwen et al. 2021). This means that ambient temperature may have a dual effect on nest building. Low temperatures should delay the onset of nest building, but at the same time should induce the construction of structurally larger nests that take longer to build. This would result in an even longer delay in the date of first egg laying. Surely by manipulating the rate of nest building (der Weduwen et al. 2021), birds can still fine tune the timing of egg laying. But in any case, the whole process may be more complicated than just optimising the laying date in accordance with available cues, while simply starting the whole exercise a number of days earlier to allow for nest building (cf. Shutt et al. 2019).

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Whether and how universally larger nests are actually built in response to lower ambient temperatures is unclear, as the evidence is mixed. Campbell et al. (2018) experimentally demonstrated that Zebra Finches *Taeniopygia guttata* build larger nests when housed in colder conditions, although another study found that this can be modified by the birds' experience (Edwards et al. 2020). Britt & Deming (2011) found a relationship between air temperature and nest mass for Blue Tits *Cyanistes caeruleus* but not for Great Tits, while Deeming et al. (2012) found the opposite in the same species. On the other hand, Mainwaring et al. (2012) and Lambrechts et al. (2016a) failed to find a correlation between ambient temperature and nest size (mass) for the same two tit species. While somewhat puzzling, this discrepancy may be explained by at least three mechanisms. First, most authors have examined ambient temperature during nest building or especially during the last phase of nest building (mostly a week before the first egg has been laid (e.g., Britt & Deeming 2011, Deeming et al. 2012, Wysocki et al. 2015, Lambrechts et al. 2016a). Yet, it is quite possible that individual decisions on nest size are shaped by cues occurring mostly before the start of nest building, as in the case of the egg laying date. In this scenario, the correlations reported in the literature can only occur in cases where these conditions persist into the nest building period.

Second, variation in nest size was shown to have a strong relationship with the identity of the female, as individual birds consistently build larger or smaller nests (Järvinen et al. 2017, O'Neill et al. 2018). Failure to account for individual variation during the analysis may obscure the signal associated with the possible effects of other factors (including weather), which may further contribute to the mixed results reported in recent years. Similarly, nest size was shown to depend on female age (e.g., Glądalski et al. 2024), condition (Mainwaring & Hartley 2009, Smith et al. 2013) or experience (Wysocki et al. 2015, Edwards et al. 2020), and the effects of these factors, if not controlled (statistically or experimentally), may overshadow the effects of temperature.

Third, another area that may give rise to conflicting results relates to the choice of cues used to assess periods of sensitivity. While different temperature metrics (e.g., daily maximum, daily mean and daily minimum temperatures) tend to be highly correlated, this is not always the case, and they may still convey different information. In particular, mean temperatures may be worse predictors of ecological phenomena than means and variances acting jointly (Zimmermann et al. 2009, Vasseur et al. 2014), primarily due to the asymmetrical shape of organismal thermal performance curves (TPC; Martin & Huey 2008, Denny 2019). Given that daily maximum (or minimum) temperature can serve as a proxy for daily temperature variability, it may also be a better predictor in phenological settings, which involve ecophysiological processes (tree bud burst, insect development) subject to constraints imposed by TPCs (see Ruel & Ayres 1999) and used as cues by birds about to breed. While some authors seeking to find temperature effects on nest size have used multiple temperature indices in their analyses, many have used only a single temperature metric, usually the daily mean (e.g., Britt & Deeming 2011, Mainwaring et al. 2012, Wysocki et al. 2015). In addition to temperature, precipitation might also be important in determining nest size, but unfortunately it is rarely analysed. For hole nesters, large nests may provide better protection against flooding, which is relatively common in natural holes due to rainwater flowing into the nest along the trunk, and sap draining from the walls of the living tree (Wesołowski et al. 2002). A large amount of moss at the base of the nest, typical of tit species, can help to absorb water in such situations, with larger nests providing better protection against soaking.

Here we report on factors influencing nest size in a population of Great Tits, a small hole-nesting passerine breeding in central Poland. Only the female of this species builds the nest, whose base is made predominantly of moss, and cup is lined with fur and hair. We wanted to find out which weather variables might affect different aspects of nest size in our study population, and especially what time period before egg laying should be considered in nest size-weather analyses. We systematically searched all possible time windows before egg laying, i.e., not only during nest building but also for some time before. We hoped to find that weather variables may indeed affect nest size, but that they may have gone undetected because the critical time windows of weather sensitivity occur well before nest building begins. To achieve this, we used systematic search routines and took advantage of a sample in which we were able to accurately account for the persistent effects of female identity by including multiple clutches laid by the same female. This paper does not explore other aspects of the relationships between nest size and female traits, but focused instead on the timing of possible weather effects on nest traits.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

METHODS

Study area and field methods

The study was conducted in 2019–2021 in an approximately 70-year-old mixed pine forest in Sękocin, about 10 km SW of Warsaw, central Poland (52°05 N, 20°52 E). Approximately 260 nest boxes are placed in 5 plots in parallel lines every 50 metres forming a grid. The boxes are made of wood with a hinged front wall for opening and the following internal dimensions: floor 11 × 11 cm (area 121 cm^2), height from bottom to entrance 21 cm. The boxes were placed about 2.5 m above the ground with entrances facing south (SE-SW). The most common hole nesters breeding in these nest boxes are Great Tits and, to much lesser extent, Pied Flycatchers *Ficedula hypoleuca*. About 40% of Great Tit pairs in the study population attempted two broods per year (Harnist 2017).

During the breeding season, nest boxes were checked every few days (ca 5–7) and the date of laying the first egg in the clutch (first egg date, FED) was determined either directly or calculated back from incomplete clutch sizes, assuming that one egg was laid per day. Adult Great Tits were caught in the period of feeding nestlings, measured (tarsus length, wing length), weighed and either ringed or identified by their existing ring. As a result, the identity of the females attending the nest was known, as was their record of previous breeding attempts. This enabled us to classify clutches of individual females as either first clutches of the year versus second or replacement clutches. More information about our study site and field methods can be found in Harnist et al. (2020) and Gołębiewska & Mazgajski (2024).

Great Tit nests were built in perforated plastic liners, so that they could be removed, weighed and measured without destroying the nest structure. Each nest was weighed and measured shortly after the start of incubation, i.e., on day 1–2 after the last egg in a clutch was laid. As both nest mass and linear measurements change throughout the nesting cycle of tits (Slagsvold 1989, Harnist et al. 2020), in line with recommendations for hole nesters (Dubiec & Mazgajski 2013, Harnist et al. 2020), we chose to take measurements early in the incubation period, long enough after the completion of nest building to allow any wet nest material to dry.

Nest mass was measured with a portable electronic scale to the nearest 0.1 g, while external measurements were made with callipers to the nearest 1 mm. We measured a number of parameters of each nest, including: (1) nest total height, from the bottom of the plastic liner to the top rim of the nest, separately along the front wall and back wall of the nest box; this is often called nest depth in other publications (O'Neill et al. 2018, Glądalski et al. 2024); (2) diameter of the nest cup (2 perpendicular measurements); (3) depth of the nest cup; (4) thickness of the nest walls at the upper rim of the nest cup (4 measurements); (5) nest bottom height, from the bottom of the nest cup to the bottom of the plastic liner; this is also called nest bottom depth or nest bottom thickness in other publications (Alvarez & Barba 2008).

To conduct the analyses in this paper, we used 3 of the 10 available nest parameters: nest mass, total nest height, and nest bottom height, to ensure comparability with the majority of published studies on the nest size of tits. As all nests were built in standardised nest boxes with the same floor dimensions, size differences between nests were mainly driven by differences in total nest height, although the latter parameter is effectively limited by the distance from the entrance hole (Mazgajski & Rykowska 2008). In any case, nest volume in this situation is a linear function of nest height. However, nest mass is not perfectly determined by nest volume, mainly due to the presence of variable amounts of air gaps in the nest (Deeming & Biddle 2015). Therefore, we decided to use nest mass as a separate parameter in our analyses. Total nest height was determined by the distance measured along the front wall of the nest, bearing in mind that the similar distance measured along the back wall is consistently smaller (Lambrechts et al. 2016b, own unpublished data). We used the nest bottom height (i.e., the depth of the nest base) as a separate variable of interest, as it has been hypothesised that tits may make the nest base of mosses in natural nest holes to serve as protection against nest flooding from rainfall, and as such may be of selective value (Wesołowski et al. 2002).

Breeding data

In 2019–2021 we found 199 Great Tit clutches in our nest box study area, but for a number of them we were unable to collect all the relevant data about breeding parameters and female identity. Therefore, as we wanted to analyse the dataset consisting of multiple nests constructed by the same females, we dropped records for nests with missing key breeding parameters or females that

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

were recorded only once. Consequently, for this analysis, we used data from 81 Great Tit clutches (44 first clutches and 37 second or replacement clutches) laid by 28 different females over 3 study years (2019–2021). Each female was represented by 2–5 clutches (mean = 2.89, SD = 0.88).

Weather data

We used daily weather data from the Warszawa-Okęcie meteorological station, located 8 km NE of the study area, obtained from the Polish Institute of Meteorology and Water Management — National Research Institute (https://danepubliczne.imgw.pl) via the 'climate' package (Czernecki et al. 2020). We used three indices of temperature (daily minimum temperature, daily average temperature, and daily maximum temperature) and one of rainfall (daily sum of precipitation), to model the relationship between the weather prior to egg laying and nest traits.

Statistical methods

All statistical analyses were conducted using R version 4.1.3 (R Core Team 2022). For each nest trait (nest mass, total nest height, bottom nest height), we started the analysis by fitting the baseline model (linear mixed model, LMM) explaining the variation in the response variable as a function of 3 predictors: study year (fixed factor), clutch type (first vs. replacement or second; fixed factor), and female identity (random factor). We then tested whether adding a weather variable aggregated over a time window (see below) as an additional predictor improved the model fit, as measured by the Akaike information criterion adjusted for small samples (AICc). Weather variables used as candidate predictors included daily minimum temperature, daily mean temperature, daily maximum temperature and daily total precipitation . We then used the sliding window approach implemented in the 'climwin' package (Bailey & van de Pol 2016, van de Pol et al. 2016) to identify the exact time window for which the given weather variable (e.g., maximum daily temperature averaged over the respective time window) best explained the variation in the nest trait of interest, in addition to that already explained by the baseline model. For each nest trait and weather variable, we tested all possible time windows over a 30-day period prior to the first egg date of a given clutch, i.e., 496 time windows ranging from 1 to 30 days (i.e., we used relative windows in 'climwin' notation). For different clutches, the associated time windows within a given year overlapped to a large extent, resulting in non-independent data points being entered into the models. Therefore, instead of taking the AICc of the best-supported model at face value and applying the classical information-theory criteria of model selection (Burnham & Anderson 2002), we used randomisation to determine the exact probability of obtaining a particular AICc value by chance given the data set (climwin::randwin function, 100 replications). We also used the Pc statistic provided by 'climwin' as an additional criterion for top model evaluation (with Pc < 0.5 suggestive of a weather signal in the data; Bailey & van de Pol 2016). Furthermore, with 496 competing models fitted for each nest trait–weather variable combination, we accounted for model selection uncertainty, by using model-averaged values defining the start and end of the time window of interest. So, instead of using the values provided by the best-supported model, we took an average from all models within the 95% confidence set, weighted by the Akaike model weights provided by 'climwin' (Helm et al. 2019).

Finally, to assess the sensitivity of our results to the inclusion of female identity effects, we repeated all sliding window analyses (3 nest variables as response, 4 weather variables as candidate predictors) with baseline models defined as simple linear models with effects of year and clutch type, i.e., ignoring the persistent effect of female identity present in the main analyses.

The proportion of variance in nest measurements explained by female identity in the baseline LMMs was estimated as unadjusted repeatabilities (also called enhanced agreement repeatabilities) in the 'rptR' package (Stoffel et al. 2017).

To estimate the daily dynamics of nest building, we used the data collected in the same study population in years 2012–2014, when we measured the nest mass of 25 nests every 2–3 days prior to egg laying, i.e., from day -15 to 0 (where 0 was assigned to FED), with each nest measured 4 to 10 times (I. Harnist et al. unpubl.). We then fitted a GLMM ('glmmTMB' package; Brooks et al. 2017) with beta distributed error to these data, using proportion of final nest mass as the response, and day before FED (fixed effect) and clutch identity (random effect) as covariates. We used estimates of day effect from this model to visualize the progress of nest construction against the estimated time windows of highest sensitivity.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

RESULTS

Weather during the study period and tit breeding statistics

The average daily mean temperature (*T_mean*) for April between 2019 and 2021 ranged from 7.0 °C to 10.6 °C, which was rather typical of the long-term average for this month (9.1 °C), while the average daily temperatures for May during our study tended to be slightly lower (12.0–13.6 °C) than the 1990–2018 average (14.2 °C). However, June temperatures were markedly higher (19.0–22.9 °C) than typically recorded over the reference period (mean 17.4 °C; Fig. 1A).

Daily maximum temperatures (*T_max*) averaged 9.9 °C (May) to 11.5 °C (April) higher than daily minimum temperatures (*T_min*). The two temperatures were highly correlated over three spring months and the entire data set ($r = 0.87$, $df = 271$, $p < 0.001$), but showed clearly weaker correlations (r from 0.64–0.73) within individual months. In April and May, daily maximum and minimum temperatures shared less than half of their variances ($r^2 = 0.48$ and 0.41, respectively).

Precipitation showed a more extreme pattern during our study period. April values were considerably lower than the long-term mean for two study years, and significantly higher in the third year. May precipitation was clearly above average in all three years. In 2020, the monthly sum of precipitation in June was three times higher than the respective average for the years 1990–2018. In the remaining two study years, June precipitation was more typical of the long-term variation (Fig. 1B).

FED distribution was clearly bimodal in all three study years. First clutches were initiated around 20 April (median Julian day = 109.5) and consisted of 9 eggs, while second and replacement clutches were laid on average on 05 June (median Julian day = 155) and consisted of 8 eggs (see Table 1 for more data).

Nest mass was highly variable, ranging from 10.7 to 54.5 g, with a coefficient of variation (CV) of 0.33. The smallest nest was 5 times lighter than the heaviest one in the studied sample. Nests from first clutches were generally heavier (31.85 g) than those from second or replacement clutches (24.38 g). Total nest height and bottom height showed the same pattern — extensive overall variability (CV = 0.25 and 0.42 respectively) with first nests being larger (higher) than second nests built in the season (Table 1). For all three nest variables analysed, additive LMMs (baseline models; see Methods) revealed that the effect of clutch

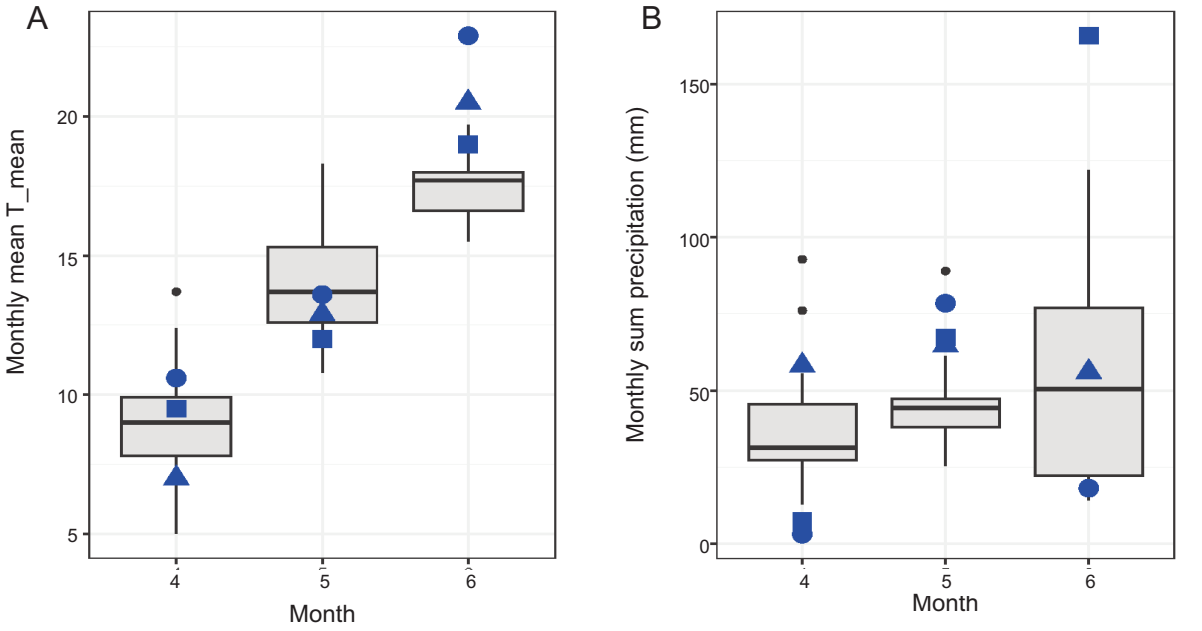

Fig. 1. Spring temperatures (A, left panel) and precipitation (B, right panel) during the study period compared to the long term averages. Shown are monthly averages of daily mean temperature (T_mean, left panel) and monthly sums of daily precipitation (right panel) for the study years 2019–2021 (blue symbols) and for the reference years 1990–2018 (box plots). Different blue symbols denote individual years (dots — 2019, squares — 2020, triangles — 2021). The lower and upper limits of the boxes are the 25th and 75th percentiles of the data, the midline is the median, and the hinges extend up to 1.5 of the interquartile range. Black dots indicate outliers.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Table 1. Breeding statistics of Great Tit clutches at Sękocin, 2019–2021 by clutch type (first vs second or replacement clutches). FED — date of first egg laid in the clutch (1 = 1 Jan.).

	First clutches (N = 44)			Second clutches (N = 37)		
Breeding parameter	mean	SD	range	mean	SD	range
FED (day of the year)	110.39	6.75	101–139	156.08	8.58	135–178
Clutch size	9.05	1.48	6–13	7.86	1.36	5–10
Nest mass (g)	31.85	9.59	16.7–54.5	24.38	7.35	0.7–44.8
Total nest height (mm)	108.26	21.10	71–160	92.85	26.98	36–144
Nest bottom height (mm)	62.13	20.60	23.2–102	51.66	26.42	5–103

type on nest size was highly significant ($p < 0.0001$ in all cases), while the effect of study year was not. However, the consistent differences between females explained most of the variation in each nest trait (unadjusted repeatabilities: nest mass — 27%, total height — 56%, bottom height — 57%).

Weather sensitivity time windows of nest traits

We found evidence of a significant relationship between Great Tit nest size and some weather variables within 30 days prior to clutch initiation in 6 out of 12 cases tested (3 nest measurements × 4 weather variables). Critical time windows of association between temperature variables and nest traits opened 19–24 days before FED, closed 6–15 days before FED and lasted 9–14 days (Table 2, Fig. 2). For precipitation, the only significant window of sensitivity opened 27 days before FED and closed 3 days before the first egg was laid. Increasing temperatures were associated with smaller and lighter nests, while increasing precipitation with heavier nests.

The baseline mixed model explaining variation in nest mass was significantly improved by the addition of minimum daily temperature averaged over days -19 to -14 ($p = 0.03$), or mean daily temperature over days -19 to -6 ($p < 0.001$), or maximum daily temperature over days -17 to -6 ($p < 0.001$) prior to the first egg date. A consideration of competing models with different window lengths (95% confidence set) resulted in slightly longer time windows: -21 to -11.1 for minimum temperature, -19.3 to -7.2 for mean temperature and -19.4

Table 2. Weather sensitivity time-windows for three nest trait variables as identified by the relative sliding window approach. For each nest trait/weather variable combination, the results of the best-supported model and the results averaged over models representing a 95% confidence set are provided. *T_min*, *T_mean*, *T_max* — daily minimum, mean and maximum temperatures respectively, averaged over the time-window duration; rain — daily precipitation sum averaged over the time-window duration; ΔAICc — difference between AICc of the top model and AICc of the baseline model (see Methods); P — significance of the result obtained by the randomization; Pc — alternative significance metric (see Bailey & van de Pol 2016).

	Best-supported model						Averaged model					
				Time-window (days prior to FED)			Time-window (days prior to FED)					
Nest trait variable/ weather variable	Δ AICc	P	Pc	Open	Close	Duration	Open		Close		Duration	
							Mean	SE	Mean	SE	Mean	SE
Nest mass												
T_min	-4.94	0.03	0.39	19	14	6	21.6	0.35	11.4	0.44	10.2	0.44
T_mean	-12.99	< 0.001	0.07	19	6	13	19.5	0.44	7.4	0.46	12.1	0.68
T_max	-16.41	< 0.001	0.05	17	6	11	20.0	0.65	6.2	0.51	13.7	0.78
rain	-18.61	< 0.001	0.05	30	2	28	26.9	0.85	2.7	0.34	24.2	0.93
Nest total height												
T_min	-5.03	0.18	0.47	22	15	7	22.5	0.30	10.1	0.37	12.4	0.39
T_mean	-8.62	0.15	0.33	23	16	7	24.1	0.30	12.3	0.47	11.8	0.54
T_max	-11.07	0.01	0.14	23	16	7	24.3	0.34	13.8	0.67	10.5	0.78
rain	-2.99	0.88	0.57	27	4	23	21.6	0.34	8.6	0.33	13.0	0.38
Nest bottom height												
T_min	-5.40	0.10	0.50	27	23	4	22.0	0.38	10.7	0.42	11.2	0.40
T_mean	-9.90	<0.001	0.27	23	16	7	23.7	0.40	14.1	0.59	9.6	0.66
T_max	-13.16	<0.001	0.07	23	16	7	24.0	0.38	15.0	0.56	8.9	0.72
rain	-4.36	0.59	0.52	24	7	17	22.1	0.33	8.0	0.32	14.1	0.40

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

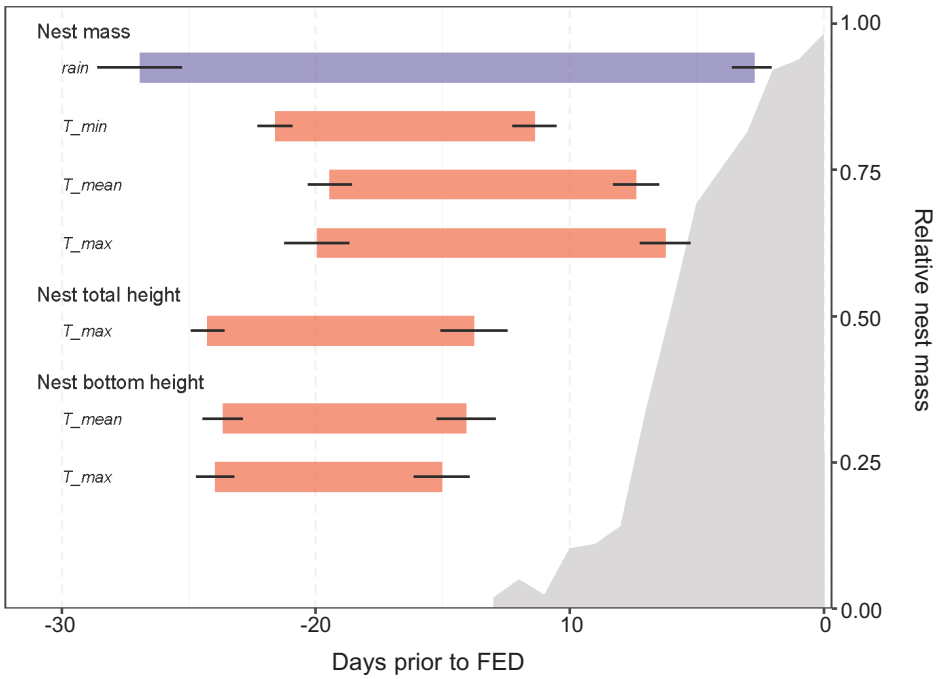

Fig. 2. Time windows of highest sensitivity of nest traits to weather variables, identified using the sliding window approach. The sensitivity windows (blue and red bars for precipitation and temperature variables, respectively) averaged over 95% model confidence sets are presented with standard errors (black lines) for their start and end dates. For comparison, the temporal dynamics of nest building in the study population is shown (grey contour; Harnist et al., unpublished data from 2012–2014, first clutches only), as measured by the cumulative proportion of final nest mass attained (right axis, Relative nest mass) by a given day before the first egg laying date (FED). See Methods for more details on the data and analyses behind the cumulative nest mass estimates.

to -6.3 for maximum temperature. Alternatively, daily precipitation averaged over 28 days (-30 to -2 for the best supported model) or 24 days before the first egg date (-26.9 to -2.7 for averaged competing models) offered comparable improvement ($p < 0.001$) over the baseline model for nest mass.

Total nest height was best described by a model that included, in addition to the effects of year, clutch type and female identity, a negative relationship with daily maximum temperature averaged over the window from day -23 to -16 before the first egg was laid. Permutations showed that, given the data, this result was unlikely to be obtained by chance ($p = 0.05$). However, this time window was not the only one that significantly improved the baseline model, with several windows extending more or less 1–3 days, providing comparable fit (as measured by delta AICc; Fig. 3). Averaging the models constituting a 95% confidence set resulted in an estimated window from day -24.3 to -13.8. For minimum and mean daily temperatures and mean daily precipitation, we did not find any time window that provided a significant improvement over the baseline model.

For nest bottom height, we found that both adding the mean daily temperature averaged over the window from day -23 to -16 or the maximum daily temperature averaged over a period from day -23 to -16 before the first egg was laid, produced models that were significantly better ($p = 0.01$ and $p < 0.001$, respectively) than the baseline model. As with the other weather variables analysed here, several time windows, slightly shorter or longer than those selected as the best, offered comparable improvement over the baseline model (Fig. 3). For maximum daily temperature, averaging parameter values across competing models (95% confidence set) resulted in a window extending from day -24.0 to -15.0 before the first egg date. For mean daily temperature, similar model averaging resulted in a window extending from day -23.7 to -14.1 (Table 2). Looking at daily minimum temperatures and mean precipitation, we did not find time windows that significantly improved the baseline model.

When the baseline mixed models were replaced by models without the persistent female identity effect, the only analysis that yielded

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

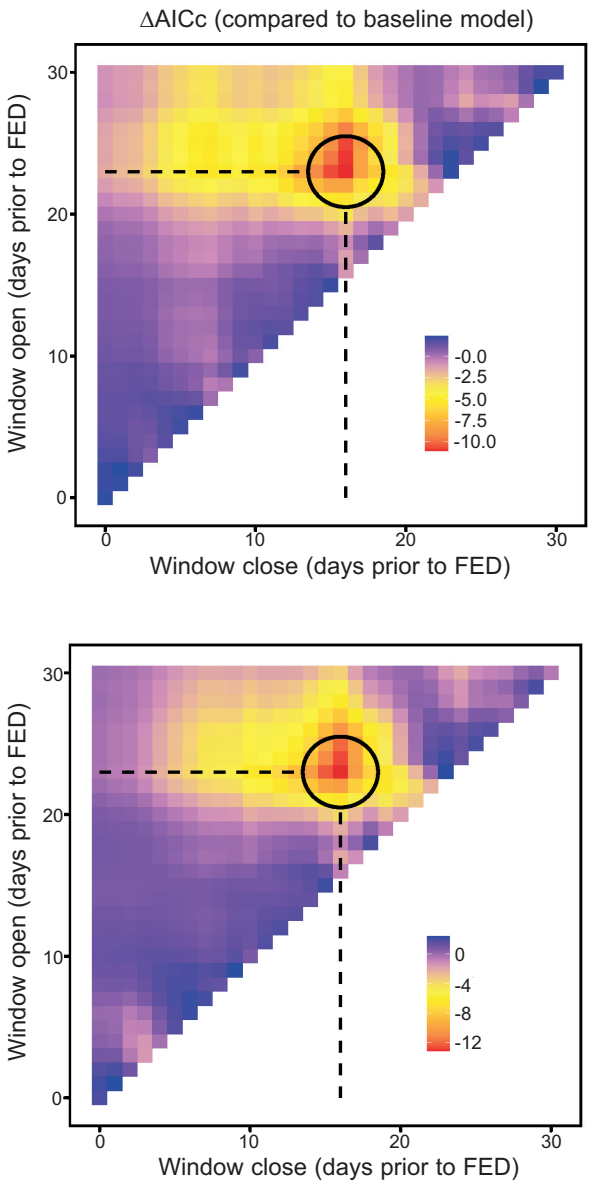

Fig. 3. Examples of heat maps presenting delta AICc (AICc of baseline model – AICc of model including a weather predictor) for all fitted weather sensitivity windows, as provided by 'climwin' (van de Pol et al. 2016). Upper panel — daily maximum temperature (*T_max*) and total nest height, lower panel — daily maximum temperature (*T_max*) and nest bottom height. Circles and dashed lines indicate the parameter combination that provides the best fit.

a significant result was the effect of averaged *T_max* on nest mass (best-supported model: $p < 0.001$, Pc = 0.51; sensitivity window of -17 to -5 days). In the remaining 11 cases, the addition of weather variables (averaged over a full range of possible windows) did not significantly improve the baseline models that only included the effects of year and clutch type.

DISCUSSION

We found that Great Tit nest size traits were related to weather conditions, in particular temperature indices averaged over time windows opening about 20–24 days before the first egg was laid. The addition of temperature variables measured during critical time windows significantly improved the fit of models explaining nest size traits as a function of the consistent effect of female identity, clutch type and year. In line with some previous results for Great and Blue Tits (Britt & Deeming 2011, Deeming et al. 2012) and Zebra Finches (Campbell et al. 2018, Edwards et al. 2020), higher and heavier nests were built at low temperatures than at high temperatures. The effects of precipitation on nest characteristics show a different pattern, as they were restricted only to nest mass and extended in a time window covering almost the whole period analysed, starting 30 days before FED and ending two days before FED.

Temperature sensitivity windows and nest size

While the effects of temperature on nest size traits have already been reported, the novelty of our results lies in identifying the timing of the sensitive periods. The Great Tits from our study population seem to use ambient temperature as a cue for nest size well before the onset of nest building. In the Sękocin tit population, nest building generally started no earlier than 14 days before FED, with a mean of -10.1 days, and 50% of the final nest mass was accumulated by day -6 (I. Harnist et al. — unpubl.). This corresponds closely to the average nest building period of 13 days found in the UK (Smith et al. 2013). Therefore, for total nest height and bottom height, the time windows of temperature sensitivity (days -23 to -16 before FED) almost did not overlap with the average nest building period (see Fig. 2). For nest mass, the time windows of temperature sensitivity extended maximally to day -6 (*T_max*), i.e., closed before half of the nest was built.

These results indicate that female Great Tits adjust their nest size to the temperatures they experience mainly before they start nest building, rather than during nest building. Therefore, within-population analyses of the effect of temperature on nest size in tits that *a priori* used the time window overlapping with the nest building period (e.g., 7 days immediately prior to the first egg date or before nest trait measurements; e.g. Britt & Deeming 2011, Lambrechts et al. 2016a) may be unable to detect any significant effects.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

We therefore suggest that a possible reason for the failure to detect a relationship between ambient temperature and the nest traits of passerines in a handful of studies (Britt & Deeming 2011, Wysocki et al. 2015, Lambrechts et al. 2016a, Lambrechts & Caro 2018, Smith et al. 2018, Sonnenberg et al. 2020) may be related to the fact that the window of temperature sensitivity was arbitrarily set only to the period of nest building, which may be too late. Our results suggest that the assumption that the nest size of Great Tits is directly influenced by weather during the nest building period, although arguably the most plausible *a priori* hypothesis, does not appear to be supported by the data. Throughout the actual nest building period (days -14 to -1 before FED), the female Great Tits in our sample were effectively insensitive to prevailing temperatures as far as nest size is concerned. This is clearly illustrated by the heat maps, which show blue areas of no model improvement across the lower left parts of the triangles (Fig. 3).

Our results also show that detecting the influence of weather in the data was largely possible only when consistent female identity effects on nest characteristics were taken into account. Except for the strongest weather effect (daily maximum temperature averaged over days -17 to -5 and nest mass), associations between weather variables and nest size could not be detected without controlling for the persistent differences between females included in the baseline mixed model. We suggest that confounding of female and weather effects on nest size may be quite common in studies that do not use measurements of multiple nests built by the same individual. As the female identity effect on nest size is typically quite strong, this may effectively hinder the detection of weather effects in such designs.

Another, rather unexpected result was that maximum daily temperature was consistently a better predictor of nest size characteristics than either minimum daily temperature or mean daily temperature. However, this may be understandable in light of a growing recognition that temperature variability often impacts the performance of ecological systems much more than the temperature mean (Zimmermann et al. 2009, Vasseur et al. 2014), largely due to the nonlinearity of thermal performance curves (TPCs), which describe the rate of physiological processes (notably metabolic rate, but also many biochemical reactions, organismal growth, reproduction rate, etc.) as a function of temperature (Dowd et al. 2015, Denny 2017, 2019, von Schmalensee et al. 2021). Although applicable to all organisms, TPCs are particularly useful to understand the performance of ectothermic animals, including insects (Colinet et al. 2015), which are often limited by low temperatures in spring, and high temperatures in summer. Briefly, when the thermal environment is temporally fluctuating (e.g., alternating between cold nights and warm days), the performance of a thermally limited organism is grossly different from that predicted by the mean temperature of the system (e.g., daily mean). For example, an insect's total daily metabolic rate may be 20–50% higher in an environment experiencing temperatures varying by 3–8 °C over the day than in an environment with a constant daily mean temperature (Ruel & Ayres 1999). Therefore, for phenological systems driven by the thermal environment (like tree bud development, insect larvae development), models using mean temperatures (or a linear relationship between temperature and response) may yield biased results, compared to models using temperature variability — either alone or in addition to mean temperature (Zimmermann et al. 2009, Vasseur et al. 2014).

In this context, it is important to note that in our data, daily maximum temperature, but not daily minimum temperature, was the variable that, in the absence of more direct measurements, captured the variation in daily temperature variability. When we used the daily temperature range (DTR = *T_max* – *T_min*) in our spring temperature time series as a simple measure of the diurnal variability of ambient temperatures, *T_max* predicted the daily range much better (Pearson's correlation between DTR and *T_max* averaged over 9 year × month time series, $r^2 = 0.32$) than *T_min* ($r^2 = 0.07$). We therefore believe that a long-recognised but still underappreciated consequence of non-linear TPCs applied to bud burst phenology and insect development provides a plausible explanation for why *T_max* is consistently the best cue identified in our analysis. Simply put, if spring phenology is, driven by variance in ambient temperatures to a significant extent, then *T_max* provides more information about the process than *T_min* and *T_mean* in our data and, as such, is likely to be the best of the three predictors used.

We found that, after controlling for the effect of female identity, birds experiencing lower temperatures build larger nests than conspecifics facing higher temperatures during their windows of sensitivity. In line with other researchers, we believe

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

this reflects an adaptive reaction of females, which adjust nest size to the environmental conditions likely to occur during incubation and the early nestling period. Larger nests, showing better insulation properties and slowing down egg cooling during female incubation recesses (Lambrechts & Caro 2022), should be at a premium during delayed, cold springs, especially given that during such adverse conditions, food supplies will be lower and females will be forced to take longer incubation breaks to replenish their energy reserves.

Interestingly, both the relative timing of critical windows (measured in days prior to FED) and the thermal sensitivity of Great Tit nest parameters (measured as the slope of nest size against temperature) did not differ between the first and second clutches in our sample. While low sample sizes preclude obtaining significant results in separate sliding window analyses for first and second clutches, the heat maps revealed the same pattern of window timing for both clutch types (data not shown). However, females about to lay a first clutch of the year face quite different conditions than females preparing to lay a second clutch. Apart from the obvious differences between temperatures in April and late May, females attempting to lay a second clutch enter the thermal sensitivity window while still feeding the nestlings of the first brood. In the study population, nestlings of the first brood usually fledge 20 days after hatching (range 17–22 days; Dubiec & Mazgajski 2023) while the first eggs of the second brood appears 9 ± 4 days after the first-brood young fledge (range 4–19 days, N = 15 females; Gołębiewska & Mazgajski 2024). Hence, the sensitivity time window for the second clutch overlaps with the feeding of the first brood's small nestlings, and generally with a period of increased energy expenditure. The totally different conditions birds have to face when building a nest for the second brood make such nests very interesting for studies, but to our knowledge, true second brood nest traits are as yet completely unexplored. In future studies, it would be very interesting to study whether female Great Tits can use information about the performance of the first brood to modify the properties of the second nest beyond those predicted by temperature, as Zebra Finches do (Edwards et al. 2020).

Precipitation effects

The effects of precipitation on nest characteristics we obtained differ from those found for temperature variables, with a significant relationship found only for nest mass — relating to precipitation averaged over a 28-day window before FED. We see in the literature that the effect of precipitation on nest mass has rarely been studied, and mostly without significant results (Lambrechts & Caro 2018). Sometimes precipitation data are mentioned in a paper, but without presenting specific results (Britt & Deeming 2011). A significant and unexpected relationship between rainfall and the nest size of tits was presented by Lambrechts et al. (2016a), who reported smaller nests built by Mediterranean Blue Tits under more rainy conditions. This contrasts with the hypothesis that the voluminous nest base built by tits from moss should serve to protect the nest contents from soaking (Wesołowski et al. 2002). If this is correct, tit nest builders should add more moss in more rainy conditions, so the nest should be larger and probably heavier, which is partly consistent with our results. In our study population, Great Tits that experienced more rain before and during nest construction built heavier but not structurally larger nests. This suggests that heavier nests may simply reflect the immediate effects of more wet nesting material being used by birds on rainy days, rather than strategic adaptations to conditions likely to occur during incubation and the early nestling period. However, we weighed the nests approximately two weeks after nest building had finished, when the bryophytes should have dried out. Therefore, at best, this can only partially explain our results. Also, if bryophytes do indeed serve an important water-absorbing function in tit nests (at least for nests located in tree cavities; cf. Wesołowski et al. 2002, Wesołowski & Wierzcholska 2018), we would expect birds to collect dry rather than wet moss as nest material between rain episodes. Finally, under the scenario where heavier nests simply reflect wetter nests, the sensitivity window for the effect of precipitation on nest mass should only overlap the nest-building period (days -14 to 0 before FED). In our data, the window extends to day -28. This leaves us with the possibility that, under rainy conditions, tits may build their nests from more densely packed materials, leaving less empty space between the individual construction pieces. Alternatively, female tits may change the proportions of different components used for nest construction (e.g., moss forming the nest base vs. hairy nest cup lining). Further studies are needed not only on the composition of bryophyte species used for nest construction (Wesołowski & Wierzcholska 2018, Glądalski et al. 2021, Fäth et al.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

2023), but also on their water uptake capacity and nest moisture retention to unravel the relationships between precipitation and tit nest size traits.

Time lags and reliability of results

An obvious question that comes to mind when looking at our results concerning the timing of sensitivity windows is why do female Great Tits about to build a nest use cues from a period starting about 10 days before the onset of nest building, rather than cues from the nest building period itself? In other words, why is the temperature sensitivity window of nest size largely decoupled from the nest building period? If nest size is to be adjusted to the thermal requirements of incubation, then the period closer to incubation (e.g., during nest building) should provide more reliable information about these future temperatures than a time window opening more than 30 days before the start of incubation (i.e., over 20 days before FED + 9–10 days of egg laying).

However, weather sensitivity windows opening long before and closing well ahead of the timing of the expression of the trait of interest are quite common in one of the largest data sets of this type analysed so far (Thackeray et al. 2016). A spectacular example here is that the laying date of Starlings *Sturnus vulgaris* in British Columbia, Canada is best predicted by mid-winter temperatures 50–90 days before FED (Williams et al. 2015). The temperature sensitivity window of Great Tit nest size traits that ends shortly before nest building commences or halfway through the expression of this trait — as we report here — are thus by no means exceptional (Thackeray et al. 2016), albeit we acknowledge that the above examples pertain to a variation in population means measured across different study years rather than to a variation across individuals within a single year or several years (absolute vs relative time window in 'climwin' notation).

On the other hand, the analytical method we used (i.e., relative sliding windows) to identify the weather sensitivity windows of nest traits may potentially yield biased results. Simmonds et al. (2019) compared five methods of identifying sensitivity windows and found that using relative sliding windows resulted in windows opening and closing notably earlier than those found using the other four methods. However, the explanations offered to account for this bias applied mostly to data collected across long series of different years, and are unlikely to apply to data dominated by variation between different individuals within the same year, as in our case. Therefore, we believe our results are reliable and that the temperature sensitivity windows of nest size preceding the nest building period can be explained in reference to biological phenomena, as proposed below.

One possibility is that tits are actually set into nest building mode earlier than the actual start of nest building. Marsh Tits nesting in natural cavities have been observed to begin nest building by cleaning the nest hole of debris and the remnants of old material from the previous year, before they start bringing in moss for the new nest of the current year (Wesołowski 2013). The cleaning phase lasted several days, advancing the entire nest building process by a few days. This behaviour may go unnoticed in birds breeding in nest boxes that are routinely cleaned of old nests, as it does not leave many evident traces to be found during standard nest box inspections. Stenning (2018) closely observed the nest building of Blue Tits and noted that the female started the whole process with a considerable amount of pecking and sweeping the inside of the nest box, an activity that can last for several days (also our own obs.). In line with this, many Blue Tits can start bringing some nest material into a nest box already up to 43 or 50 days before FED (Stenning 2018, der Weduwen et al. 2021), despite the mean nest building period of 16 or 10.6 days, respectively. Thus, female tits probably start the nest building process with a cleaning phase that may often remain cryptic in standard nest box studies. Presumably, the sensitivity window starting around 24 days before FED, as found in this study, overlaps with the cleaning stage, during which birds may use ambient temperature cues to decide on nest size and the timing of egg laying, but still do not bring much nest material into the nest box, focusing instead on adjusting the interior of the cavity. Additionally, Great Tit females may roost in chosen nest boxes some days or even weeks before nest building begins (Gosler 1993). It is tempting to think that the female may use information on the thermal properties of the nest cavity, compared against the temperature of the outside environment, to adjust the size and properties of the nest built later on in this place. This would again explain the start of the temperature sensitivity time window a couple of days before actual nest building commences.

Still another, not mutually exclusive explanation for such an extended period of sensitivity of nest traits to weather conditions relates to the

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

representativeness of nest-box studies to the natural conditions experienced by Great Tits during their evolutionary history. The majority of tit studies have been conducted on birds breeding in nest boxes. However, some experiments on the nest site choice of this species suggest that these birds prefer much larger and deeper nest boxes than normally used in nest-box studies. Importantly, in natural conditions, Great Tits choose much larger (mostly deeper) cavities that other hole nesters (see Maziarz et al. 2015). If the duration of nest building is related to the final size of the nest (van Weduwen et al. 2021), then we could assume, that in natural conditions, birds breeding in tree cavities should start nest building considerably earlier in order to build much larger nests than those we observe in nest boxes. Therefore, the behavioural "readiness" for nest building and associated weather sensitivity of nest traits that starts over 20 days before FED need not be seen as actually decoupled from the timing of nest building in natural conditions. However, testing this hypothesis requires much more data on nest building duration, the daily rate of nest building, etc., coming from different populations, including birds nesting in natural holes.

Obviously, more research is needed to confirm whether the results we obtained in our study are applicable to other populations of the species. The Great Tit nests we analysed are larger (higher and heavier) than nests from other populations studied so far in relation to weather conditions (e.g., Britt & Deeming 2011, Lambrechts et al. 2016a). This could be related to the size of the nest boxes used by the birds, as tits adjust nest size — mostly nest height — to the size of the breeding cavity, and build smaller nests in shallow nest boxes (e.g., Mazgajski & Rykowska 2008, Bueno-Enciso et al. 2016). Therefore, the size of the nest box used could possibly affect both the duration of nest building as well as the microclimate of the breeding site, hence sensitivity to weather conditions and nest size adjustment. In this way, sensitivity to the weather time window could differ between populations, and of course between species. Such differences between populations and closely related species may possibly explain the conflicting results reported for Great and Blue Tits, where significant temperature-nest size relationships were found for one species but not the other, and the opposite results being found in other studies (cf., e.g., Britt & Deeming 2011, and Deeming et al. 2012 for Great Britain). Similar analyses performed for other species, especially hole nesters, where data collection for a nest box population is relatively easy, would be useful to better understand the factors affecting the relationships between temperature and nest size adjustments.

CONCLUSIONS

Our study confirms that the Great Tits which start breeding at lower temperatures build larger nests, but found that this may often go unnoticed in standard analyses, as females rely on the temperatures experienced prior to nest construction, i.e., about 20 days before FED. Our results suggest that nest building and the sensitivity of nest traits to temperature (or more generally to weather conditions) should be considered as another stage of reproduction subject to evolutionary optimisation, alongside the well-known and frequently studied timing of egg laying and clutch size. Birds may have to decide whether to start egg laying earlier, which would usually require the construction of a larger nest and may delay their FED, or to build a larger nest more quickly at some cost (physiological stress, see Moreno et al. 2008, Mainwaring & Hartley 2013), or to delay egg laying by a few days, which may allow the construction of smaller nests, but also at the cost of reduced fitness due to delayed FED. In any case, building larger nests may contribute to the costs of early laying faced by the very earliest breeders and attributed to the increased costs of egg production and incubation at low temperatures (Perrins 1970, Drent 2006, Visser et al. 2012). All this adds another layer of complexity to thinking about the factors affecting the timing of breeding in birds, especially in an era of climate change.

ACKNOWLEDGEMENTS

This research is part of a project financed by Polish National Science Centre grant no. 2017/27/B/NZ8/03118 (awarded to TDM). We thank Anna Dębska, Ewa Nalepa and Jacek Hikisz for helping during fieldwork, the Forest Research Institute for logistical support and Michał Glądalski for comments on an earlier draft of the manuscript. English was verified by Barbara Przybylska.

REFERENCES

Alabrudzińska J., Kaliński A., Słomczyński R., Wawrzyniak J., Zieliński P., Bańbura J. 2003. Effects of nest characteristics on breeding success of Great Tits *Parus major*. Acta Ornithol. 38: 151–154.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Álvarez E., Barba E. 2008. Nest quality in relation to adult bird condition and its impact on reproduction in Great Tits *Parus major*. Acta Ornithol. 43: 3–9.

Antonov A. 2004. Smaller Eastern Olivaceous Warbler *Hippolais pallida elaeica* nests suffer less predation than larger ones. Acta Ornithol. 39: 87–92.

Bailey L. D., van de Pol M. 2016. Climwin: An R toolbox for climate window analysis. PLoS One 11 (12): e0167980.

Both C. 2010. Food availability, mistiming, and climatic change. In: Moller A. P., Fiedler W., Berthold P. (Eds). Effects of climate change on birds. Oxford University Press, pp. 129–147.

Both C., Visser M. E. 2005. The effect of climate change on the correlation between avian life-history traits. Glob. Chang. Biol. 11: 1606–1613.

Britt J., Deeming D. C. 2011. First-egg date and air temperature affect nest construction in Blue Tits *Cyanistes caeruleus*, but not in Great Tits *Parus major*. Bird Study 58: 78–89.

Brooks M. E., Kristensen K., van Benthem K. J., Magnusson A., Berg C. W., Nielsen A., Skaug H. J., Mächler M., Bolker B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R Journal 9: 378–400.

Bueno-Enciso J., Ferrer E. S., Barrientos R., Sanz J. J. 2016. Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. J. of Ornithol. 157: 759–772.

Burnham K. P., Anderson D. R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer Science+Business Media.

Campbell B. L., Hurley L. L., Griffith S. C. 2018. Behavioural plasticity under a changing climate; how an experimental local climate affects the nest construction of the zebra finch *Taeniopygia guttata*. J. Avian Biol. 49: e01717.

Charmantier A., McCleery R. H., Cole L. R., Perrins C., Kruuk L. E. B., Sheldon B. C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320: 800–803.

Chmura H. E., Kharouba H. M., Ashander J., Ehlman S. M., Rivest E. B., Yang L. H. 2019. The mechanisms of phenology: the patterns and processes of phenological shifts. Ecol. Monogr. 89: 1–22.

Cohen J. M., Lajeunesse M. J., Rohr J. R. 2018. A global synthesis of animal phenological responses to climate change. Nat. Clim. Chang. 8: 224–228

Colinet H., Sinclair B. J., Vernon P., Renault D. 2015. Insects in fluctuating thermal environments. Annu. Rev. Entomol. 60: 123–140.

Cresswell W., McCleery R. 2003. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. J. Anim. Ecol. 72: 356–366.

Crossman C. A., Rohwer V. G., Martin P. R. 2011. Variation in the structure of bird nests between northern Manitoba and southeastern Ontario. PLoS One 6(4): e19086.

Czernecki B., Glogowski A., Nowosad J. 2020. Climate: An R package to access free in-situ meteorological and hydrological datasets for environmental assessment. Sustainability 12: 394.

Daan S., Dijkstra C., Drent R., Meijer T. 1989. Food supply and the annual timing of avian reproduction. Acta 19th Int. Ornithol. Congr., University of Ottawa Press, pp. 392–407.

Daan S., Tinbergen J. M. 1997. Adaptation of life histories. In: Krebs J. R., Davies N. B. (Eds). Behavioural ecology: An evolutionary approach. 4th ed. Blackwell Science, pp. 311–333.

Deeming D. C. 2023. A review of the roles materials play in determining functional properties of bird nests. Acta Ornithol. 58: 1–28.

Deeming D. C., Biddle L. E. 2015. Thermal properties of bird nests depend on air-gaps between the materials. Acta Ornithol. 50: 121–125.

Deeming D. C., Mainwaring M. C., Hartley I. R., Reynolds S. J. 2012. Local temperature and not latitude determines the design of Blue Tit and Great Tit nests. Avian Biol. Res. 5: 203–208.

Denny M. 2017. The fallacy of the average: On the ubiquity, utility and continuing novelty of Jensen's inequality. J. Exp. Biol. 220: 139–146.

Denny M. 2019. Performance in a variable world: using Jensen's inequality to scale up from individuals to populations. Conserv. Physiol. 7: coz053.

der Weduwen D., Keogan K., Samplonius J. M., Phillimore A. B., Shutt J. D. 2021. The correlates of intraspecific variation in nest height and nest building duration in the blue tit *Cyanistes caeruleus*. J. Avian Biol. 2021: e02528.

Dowd W. W., King F. A., Denny M. W. 2015. Thermal variation, thermal extremes and the physiological performance of individuals. J. Exp. Biol. 218: 1956–1967.

Drent R. H. 2006. The timing of birds' breeding seasons: The Perrins hypothesis revisited especially for migrants. Ardea 94: 305–322.

Dubiec A., Mazgajski T. D. 2013. Nest mass variation over the nesting cycle in the Pied Flycatcher (*Ficedula hypoleuca*). Avian Biol. Res. 6: 127–132.

Dubiec A., Mazgajski T.D. 2023. Assessing timing of fledging in a cavity-nesting passerine using temperature data loggers. Ornis Fennica 100: 123–134.

Dunn P. O. 2019. Changes in timing of breeding and reproductive success in birds. In: Dunn P. O., Moller A. P. (Eds). Effects of climate change on birds. 2nd ed. Oxford University Press, pp. 108–119.

Dunn P. O., Winkler D. W. 2010. Effects of climate change on timing of breeding and reproductive success in birds. In: Moller A. P., Fiedler W., Berthold P. (Eds). Effects of climate change on birds. Oxford University Press, pp. 113–128.

Edwards S. C., Shoot T. T., Martin R. J., Sherry D. F., Healy S. D. 2020. It's not all about temperature: Breeding success also affects nest design. Behav. Ecol. 31: 1065–1072.

Fäth L., Obermaier E., Pfeifer R. 2023. Picky Blue Tits — selective moss utilization for nest construction in *Cyanistes caeruleus*. Ornithol. Anzeiger 61: 1–15.

Glądalski M., Bańbura M., Kaliński A., Markowski M., Skwarska J., Wawrzyniak J., Zieliński P., Bańbura J. 2016. Effects of extreme thermal conditions on plasticity in breeding phenology and double-broodedness of Great Tits and Blue Tits in central Poland in 2013 and 2014. Int. J. Biometeorol. 60: 1795–1800,

Glądalski M., Kaliński A., Markowski M., Skwarska J., Wawrzyniak J., Bańbura J. 2024. Nest size parameters of Great Tits and Blue Tits: a long-term study. J. Ornithol. 165: 381–389.

Glądalski M., Wolski G. J., Bańbura M., Kaliński A., Markowski M., Skwarska J., Wawrzyniak J., Bańbura J. 2021. Differences in use of bryophyte species in tit nests between two contrasting habitats: an urban park and a forest. Eur. Zool. J. 88: 807–815.

Gołębiewska A., Mazgajski T. D. 2024. A novel non-invasive method for measuring the body mass of hole nesting birds during breeding. Pol. J. Ecol. 72: 65–74.

Gosler A.G. 1993. The Great Tit. Hamlyn Species Guides. Paul Hamlyn, London.

Hansell M. 2000. Bird nests and construction behaviour. Cambridge University Press, Cambridge, UK.

Hansel M. 2005. Animal architecture. Oxford U. Press, USA.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Harnist I. 2017 [Effects of nest building investments on the Great Tit *Parus major* fitness]. PhD Thesis, Museum and Institute of Zoology Polish Academy of Sciences, Warszawa Poland. (in Polish, with English summary)

Harnist I., Dubiec A., Mazgajski T. D. 2020. Changes of nest mass in relation to nesting stages in the Great Tit *Parus major*. Bird Study 67: 292–299.

Helm B., Van Doren B. M., Hoffmann D., Hoffmann U. 2019. Evolutionary response to climate change in migratory Pied Flycatchers. Curr. Biol. 29: 3714–3719.

Järvinen P., Kluen E., Brommer J. E. 2017. Low heritability of nest construction in a wild bird. Biol. Lett. 13: 20170246.

Jelínek V., Požgayová M., Honza M., Procházka P. 2016. Nest as an extended phenotype signal of female quality in the great reed warbler. J. Avian Biol. 47: 428–437.

Kluijver H. N. 1951. The population ecology of the great tit, *Parus m. major* L. Ardea 39: 1–135.

Kluyver H. N. 1952. Notes on body weight and time of breeding in the Great Tit, *Parus m. major* L. Ardea 40: 123–141.

Lambrechts M. M., Blondel J., Bernard C., Caro S. P., et al. 2016a. Exploring biotic and abiotic determinants of nest size in Mediterranean Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*). Ethology 122: 492–501.

Lambrechts M. M., Blondel J., de Franceschi C., Doutrelant C. 2017. Nest size is positively correlated with fledging success in Corsican Blue Tits (*Cyanistes caeruleus*) in an insular oak-dominated habitat mosaic. J. Ornithol. 158: 125–132.

Lambrechts M. M., Caro S. P. 2018. Experimental manipulation of photoperiod and temperature does not influence nest size in Blue and Great tits. Auk 135: 218–227.

Lambrechts M. M., Caro S. P. 2022. Egg cooling associated with nest size in a passerine bird. J. Therm. Biol. 110: 103383.

Lambrechts M. M., Haurez J., Bodineau G., Gagliardi G., et al. 2016b. Coal Tits *Periparus ater* build larger nests than Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* living in the same Mediterranean coniferous woodland habitat. Acta Ornithol. 51: 123–129.

Mainwaring M. C., Hartley I. R. 2009. Experimental evidence for state-dependent nest weight in the blue tit, *Cyanistes caeruleus*. Behav. Processes 81: 144–146.

Mainwaring M. C., Hartley I. R. 2013. The energetic costs of nest building in birds. Avian Biol. Res. 6: 12–17.

Mainwaring M. C., Hartley I. R., Bearhop S., Brulez K., du Feu C. R., Murphy G., Plummer K. E., Webber S. L., Reynolds S. J., Deeming D. C. 2012. Latitudinal variation in blue tit and great tit nest characteristics indicates environmental adjustment. J. Biogeogr. 39: 1669–1677.

Martin T. L., Huey R. B. 2008. Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. Am. Nat. 171: 102–118.

Mazgajski T. D., Rykowska Z. 2008. Dependence of nest mass on nest hole depth in the Great Tit *Parus major*. Acta Ornithol. 43: 49–55.

Maziarz M., Wesołowski T., Hebda G., Cholewa M. 2015. Natural nest-sites of Great Tits (Parus major) in a primeval temperate forest (Białowieża National Park, Poland). J. Ornithol. 156: 613–623.

McLean N., Kruuk L. E. B., van der Jeugd H. P., Leech D., van Turnhout C. A. M., van de Pol M. 2022. Warming temperatures drive at least half of the magnitude of long-term trait changes in European birds. Proc. Natl. Acad. Sci. U. S. A. 119: e2105416119.

Moreno J., Martínez J., Corral C., Lobato E., Merino S., Morales J., Martínez-de la Puente J., Tomás G. 2008. Nest construction rate and stress in female Pied Flycatchers *Ficedula hypoleuca*. Acta Ornithol. 43: 57–64.

O'Neill L. G., Parker T. H., Griffith S. C. 2018. Nest size is predicted by female identity and the local environment in the blue tit (*Cyanistes caeruleus*), but is not related to the nest size of the genetic or foster mother. R. Soc. Open Sci. 5: 172036.

Perez D. M., Gardner J. L., Medina I. 2020. Climate as an evolutionary driver of nest morphology in birds: A review. Front. Ecol. Evol. 8: 566018.

Perrins C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242–255.

Phillimore A. B., Leech D. I., Pearce-Higgins J. W., Hadfield J. D. 2016. Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. Glob. Chang. Biol. 22: 3259–3272.

Powell L. A., Rangen K. L. 2000. Variation in Wood Thrush nest dimensions and construction. North Am. Bird Bander 25: 89–96.

R Core Team 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Rohwer V. G., Law J. S. Y. 2010. Geographic variation in nests of Yellow Warblers breeding in Churchill, Manitoba, and Elgin, Ontario. Condor 112: 596–604.

Ruel J. J., Ayres M. P. 1999. Jensen's inequality predicts effects of environmental variation. Trends Ecol. Evol. 14: 361–366.

Shutt J. D., Cabello I. B., Keogan K., Leech D. I., Samplonius J. M., Whittle L., Burgess M. D., Phillimore A. B. 2019. The environmental predictors of spatiotemporal variation in the breeding phenology of a passerine bird. Proc. R. Soc. B 286: 20190952.

Simmonds E. G., Cole E. F., Sheldon B. C. 2019. Cue identification in phenology: A case study of the predictive performance of current statistical tools. J. Anim. Ecol. 88: 1428–1440.

Slagsvold T. 1989. Experiments on clutch size and nest size in passerine birds. Oecologia 80: 297–302.

Smith J. A., Harrison T. J. E., Martin G. R., Reynolds S. J. 2013. Feathering the nest: Food supplementation influences nest construction by Blue (*Cyanistes caeruleus*) and Great Tits (*Parus major*). Avian Biol. Res. 6: 18–25.

Smith M. G., Kaiser S. A., Sillett T. S., Webster M. S. 2018. Variation in nest characteristics and brooding patterns of female Black-throated Blue Warblers is associated with thermal cues. Auk 135: 733–747.

Sonnenberg B. R., Branch C. L., Benedict L. M., Pitera A. M., Pravosudov V. V. 2020. Nest construction, ambient temperature and reproductive success in a cavity-nesting bird. Anim. Behav. 165: 43–58.

Stenning M. J. 2018. The Blue Tit. T & AD Poyser.

Stoffel M. A., Nakagawa S., Schielzeth H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol. Evol. 8: 1639–1644.

Thackeray S. J., Henrys P. A., Hemming D., Bell J. R., et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535: 241–245.

Thomas D. W., Bourgault P., Shipley B., Perret P., Blondel J. 2010. Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the Corsican Blue Tit (*Cyanistes caeruleus*). Auk 127: 129–139.

van de Pol M., Bailey L. D., McLean N., Rijsdijk L., Lawson C. R., Brouwer L. 2016. Identifying the best climatic predictors in ecology and evolution. Methods Ecol. Evol. 7: 1246–1257.

Vasseur D. A., DeLong J. P., Gilbert B., Greig H. S., Harley C. D. G., McCann K. S., Savage V., Tunney T. D., O'Connor M. I. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proc. R. Soc. B. 281: 20132612.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Verhulst S., Nilsson J. Å. 2008. The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. Philos. Trans. R. Soc. B Biol. Sci. 363: 399–410.
Visser M. E., te Marvelde L., Lof M. E. 2012. Adaptive phenological mismatches of birds and their food in a warming world. J. Ornithol. 153: S75–S84.
von Haartman L. 1990. Breeding time of Pied Flycatcher *Ficedula hypoleuca*. In: Blondel J., Gosler A., Lebreton J.-D., McCleery R. (Eds). Population biology of passerine birds. An integrated approach. Springer-Verlag, Berlin, pp. 1–16.
von Schmalensee L., Hulda Gunnarsdóttir K., Näslund J., Gotthard K., Lehmann P. 2021. Thermal performance under constant temperatures can accurately predict insect development times across naturally variable microclimates. Ecol. Lett. 24: 1633–1645.
Wesołowski T. 2013. Timing and stages of nest-building by Marsh Tits (*Poecile palustris*) in a primeval forest. Avian Biol. Res. 6: 31–38.
Wesołowski T. 2023. Weather, food and predation shape the timing of Marsh Tit breeding in primaeval conditions: a long-term study. J. Ornithol. 164: 253–274.
Wesolowski T., Czeszczewik D., Rowiński P., Walankiewicz W. 2002. Nest soaking in natural holes — A serious cause of breeding failure? Ornis Fennica 79: 132–138.
Wesołowski T., Wierzcholska S. 2018. Tits as bryologists: patterns of bryophyte use in nests of three species cohabiting a primeval forest. J. Ornithol. 159: 733–745.
Williams T. D. 2012. Physiological adaptations for breeding in birds. Princeton University Press.
Williams T. D., Bourgeon S., Cornell A., Ferguson L., Fowler M., Fronstin R. B., Love O. P. 2015. Mid-winter temperatures, not spring temperatures, predict breeding phenology in the European starling *Sturnus vulgaris*. R. Soc. Open Sci. 2: 140301.
Woods H. A., Pincebourde S., Dillon M. E., Terblanche J. S. 2021. Extended phenotypes: buffers or amplifiers of climate change? Trends Ecol. Evol. 36: 889–898.
Wysocki D., Jankowiak Ł., Greño J. L., Cichocka A., Sondej I., Michalska B. 2015. Factors affecting nest size in a population of Blackbirds *Turdus merula*. Bird Study 62: 208–216.
Zimmermann N. E., Yoccoz N. G., Edwards T. C., Meier E. S., Thuiller W., Guisan A., Schmatz D. R., Pearman P. B. 2009. Climatic extremes improve predictions of spatial patterns of tree species. Proc. Natl. Acad. Sci. U. S. A. 106: 19723–19728.

STRESZCZENIE

[Bogatki dostosowują wielkość gniazda do warunków pogodowych panujących przed rozpoczęciem jego budowy]

Biorąc pod uwagę rolę, jaką pełnią gniazda, należy spodziewać się związku pomiędzy warunkami pogodowymi, głównie temperaturą, a cechami gniazda, takimi jak wielkość czy materiały użyte do jego budowy. Jednak wiele dotychczasowych badań, prowadzonych głównie na niewielkich wróblowych, nie wykazało istotnych związków między parametrami gniazda a pogodą panującą w zdefiniowanym *a priori* okresie. Okres ten zwykle obejmował ostatni tydzień przed złożeniem pierwszego jaja. Biorąc jednak pod uwagę, że u poszczególnych gatunków ptaków średni czas budowy gniazda jest zwykle dłuższy, okres ten najczęściej odpowiadał końcowym etapom budowy gniazda. Możliwe jest więc, że dotychczasowy sposób doboru okresu, dla którego badano potencjalny wpływ warunków pogodowych na parametry gniazda, nie był właściwy. Dodatkowo, wielkość gniazda jest cechą silnie zmienną osobniczo. W związku z tym unikalny identyfikator osobnika powinien być uwzględniany w analizach statystycznych. Celem badań było zidentyfikowanie okien czasowych, dla których brane pod uwagę czynniki pogodowe najlepiej wyjaśniały zmienność cech gniazda, przy jednoczesnym uwzględnieniu w analizach efektu roku, typu lęgu (pierwszy lub drugi) i osobnika.

Badania prowadzono w populacji lęgowej bogatki gniazdującej w skrzynkach lęgowych w Lesie Sękocińskim k. Warszawy. Ptaki budowały gniazda w perforowanych plastikowych pudełkach, co umożliwiało ich wyjmowanie i pomiary bez naruszania ich struktury. Gniazda z pierwszych i drugich lęgów zostały zmierzone (całkowita wysokość gniazda i grubość dna) i zważone na początku inkubacji. Samice zostały schwytane podczas karmienia piskląt. Zebrano również dane dotyczące biologii lęgowej, w tym o dacie złożenia pierwszego jaja (FED — first egg date) dla każdego lęgu. Jako czynniki pogodowe potencjalnie wpływające na wielkość gniazda uwzględniono dzienną sumę opadów i trzy parametry temperatury: średnią, minimalną i maksymalną temperaturę dzienną. Korzystając z metody analitycznej „sliding window" (van de Pol et al. 2016) dla każdej cechy gniazda i czynnika pogodowego przetestowano wszystkie możliwe okna czasowe w okresie 30 dni przed FED szukając takiego, dla którego brany pod uwagę czynnik pogodowy najlepiej wyjaśniał zmienność danej cechy gniazda.

Pogoda w okresie prowadzenia badań tj. kwiecień–czerwiec 2019–2021 nie odbiegała istotnie od średniej wieloletniej dla tych miesięcy (Fig. 1). Gniazda z lęgów pierwszych były większe niż te z lęgów powtarzanych lub drugich (Tab. 1). Wcześniejsze badania wykazały, że bogatki z populacji w Lesie Sękocińskim budują gniazda przez średnio 10 dni przed złożeniem pierwszego jaja. Tymczasem stwierdzono, że okna czasowe wskazujące na związek pomiędzy temperaturą a cechami gniazda otwierały się 19–24 dni przed FED, a zamykały 6–15 dni przed FED, a więc trwały 9–14 dni, w znacznej części przed rozpoczęciem budowy gniazda przez ptaki (Fig. 2, Tab. 2).

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Wyniki analiz wskazywały na pewną zmienność otwarcia i zamknięcia okien czasowych, dla których istnieje związek pomiędzy zmiennymi pogodowymi a poszczególnymi cechami gniazda (Fig. 3). Jednak zawsze otwarcie okien przypadało znacznie wcześniej niż przystępowanie sikor do budowy gniazda (Fig. 2). W przypadku opadów atmosferycznych, najsilniejszy związek między tym parametrem pogodowym a wielkością gniazda, stwierdzono dla okna otwierającego się 27 dni przed FED i zamykającego 3 dni przed FED (Fig. 2, Tab. 2). Maksymalna dzienna temperatura była lepszym predyktorem parametrów gniazda niż minimalna lub średnia dzienna temperatura (Tab. 2).

Uzyskane wyniki wskazują, że samice bogatki dostosowują wielkość gniazda do temperatur, których doświadczają głównie przed rozpoczęciem budowy swojego gniazda, a nie — jak można byłoby zakładać i było to uwzględniane do tej pory — już w trakcie jego budowy.

Downloaded From: https://bioone.org/journals/Acta-Ornithologica on 24 Mar 2025
Terms of Use: https://bioone.org/terms-of-use