Interaction of climate change with effects of conspecific and heterospecific density on reproduction

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Abstract

We studied the relationship between temperature and the coexistence of great tit *Parus major* and blue tit *Cyanistes caeruleus*, breeding in 75 study plots across Europe and North Africa. We expected an advance in laying date and a reduction in clutch size during warmer springs as a general response to climate warming and a delay in laying date and a reduction in clutch size during warmer winters due to density-dependent effects. As expected, as spring temperature increases laying date advances and as winter temperature increases clutch size is reduced in both species. Density of great tit affected the relationship between winter temperature and laying date in great and blue tit. Specifically, as density of great tit increased and temperature in winter increased both species started to reproduce later. Density of blue tit affected the relationship between spring temperature and blue and great tit laying date. Thus, both species start to reproduce earlier with increasing spring temperature as density of blue tit increases, which was not an expected outcome, since we expected that increasing spring temperature should advance laying date, while increasing density should delay it cancelling each other out. Climate warming and its interaction with density affects clutch size of great tits but not of blue tits. As predicted, great tit clutch size is reduced more with density of blue tits as temperature in winter increases. The relationship between spring temperature and density on clutch size of great tits depends on whether the increase is in density of great tit or blue tit. Therefore, an increase in temperature negatively affected the coexistence of blue and great tits differently in both species. Thus, blue tit clutch size was unaffected by the interaction effect of density with temperature, while great tit clutch size was affected in multiple ways by these interactions terms.

Keywords: Blue tit, clutch size, *Cyanistes caeruleus*, great tit, interspecific competition, intraspecific competition, laying date, *Parus major*, temperature anomaly

Introduction

Climate change has been predicted to affect both intra- and interspecific competition either through effects on the abundance of limiting resources, through changes in the abundance of interacting species or through changes in species distribution (Møller et al. 2010, 2019). It is well known that density-dependent effects on fecundity or other demographic traits can regulate populations as a result of intra- and/or interspecific competition. There are two mechanisms that explain density-dependence in fecundity. First, as density increases breeding habitats are occupied in sequential order of quality. High quality sites are occupied firsts and poor quality sites later (i.e. those that yield lower than average fecundity) resulting in a decrease of reproductive parameters at the population level (i.e. Habitat Heterogeneity Hypothesis) (e.g. Dhondt et al. 1992). This hypothesis can be extended to the individual level whereby high quality or older individuals settle first and hence occupy the high quality sites while low quality individuals appear later and occupy low quality sites. This also would enhance the decrease in reproductive parameters at the population level (e.g. Balbontín and Ferrer 2008). Second, increased density can also reduce reproductive parameters due to antagonistic encounters amongst individuals (i.e. Interference Hypothesis) (e.g. Dhondt and Schillemans 1983) or through competition for food. In birds, advanced phenology is correlated with increased fecundity (Kluijver 1951, Winkler and Allen 1996, Smith and Moore 2004). Thus, it is expected that competition caused by increased density would result in delayed breeding at the population level and hence reduce fecundity (e.g. clutch size). Intra- and interspecific competition are known to affect laying date and clutch size in hole-nesting birds (Dhondt 2010, 2012, Stenseth et al. 2015, Møller et al. 2018). However, some studies suggest that such effects of competition are significant only in specific plots or specific periods, raising questions about the generality of these phenomena, but also about their underlying causes (Alatalo and Lundberg 1984, Török and Tóth 1988, Dhondt et al.1992).

Birds advance the timing of migration or breeding in response to climate warming (Parmesan and Yohe 2003). This response has been attributed to improve the synchronization of the timing of reproduction with the timing of prey emergence at lower trophic levels. Thus, the peak in food abundance (e.g. caterpillar) would match with the peak of maximum demand of chicks during the nestling stage. However, this possible mismatch could vary across Europe (e.g., Visser et al. 1998, 2009).. Although the relationship between laying date and climate warming is well known, we know little about the relationship between clutch size and temperature. For instance, a warmer spring could provide a more favourable ambient environment for females that might result in an increase in reproductive investment. However, it has been suggested that a reduction in clutch size could be an alternative strategy to improve reproductive adjustment with lower trophic levels (e.g. Bleu et al. 2017).

Female great and blue tits lay a clutch of 7-9 eggs and 7-13 eggs, respectively (e.g., Perrins 1991). The species differ in life-history strategies in that the probability to lay a second brood is lower in blue compared to great tit (e.g. Gibb and Betts 1963, Visser et al. 2003). As double-brooded species have more difficulty to cope with climate change than single-brood species (e.g. Husby et al. 2009) we expected a difference in response to climate change of blue tits compared to great tits. Blue tit should respond more strongly to increasing temperatures since it is a mainly single-brood species.

During the breeding season interspecific competition for food occurs when the smaller blue tit consumes smaller instar of the same caterpillar species as eaten by the larger great tit. This results in pre-emptive food consumption that differentially impairs the great tit, which is therefore the inferior competitor (Dhondt 2012). On the other hand, competition for access to nest boxes favours great tits when large-holed nest boxes are available (Dhondt and Eyckerman 1980). Great tits outcompete blue tits by excluding blue tits from boxes used as roosting or breeding sites, even when boxes are super-abundant (Dhondt 2012).

During the non-breeding season great and blue tit adult survival rate is affected by winter severity (e.g. Robinson et al. 2007, Pearce-Higgins and Green 2014). Winters with abundant and extended snow cover decrease survival rate of adult and one-year old birds and consequently population size is reduced during the next breeding season. These effects of winter weather on survival have been attributed to reduced food supply in snowy winters (e.g., beech mast) (Pearce-Higgins and Green 2014 and reference herein). Thus, we expected an increase in population size (i.e. density) after warmer winters. Specifically, as density increased, the proportion of one-year old individuals being part of the populations this effect should specifically affect short-lived species. This could constitute part of the mechanism that could delay laying date and reduce clutch size due to density-dependent effects (e.g. Dhondt et al. 1992, Balbontín and Ferrer 2008).

Recently, Møller et al. (2018) published extensive analyses of effects of competition on laying date and clutch size in great and blue tit across Europe and North Africa. Here we expand these analyses by testing for the first time whether the effects of climate change during the last 50 years significantly influenced intra- and interspecific competition by measuring their presumed effect on lay date and clutch size while controlling statistically for a number of variables that are known to predict lay date and clutch size in blue and great tit (Møller et al. 2014a). We did so by analysing a long-term dataset of 75 studies of two species of secondary hole nesting birds across Europe and North Africa. We used density (number of occupied nestboxes per ha) as a proxy for intensity of competition (Dhondt 2012). Intensity of competition could be measured as the slope of density on a demographic parameter (e.g. laying date or clutch size). Therefore, we included density as an independent variable in statistical models were the dependent variable was laying date or clutch size to measure intensity of competition (Welden and Slauson 1986). We used temperature anomalies during winter and spring as a proxy of climate change.

The objectives of this study are to test whether laying date advanced and clutch size change with increasing temperature, whether this effect was modified by density; and whether the intensity of intra- and interspecific competition was impacted by increasing temperature anomalies.

We predicted that (1) in warmer winters survival rates should increase, particularly for yearling birds (i.e. those that lay smaller clutches and lay later) in both great and blue tits. Hence inter- and intraspecific density should increase resulting in a delayed laying date and a reduced clutch size. The relationships between temperature anomalies in winter and laying date and clutch size are predicted to increase with density. Thus, we expected a greater delay in laying date and a greater reduction in clutch size with increased winter temperature anomalies (for details see Table 1). (2) In warmer springs (i.e. with increased spring temperature anomalies) a more proximal cue for seasonally breeding species, we expected laying date to advance in both great and blue tit, with a stronger response in blue tits. If this results in a mismatch with lower trophic levels, tits should adaptively reduce clutch size to cope with the reduced food availability when feeding nestlings. We thus expect that positive spring temperature anomalies will lead to a reduced clutch size with a stronger effect in great tits. We did not predict an effect for the outcome of the interaction between temperature anomalies in spring and density on laying date. Because warming should advance laying, and competition should delay laying, both effects could cancel each other out. Likewise, competition and its interaction with temperature anomalies in spring should reduce clutch size in great tits more than blue tits. This is expected because the latter outcompetes the former for food, and also because blue tits should respond more rapidly to temperatures in spring since it is mainly a single-brood species (for details see Table 1).

Methods

Study sites and data sets

We obtained information on density of occupied nest boxes per ha, nest box size, clutch size, laying date and ecological variables from all studies considered in this paper for two common species of secondary hole-nesters, the great tit and the blue tit, across Europe and North Africa, as described in detail elsewhere (Møller et al. 2014a, b). Density of great or blue tits was estimated as the number of occupied nest boxes per ha. Nest boxes have entrance holes that could be large enough for great tits (32 mm diameter) and in some plots have additional small-holed nest boxes available for blue tits (26 mm diameter). Nest boxes usually are available in all plots at high densities (e.g., >6.6.ha^{-1}) and did not limit population size. In total, we calculated 919 yearly mean laying dates and 916 yearly mean clutch sizes across 75 study plots with both great and blue tits breeding during the period 1957-2012 (Møller et al. 2014a, b). Study years started in 1957 in Vlieland and ended in 2012 in several study plots. The mean (SD) numbers of years monitored was 11.49 (14.66) (range: 1-55 years). The mean (SD) Nearest Neighbour Distance was 173.6 (115.4) km.

The abundance of great and blue tits changes across years within study plots. The average abundance of great tits was 18 (range: 1-137) occupied nest boxes and for blue tits 17 (range: 1-99) occupied nest boxes. The average density was 0.68 breeding pairs / ha for great tit and 0.65 breeding pairs / ha for blue tit. We included only study plots in which both great and blue tits had been recorded breeding at least once in order to ensure that all study plots contained suitable habitats, breeding sites and nest boxes for both species. Although the taxonomy of tits is currently under revision (Stenning 2018), we used two taxa of tits (great tit and blue tit) with comparable ecologies without considering that some populations in the Canary Islands and North Africa may constitute the separate species *Cyanistes teneriffae* (Stenning 2018).

We restricted the analyses to first clutches, or early clutches known to be initiated less than 30 days after the first egg was laid in a given year in a study area to standardize sampling procedures (cf. Nager and van Noordwijk 1995). We assumed that the very small number of unidentified early repeat clutches that usually result from perturbations (e.g. Haywood 1993), or lay-dates calculated from information obtained from different breeding stages (e.g. Lambrechts et al. 1997), did not substantially alter the overall average clutch size and average lay date per study plot. Second or late clutches were excluded from analyses because they are usually smaller than first or early clutches and their frequency varies between years and habitats (e.g. Kluijver 1951, Lambrechts et al. 2008).

All data are available at DOI: doi:10.5061/dryad.p763611.

Life-history traits and environmental factors

Information on latitude, longitude and altitude was provided by the authors of earlier studies or found in publications (for details, see Vaugoyeau et al. 2016, Møller et al. 2014a, b, 2018). Tree species vary significantly in timing and amount of invertebrates available for raising offspring in tits (e.g. Kennedy and Southwood 1984, Lambrechts et al. 2008). We classified vegetation as 'deciduous' habitat dominated by non-evergreen broad-leaved deciduous trees (*Alnus, Betula, Carpinus, Citrus, Fagus, Fraxinus, Malus, Quercus,* including *Q. faginea*), 'evergreen' habitat dominated by non-coniferous broad-leaved evergreen trees (*Q. ilex, Q. suber*), 'coniferous' habitat dominated by coniferous trees (*Abies, Cedrus, Picea, Pinus*), or 'mixed' habitats formed by a combination of the former tree vegetation classes (e.g. deciduous mixed with evergreen). Study plots were classified as either rural or urban, using the classifications provided by the original studies. Urban areas were characterized by city parks, gardens and similar habitats in close proximity to humans, while forests, plantations and similar habitats were classified as rural. Only nest box studies were included. We calculated the internal floor area (in cm²) of nest boxes, using publications (e.g. Lambrechts et al. 2010) or additional information provided by participants. The material constituting the nest box was divided into two broad binary classes that are readily distinguishable: wood scored as 1, which includes tree trunks, plywood, board-masonite, or board (e.g. Gustafsson and Nilsson 1985) and concrete scored as 0 (a mixture of cement and other materials; Lambrechts et al. 2010). We included all these input variables in the statistical models because previous studies have indicated that each of these variables are significant predictors of laying date and clutch size (Lambrechts *et al.* 2010; Møller *et al.* 2014a, b; Vaugoyeau *et al.* 2016).

Major life history traits are known to vary among years. For instance, in local study plots biotic (e.g. resource availability, intra- or interspecific interactions) and abiotic factors (e.g. weather) can vary substantially among years perhaps explaining within-plot variation in average clutch size (e.g. Kluijver 1951, Perrins 1965, Both 2000). We thus used study year as a random factor in all analyses.

Temperature

We used temperature anomalies rather than temperatures themselves to characterize climate across the very large geographic area of the study because we were interested in the effect of temperature change at each study site. Temperature anomaly is defined as a departure from a reference value or long-term average. A positive anomaly indicates that the observed temperature was warmer than the reference value, while a negative anomaly indicates that the observed temperature was cooler than the reference value. If, for example, the reference value is 15ºC and the measured temperature is 17ºC, then the temperature anomaly is +2ºC (17ºC – 15ºC (CMB and Crouch 2012). Mean great tit laying date was 22nd April (range: 19th March-12th May, n=75 study plots) and mean blue tit laying date was 23rd April (range: 17th March-13th May, n=75 study plots). Thus, we selected mean spring temperature anomalies during March-May as an appropriate time window that would reflected the temperatures experienced prior to the start of reproduction for all plots. Likewise, we used the mean winter temperature anomalies during December-February and mean annual temperature anomalies estimated as the temperature anomaly for every year. These temperature anomalies were calculated with respect to the average temperature obtained for the time window 1980-2010 taken for each study plot. Temperature anomalies for each study plot were extracted from a 5 x 5 degree-grid where temperature anomalies were calculated by averaging the anomalies for each meteorological station that is found within a grid point (https://www.ncdc.noaa.gov/cag/). Temperature anomalies tend to be highly positively correlated across distances of less than 1000's km (Hansen and Lebedeff 1987) and hence using a 5 x 5 degree grid was adequate.

Statistical analyses

We tested whether temperature anomaly interacts with density affecting the competitive or coexistence relationship between great and blue tits to affect laying date and clutch size by evaluating possible candidate models obtained from four general linear mixed models. We evaluated predictors explaining four response variables (i.e. laying date of great and blue tits and clutch size of great and blue tits, respectively) by defining for each response a full model. The models were set with the aim to test the predictions stated in Table 1 (see full model formula in foot notes). Each of these full models included the density of great and blue tits and temperature anomaly of spring and winter. We explicitly included the interaction term between (winter or spring) temperature anomaly and density of great or blue tits to test the hypothesis that an increase in temperature anomaly could affect laying date or clutch size of either species. We also included the previously listed confounding variables that have been shown to affect laying date or clutch size of great and blue tits. These input variables were latitude, longitude, altitude, nest box material (wood or concrete), nest floor surface, urbanization (rural or urban) and habitat (coniferous, deciduous, mixed or evergreen). The full model was a linear mixed effect model in which we included these predictors as fixed effects and two random intercepts for study plot and year that were retained in all models. We included in the same model density of blue and great tit and temperature anomaly in spring and winter because these variables were only moderately positively correlated (density of great tit *vs* density of blue tit: $r_s = 0.441$, $P < 0.001$; temperature anomaly in spring *vs* temperature anomaly in winter: $r_s = 0.497$, $P < 0.001$). We calculated Variance Inflation Factors (VIF) in the four models (Freund et al. 2003). All predictors showed low VIF values less than 5.0.

For all models we first standardized the input variables entering the full model by scaling them after centering their mean and dividing by two standard deviations, which allowed comparison on the same scale of coefficients of binary factors and covariates. Therefore, the parameter estimates were standardized effect sizes on a comparable scale (Gelman 2008, Grueber et al. 2011). In total, for the analyses on laying date we included in each full model 15 predictor terms resulting in $2^{15} = 32{,}768$ candidate models. For the analyses on clutch size we also included laying date in each full model which resulted in 16 terms or $2^{16} = 65{,}536$ candidate models. Top models of all possible candidates were determined using Akaike Information Criterion with a correction for small sample size (AICc). We calculated Akaike weight (*w*) for each candidate model that can be interpreted as the probability that it is the best model, given the data and set of candidate models (Burnham and Anderson, 2002). The reference level of the fixed factor ‘habitat’ was ‘conifer’, and for ‘urbanization’ it was ‘rural’ and for ‘material’ it was ‘concrete’ in all models. The final model was obtained by averaging the parameter estimates from top models at a cut-off criterion of AIC < 6.0 (Richards 2008). We employed the package MuMIn (Bartón 2009) and the package lme4 (Bates and Maechler 2009) using R version 3.3.2 (R Development Core Team 2019). The confidence intervals (CI 95%) were calculated from the final model using the parameter estimates (effect size) and the associated SE obtained after model averaging. We assumed that a predictor term significantly contributed to explaining the response variable when the CI for the estimated parameter excluded zero (Grueber et al. 2011).

Results

Temporal trend in temperature anomaly

The annual temperature anomaly (January-December) increased on average +0.027ºC / year (*F* = 307.4, df = 1, 462, $p < 0.0001$, estimate (SE) = 0.027 (0.001)). Spring temperature anomaly for March-May increased on average by +0.033ºC /year (*F* = 202.60, df = 1, 462, $p < 0.0001$, estimate (SE) = 0.033 (0.002)). Winter temperature anomaly for December-February increased on average by +0.011ºC / year (*F* = 12.06, df = 1, 462, $p < 0.0006$, estimate (SE) = 0.011 (0.003)). These results were obtained for three different linear mixed-effect models where study plot was included as a random term with temperature anomaly (year, winter or spring) as the dependent variable and year (centered as its overall mean) included as a fixed effect. The inclusion of a random slope for year within study plot did not improve the models (e.g., analyses where models with and without a random slope for year: Temperature anomaly (year): Likelihood-ratio = 0.078, *P* = 0.96; Temperature anomaly (spring): L-ratio = 0.000, p= 1.0; Temperature anomaly (winter): L-ratio = 0.000, p = 1.0), and, therefore, a common slope for year was assumed in these analyses. Thus, the increase in temperature anomaly did not differ significantly amongst study plots.

Inter- and intraspecific competition and response to climate change

Great tit timing of reproduction

The models of the analyses for great tit showed that laying date advanced with increasing spring temperature anomaly (Table 2, Fig. 1). The interaction term between spring temperature anomaly and blue tit density, on the one hand, and winter temperature anomaly and great tit density, on the other, also influenced great tit laying date significantly. Thus, great tits laid earlier as spring temperature anomaly increased and laying date advanced more steeply with spring temperature anomaly as blue tit density increased (Fig. 3a). In contrast, great tit laying date was delayed with winter temperature anomaly as great tit density increased (Fig. 3b). These effects were found while controlling for confounding variables known to affect laying date, such as latitude, longitude, altitude, habitat, urbanization, nest floor surface and nest-box material.

Blue tit timing of reproduction

The final model for blue tit laying date was similar to that for great tits. Across Europe and North Africa blue tits advanced laying date as spring temperature anomaly increased (Table 3, Fig. 1). Similarly to the results in great tits, blue tit lay date was significantly correlated with the interaction between spring temperature anomalies and heterospecific density, and in this case it was also correlated with the interaction between spring temperature anomalies and conspecific density. Likewise, blue tit laying date was significantly correlated with the interaction of great tit density with winter temperature anomaly. Thus, blue tits laid earlier as spring temperature anomalies increased and laying date advanced more steeply with spring temperature anomaly as blue tit density increased, this effect being modulated by the interaction of temperature anomaly both with great and blue tit density (e.g. Fig. 4a for the interaction between density of blue tit and spring temperature anomaly on laying date of blue tit). In contrast, blue tit laying date was delayed more steeply with winter temperature anomaly as density of great tits increased (Fig. 4b). This was the case for the model analysing great tit laying date (Fig. 3b). These effects were found while controlling for confounding variables known to affect laying date, such as latitude, longitude, altitude, habitat, urbanization, nest floor surface and nest-box material.

Effects on great tit clutch size

Across Europe and North Africa great tit clutch size decreased as winter temperature anomaly increased, and it was not correlated with the main effect of spring temperature anomaly (Table 4, Fig. 2). We found opposite interaction effects between temperature anomaly in spring and winter and the density of blue tits on clutch size of great tits. We also found opposite effects (i.e. different sign) on the interaction between spring temperature anomaly and density of great or blue tit on great tit clutch size. Thus, there was a negative interaction between spring temperature anomaly and great tit density on great tit clutch size, and a positive interaction between effect of spring temperature anomaly and blue tit density on great tit clutch size. Thus, great tit clutch size was further reduced with increasing spring temperature anomaly as great tit density increased, and with increasing winter temperature anomaly as blue tit density increased (Figs 5a-b). In contrast, clutch size increased with increasing spring temperature anomaly when blue tit density increased (Fig. 5c). These effects were found while controlling for confounding variables known to affect laying date, such as latitude, longitude, altitude, habitat, urbanization, nest floor surface and nest-box material.

Effects on blue tit clutch size

Opposite to what we found for great tit clutch size, we did not find any interaction effect between temperature anomaly in either spring or winter and the density of either great or blue tit on clutch size of blue tit. These effects were found while controlling for confounding variables known to affect clutch size, such as laying date, latitude, longitude, altitude, habitat, urbanization, nest floor surface and nest box material.

Discussion

An increase in temperature anomaly due to climate warming was correlated with the timing of breeding and clutch size in great and blue tits across large spatial and temporal scales in Europe and North Africa. This is not a novel finding since effects of temperature anomaly on laying date and clutch size have previously been found in these species (e.g. Visser et al. 1998, 2003). What is novel though is that the strength of the effects of temperature anomaly on laying date and clutch size varied with density, as shown by multiple significant interaction terms between density and temperature anomaly in both winter and spring. Furthermore, this is the first study showing that the effect of temperature anomaly on laying date and clutch size is widespread across large spatial and temporal scales in these coexisting tits.

In this study we focused on how intra- and interspecific density interacted with climate warming, and how this affected two species of coexisting tits. Blue and great tit advanced laying date as spring temperature increased (Prediction 1: supported). In contrast, winter temperature did not correlate with laying date of either great or blue tit (Prediction 2: not supported). However, when winter temperature increased both great and blue tits delayed laying date as density increased (Prediction 3: supported). Specifically, that was the case for laying date of great tits when intraspecific density increased and for laying date of blue tits when heterospecific density increased. In contrast, when spring temperatures increased both great and blue tits advanced laying date as density increased (prediction 4: not supported). Specifically, it occurs for laying date of great tits when heterospecific density increased, and for laying date of blue tits when both hetero- and conspecific density increased.

We expected that an increase in spring temperature anomalies should advance laying date, and that an increase in density should delay laying, which could cancel the effect of spring temperature anomaly on laying date (Prediction 4). As expected, an increase in spring temperature anomaly resulted in a similar advance in laying date in the two tits species. In contrast, sites where density of conspecifics or heterospecifics is high, an additional increase in temperature anomaly in spring resulted in further advance in laying date. It is well known that social information gathered from conspecifics and heterospecifics show that similar ecological niches could serve as important cues to select breeding habitat or to change behaviour related to the acquisition of food, as has been already demonstrated in birds, including great tit (e.g. Aplin et al. 2015, Samplonius et al. 2017). For instance, migratory pied flycatcher *Ficedula hypoleuca* could gather social information from the breeding phenology of great tits as a social cue to select its breeding habitat later during their breeding season (Samplonius and Both 2017). It could be possible that the presence of more conspecifics or heterospecifics could act as social cues that serve great and blue tits to advance laying date more to cope with an earlier emergence of caterpillars and hence improving their responses to climate change. That would be the case when advanced laying date results in a higher degree of synchrony between emergence of food and timing of breeding.

It is also possible that great and blue tit interact with other migrant or resident species. For instance, it is known that great and blue tits could compete with pied flycatcher (*Ficedula hypoleuca*). However, it has been shown that the two species of tit affect pied flycatcher but not the reverse (Wittwer et al. 2015).Although, there could be other interacting species we consider that the most important competitive interaction was recorded in this study. This question could be subject to experimental and observational future studies.

Interestingly, as winter temperatures increased, clutch size declined in both great and blue tits (Prediction 6: supported). It should be highlighted, that winter temperature was more strongly correlated with great tit than blue tit since clutch size is reduced more after warmer winters in the former species. In contrast, spring temperatures were not correlated with clutch size in either species (Prediction 5: not supported). Climate warming and its interaction with density affected clutch size of great and blue tits differently. Thus, we did not find any significant interaction between winter or spring temperature and density of great or blue tits on clutch size of blue tits. However, that was not the case for great tits since spring and winter temperature interacted with density affecting great tit clutch size. Thus, clutch size of great tit was reduced more when spring temperature and density of conspecifics (i.e. great tits) increased (Prediction 7: supported), but it increased more steeply when spring temperature and density of heterospecifics (i.e. blue tits) increased (Prediction 7: not supported). Furthermore, winter temperature interacted with competition affecting only clutch size of great tits. Thus, clutch size of great tit was reduced more strongly when winter temperature and density of heterospecific (i.e. blue tits) increased which is in line with results of Dhondt (2010) in which he reports a stronger effect of density on clutch size of great tit than blue tit (Prediction 8: supported).

Density-dependence could result in a delay in laying date and a reduction in clutch size (Stenseth et al. 2015). An increase in intra- or interspecific competition (resulting from higher densities) could affect the response to climate warming (Stenseth et al. 2015). If that was the case, we would expect a significant interaction between density and temperature anomaly on laying date and clutch size. Indeed, an increase in winter temperature interacted with density of great tit by delaying laying date of both great and blue tit (Prediction 3: supported). An increase in winter temperature anomaly could increase adult survival in both species, specifically in blue tits, and this could affect the intensity of competition the subsequent spring, which in turn could reduce clutch size and delay laying at the population level due to density-dependent processes including an increase in the proportion of young inexperienced breeders (e.g. Dhondt et al. 1992, Ferrer and Donazar 1996). Importantly, that is what we found for the interactions between winter temperature and density for laying date of great and blue tit and for clutch size of great tit. Alternatively, energetic constraints imposed during winter may also have physiological consequences that may affect laying date. Warm winters may select for metabolic genotypes with a reduced rate of living resulting in smaller clutches (Nilsson and Nilsson 2016). However, our statistical analyses still showed a relationship between temperature anomaly and life history traits after adjustment for density, implying that there are genuine temperature anomaly effects.

Warm springs imply faster caterpillar development, and birds have to speed up to keep up with the caterpillars. One way of doing so is by laying fewer eggs, or by starting incubation earlier (Matthysen et al. 2011). Therefore, it would be possible that the advance in laying date would not suffice to match the emergence of caterpillars, the main food for nestling tits (Perrins 1965, Both et al. 2009). Reduced clutch size may constitute an additional reproductive strategy to decrease the mismatch by advancing incubation, as experimentally shown in the great tit (Bleu et al. 2017). Therefore, a mismatch between emergence of food and timing of reproduction could also occur at large spatial and temporal scales across the breeding season, as already shown for specific European populations of birds (e.g. Visser et al. 1998, Both et al. 2009). In contrast, there is only little evidence of mismatch between blue and great tits and their food resources except for summers with warmer spring (Burgess et al. 2018). Therefore, there are different explanations for the observed reduction in clutch size with increasing temperatures in winter, and this should be explored further in future studies.

Since increasing temperature anomaly in winter reduced clutch size of both species, the abundance of both species should be affected equally by climate warming. However, winter temperature anomaly has a stronger effect on clutch size in great tit (estimate (SE) =-0.506 (0.079), Table 4) than in blue tit (estimate (SE)=-0.159 (0.067), Table 5). However, clutch size is only a component of fitness and we need future studies to try to find out how these contrasting effects translate into differences in population sizes between these tits species. The interacting effect of climate warming with density affected clutch size of great tit while it did not affect clutch size of blue tits. For instance, an increase in spring temperature interacted differently with density of blue tit compared to the effect of density of great tits on their clutch size. Specifically, increasing spring temperature interacted with density of blue tits increasing clutch size of great tit (i.e. rejecting prediction 7), while increasing spring temperatures interacted with density of great tits to decrease clutch size of great tits (i.e. supporting prediction 7). In contrast, the interaction between spring temperature anomaly and density of great or blue tits on clutch size of blue tits was not significant. That is in accordance with prediction 7 since we predicted stronger effects on great compared with blue tits. Therefore, a rapid advance in laying date with density and temperature anomaly did not provide a reproductive advantage for great tits, while that could be the case for blue tits since clutch size was not reduced in blue tits when temperature anomaly and density interacted to affect clutch size. The difference in response to clutch size in great compared to blue tits could be related that either blue tits consume earlier instars of caterpillar larvae that emerge earlier or to that the two species may forage in different micro-habitats, such as different heights in trees with great tits consuming more food on the ground (Slagsvold and Wiebe 2007). The phenology of invertebrate prey may differ between such micro-habitats (Tremblay et al. 2005, Visser et al. 2003), and, therefore, the difference in prey response to climate change by the two species could explain small differences in timing of breeding. Therefore, if these trends in climate warming continue at similar rates, these interspecific differences could translate into differences in abundance or population size favouring blue tit since this species seems to be less affected by climate warming than great tit.

In conclusion, when studying the effects of increasing temperature anomalies on timing of reproduction and clutch size at large spatial and temporal scales, we found that great and blue tits responded to climate warming by advancing timing of reproduction. However, this advance in breeding date with increasing temperature anomaly did not prevent a reduction in clutch size due to increasing temperature anomalies and increasing densities. In addition, the response to increasing temperature anomaly interacted with density by advancing laying date even more at higher densities. This interaction reduced clutch size in great, but not in blue tits. Further studies are needed to examine how intra- and interspecific relationships interact with temperature anomalies, on timing of breeding and breeding success, which may ultimately affect fitness and population size.

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Author contributions

A.P.M. and J.B. conceived the idea. A.P.M. and J.B. analysed data and A.P.M. J.B. and A.A.D. wrote the manuscript. A.P.M., A.A.D., F.A., A.A., J.Ba., E.B., C.B., JcB.,J.C.B., J.C., F.C., M.C., M.Ch.,C.C., A.D., M.E., T.E., P.N.F., J.T.F., A.G., A.E.G., A.G.G., L.G., I.H., I.R.H., P.H., S.A.H., S.J., A.J., R.J.,E.K., I.K., T.L., B.L., E.L.,O.L, M.C.M., R.M., B.M., E.M.,T.D.M., S.M., C.M., M.M., R.G.N., J.-Å.N., S.G.N., A.C.N., M.V.N., M.O.,C.S.P., R.P., I.P., V.R., H.R.,Hu.R., S.R.,J.C.S.,J.T.S.,L.P.S, T.S.,T.So. A.S., M.J.S., J.T.,P.T., A.J.v.N., W.W., and M.M.L. collected data and approved final manuscript.

Conflicts of interest

The authors declare not conflicts of interest

Permits

The data used in every study plot have the appropriated permits issued for each country or region government.

Data accessibility

Data are available from the Dryad Digital Repository upon acceptance.

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Figure legends

Figure 1 Effects of temperature anomaly (ºC) in spring and winter on laying date of great and blue tits where 1 = January 1st. The lines (± 95% CI) are the predicted values obtained from a linear mixed-effect model where latitude, longitude and altitude and nest floor surface are maintained at their mean values and habitat, urbanization and nest box material at their reference values (i.e., conifer, rural habitat and box material concrete). Black lines represent effect size and did not include zero in 95% CI and grey lines represent effect size and did include zero in 95% CI (see Tables 3 and 4 for details)

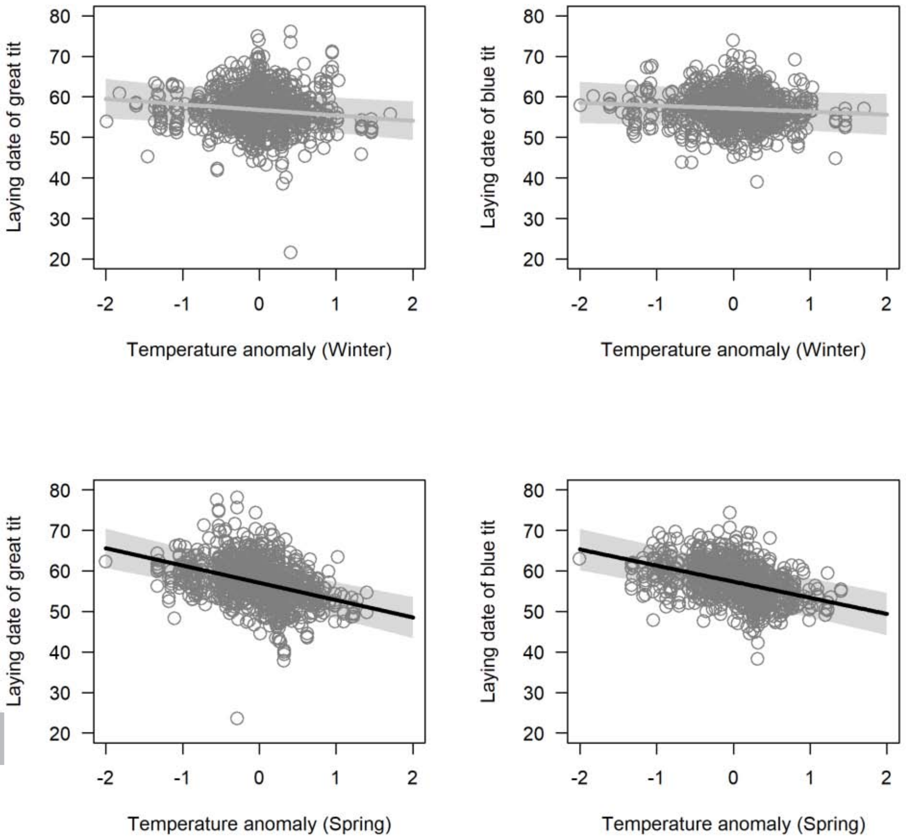

Figure 2 Effects of temperature anomaly (ºC) in spring and winter on clutch size of great and blue tits. The lines (±95% CI) are the predicted values obtained from a linear mixed-effect models where latitude, longitude and altitude and nest floor surface are maintained at their mean values and habitat, urbanization and material at their reference values (i.e., conifer, natural habitat and the construction material concrete, respectively). Black lines represent effect sizes that did not included zero in 95% CI and grey lines represent effect sizes that did included zero in 95% CI (see Tables 5 and 6 for details)

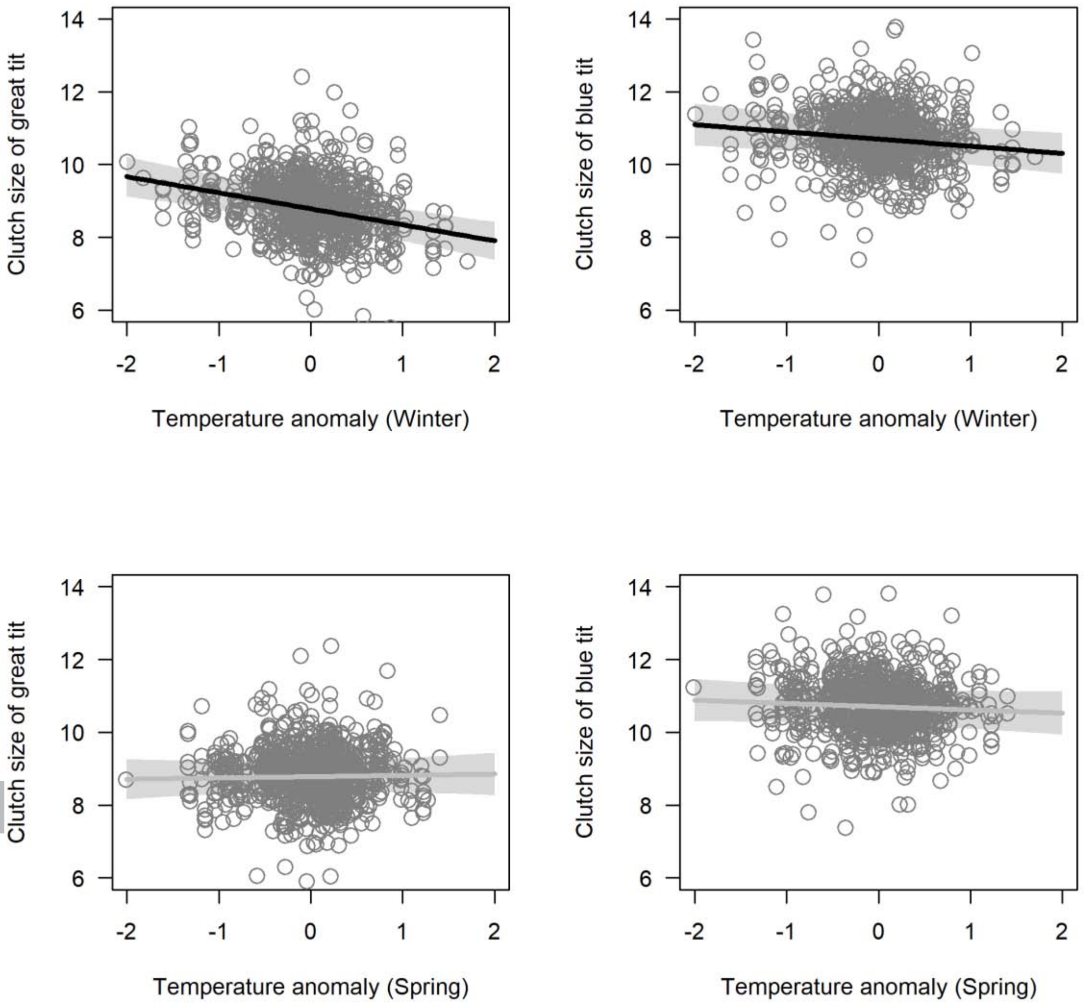

Figure 3 Effects of the interaction term of temperature anomaly (ºC) in spring and density (number of nest boxes ha^{-1}) of great tits on laying date of great tits (a) and effects of the interaction term of temperature anomaly in winter and density of great tits on laying date of great tits (b). The surfaces represent the predicted values at average values for other predictors included in the model obtained from a final model after averaging the top models obtained from 32,768 candidate models

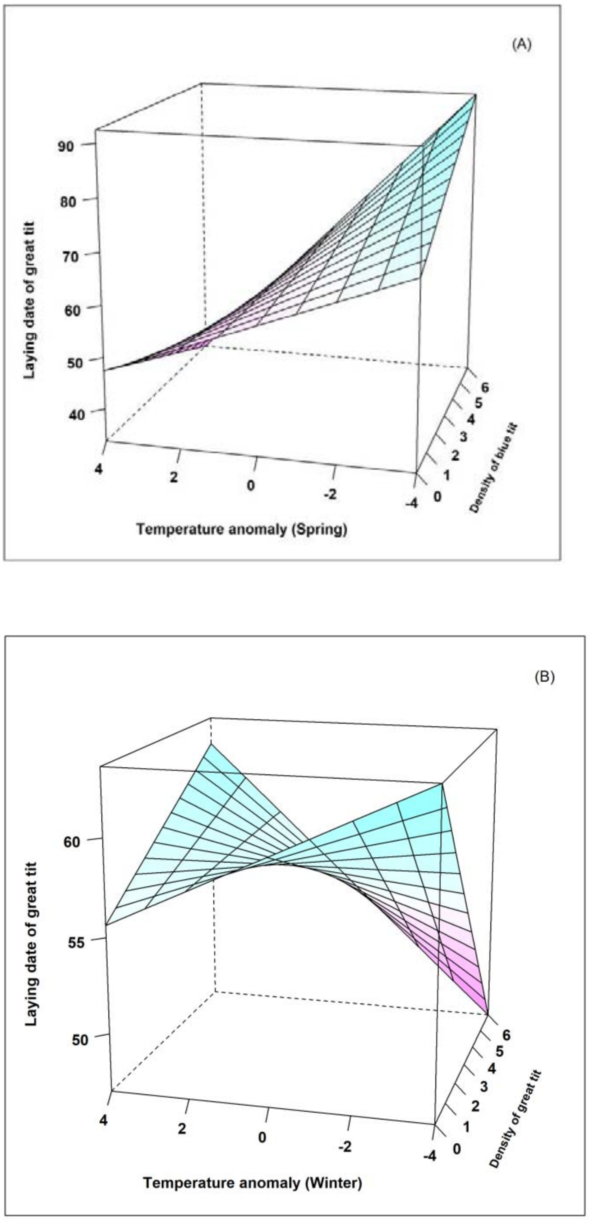

Figure 4 Effects of the interaction term of temperature anomaly (ºC) in spring and density (number of nest boxes ha^{-1}) of blue tits on laying date of blue tits (a) and effects of the interaction term of temperature anomaly in winter and density of great tits on laying date of blue tits (b). The surfaces represent the predicted values at average values for other predictors included in the model obtained from a final model after averaging the top models obtained from 32,768 candidate models

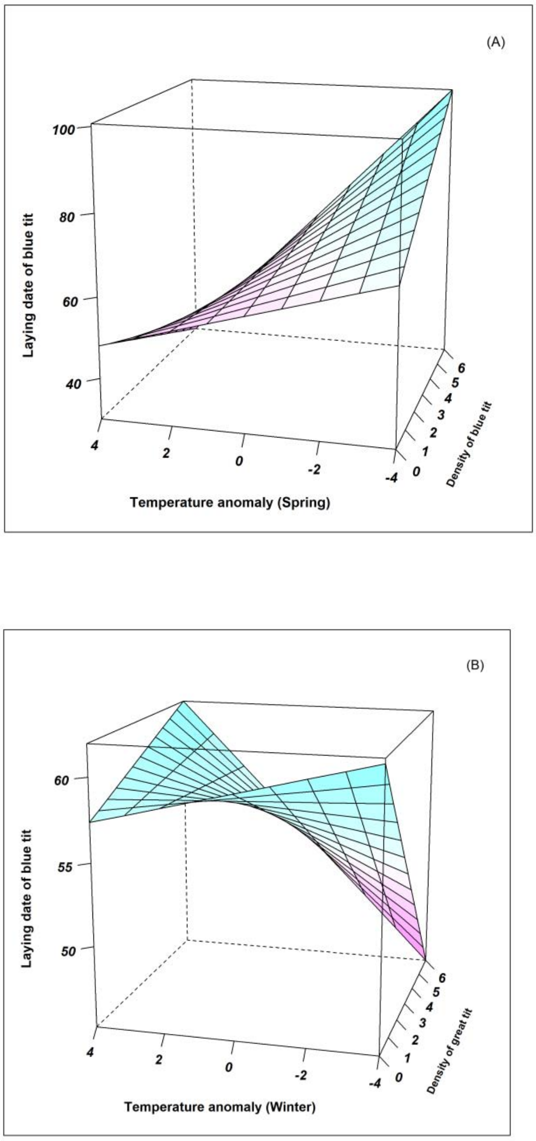

Figure 5 Effects of the interaction term of temperature anomaly (ºC) in spring and density of great tits (nest boxes ha^{-1}) on clutch size of great tits (a) and the interaction term of temperature anomaly (ºC) in winter and density of blue tits on clutch size of great tits (b) and the interaction term of temperature anomaly (ºC) in spring and density of blue tits (nest boxes ha^{-1}) on clutch size of great tits (c). The surfaces represent the predicted values at average values for other predictors included in the model obtained from a final model after averaging the top models obtained from 65,536 candidate models

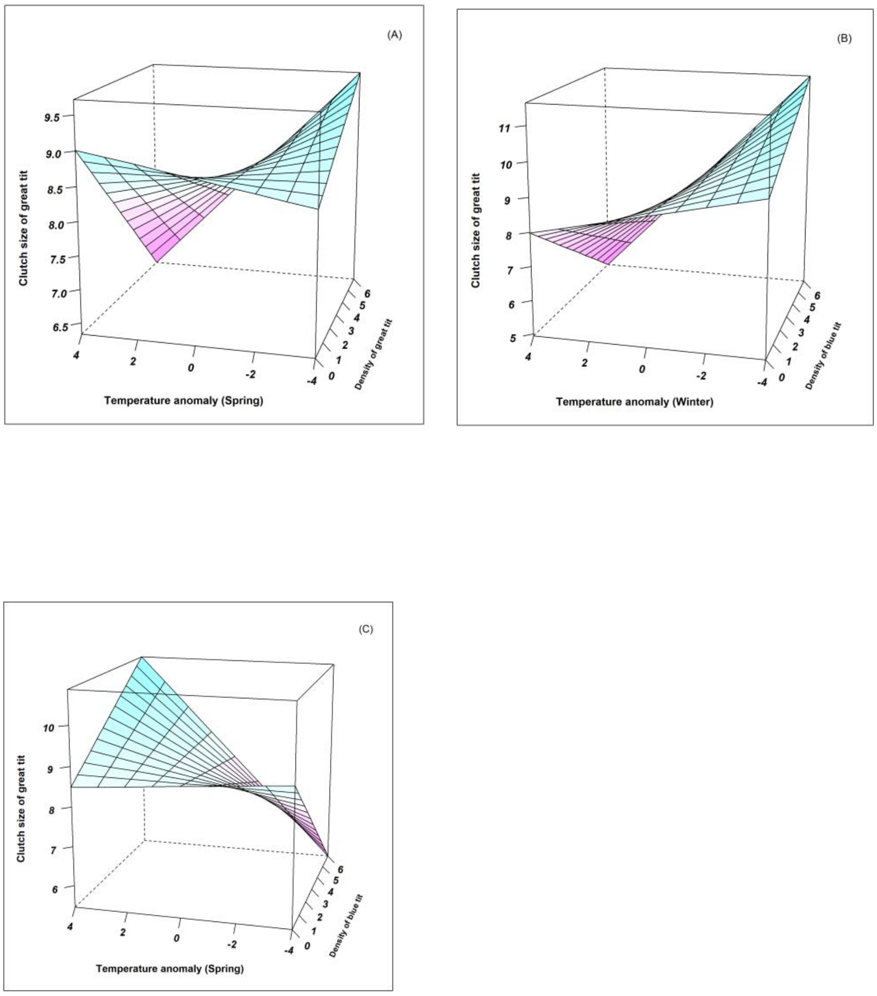

Table Legends

Table 1 Predictions from hypotheses about response to climate warming and its interaction with density in great and blue tits studied across 75 study sites in Europe and North Africa. The predictions are depicted as expected from statistical models described in Methods and presented in Tables 2-5. GT is great tit. BT is Blue tit. T^a = temperature anomaly. Nfloor= N[illegible] surface (mm). Models were run separately for GT and BT laying date and clutch size, respectively. Full models are in Table foot. Symbol | refers to the random effects part of the formula. Pred. is prediction number. Model formula only depicted the variables of interest related to the predicted relationship.

Pred.	Model formula	Predict relationship
1	Laying date (GT)~β_0+β_1 x T^a spring	$\beta_1 \neq 0$ and $\beta_1 < 0$. Laying date advance as T^a spring increases
	Laying date (BT)~β_0+β_2 x T^a spring	$\beta_2 \neq 0$ and $\beta_2 < 0$. Idem.
		$\beta_2 > \beta_1$. BT advance more laying date than GT as T^a spring increases
2	Laying date~β_0+β_1 x T^a winter	$\beta_1 \neq 0$ and $\beta_1 > 0$. Laying date delayed as T^a winter increases
3	Laying date~β_0+β_7 x (T^a winter: Density)	$\beta_7 \neq 0$ and $\beta_7 > 0$.Laying date delayed more with density as T^a winter increases
4	Laying date~β_0+β_7 x (T^a spring: Density)	$\beta_7 = 0$ No effect
5	Clutch size (GT)~β_0+β_1 x T^a spring	$\beta_1 \neq 0$ and $\beta_1 < 0$. Clutch size is reduced as T^a spring increases
	Clutch size (BT)~β_0+β_2 x T^a spring	$\beta_2 \neq 0$ and $\beta_2 < 0$. Idem.
		$\beta_1 < \beta_2$. GT reduced more clutch size than BT as T^a spring increases
6	Clutch size~β_0+ β_1 x T^a winter	$\beta_1 \neq 0$ and $\beta_1 < 0$. Clutch size is reduced as T^a spring increases

7	Clutch size~$\beta_0+\beta_7$ x (T^a winter: Density)	$\beta_7 \neq 0$ and $\beta_7<0$.Clutch size is reduced more with density as T^a winter increases
8	Clutch size~$\beta_0+\beta_7$ x (T^a spring: Density)	$\beta_7 \neq 0$ and $\beta_7<0$.Clutch size is reduced more with density as T^a spring increases

Laying date ~ $\beta_0+\beta_1$ x T^a [illegible] T^a winter+ β_3 x Density GT+ β_4 x Density BT + β_5 x (T^a spring: Density GT)+ β_6 x (T^a spring: Density BT)+ β_7 x (T^a winter: Density GT)+ β_8 x (T^a winter: Density BT)+ β_9 x Latitude+ β_{10} x Longitude+ β_{11} x Altitude+ β_{12} x Habitat+ β_{13} x Urbanization+ β_{14} x Nfloor+ β_{15} x Nest material+(1 | Site)+(1|Year)

Clutch size ~ $\beta_0+\beta_1$ x T^a spring+ [illegible] T^a winter+ β_3 x Density GT+ β_4 x Density BT + β_5 x (T^a spring: Density GT)+ β_6 x (T^a spring: Density BT)+ β_7 x (T^a winter: Density GT)+ β_8 x (T^a winter: Density BT)+ β_9 x Laying date +β_{10} x Latitude+ β_{11} x Longitude+ β_{12} x Altitude+ β_{13} x Habitat+ β_{14} x Urbanization+ β_{15} x Nfloor+ β_{16} x Nest material+(1 | Site)+(1|Year).

Table 2 Summary results after model averaging of the effects of temperature anomaly in spring and winter and density of great and blue tits on laying date of great tits across Europe and North Africa. Estimates (SE) and 95% CI are reported. The model also included other potential predictors of laying date of great tit. Sample size is 919 observations on yearly average laying date taken across 75 sites across Europe. Effects in bold font are statistically significant

Parameter	Estimate	SE	CI (95%)
Intercept	58.910	2.130	(54.729, 63.091)
Density of Blue tit (BT)	1.497	0.766	(-0.006, 3.002)
Density of Great tit (GT)	**-1.730**	**0.611**	**(-2.928, -0.530)**
Latitude	**8.766**	**2.738**	**(3.392, 14.139)**
Longitude	**5.295**	**1.918**	**(1.531, 9.060)**
Floor surface (nest)	0.069	1.145	(-2.177, 2.317)
T^a Spring	**-5.100**	**0.626**	**(-6.330, -3.870)**
T^a winter	-0.977	0.559	(-2.075, 0.121)
T^a Spring x BT	**-2.452**	**0.849**	**(-4.199, -0.875)**
T^a Spring x GT	-1.267	0.760	(-2.759, 0.224)
T^a Winter x BT	-0.521	0.913	(-2.313, 1.270)
T^a Winter x GT	**1.535**	**0.702**	**(0.157, 2.914)**
Altitude	0.389	2.577	(-4.668, 5.448)
Material	2.027	1.837	(-1.577, 5.632)
Urbanization	**-2.553**	**1.259**	**(-5.026, -0.081)**
Habitat (Deciduous)	**-4.858**	**2.461**	**(-9.689, -0.027)**
Habitat (Evergreen)	1.395	3.603	(-5.677, 8.467)
Habitat (Mixed)	**-3.432**	**1.039**	**(-5.471, -1.392)**

*Effect sizes have been standardized to two SD following Gelman (2008). Reference levels were (no) urbanized for urbanization and (conifer) for habitat. Parameter estimates for predictors with confidence intervals not including zero are highlighted in bold. CI is confidence interval

Table 3 Summary results after model averaging of the effects of temperature anomaly in spring and winter and density of great and blue tit on laying date of blue tit across Europe and North Africa. Estimates (SE) and 95% CI are reported. The model also included other potential predictors of laying date of great tit. Sample size is 919 observations on yearly average laying date taken across 75 sites across Europe. Effects in bold font are statistically significant

Parameter	Estimate	SE	CI (95%)
Intercept	58.836	2.273	(54.374, 63.299)
Density of Blue tit (BT)	**1.946**	**0.651**	**(0.667, 3.224)**
Density of Great tit (GT)	**-1.713**	**0.519**	**(-2.732, -0.693)**
Latitude	**22.628**	**2.738**	**(16.475, 28.782)**
Longitude	0.079	2.155	(-4.150, 4.309)
Floor surface (nest)	**-2.191**	**1.038**	**(-4.229, -0.153)**
T^a Spring	**-4.925**	**0.526**	**(-5.959, -3.891)**
T^a winter	-0.469	0.471	(-1.394, 0.454)
T^a Spring x BT	**-2.794**	**0.732**	**(-4.232, -1.357)**
T^a Spring x GT	**-1.512**	**0.654**	**(-2.796, -0.227)**
T^a Winter x BT	-0.652	0.731	(-2.087, 0.872)
T^a Winter x GT	**1.472**	**0.571**	**(0.350, 2.594)**
Altitude	**15.362**	**2.620**	**(10.219, 20.506)**
Material	1.307	1.907	(-2.436, 5.051)
Urbanization	**-2.592**	**1.080**	**(-4.713, -0.472)**
Habitat (Deciduous)	**-5.985**	**2.626**	**(-11.139, -0.831)**
Habitat (Evergreen)	6.846	3.793	(-0.598, 14.290)
Habitat (Mixed)	**-3.684**	**0.883**	**(-5.418, -1.951)**

*Effect sizes have been standardized to two SD following Gelman (2008). Reference levels were (no) urbanized for urbanization and (conifer) for habitat. Parameter estimates for predictors with confidence intervals not including zero are highlighted in bold. CI is confidence interval

Table 4 Summary results after model averaging of the effects of temperature anomaly in spring and winter and density of great and blue tit on clutch size of great tit across Europe and North Africa. Estimates (SE) and 95% CI are reported. The model also included other potential predictors of clutch size of great tit. Sample size is 916 observations on yearly average laying date taken across 75 sites across Europe.

Effects in bold font are statistically significant

Parameter	Estimate	SE	CI (95%)
Intercept	8.642	0.200	(8.247, 9.036)
Laying date of Great tit	**-0.839**	**0.094**	**(-1.024, -0.653)**
Density of Blue tit (BT)	-0.150	0.102	(-0.351, 0.050)
Density of Great tit (GT)	**-0.203**	**0.080**	**(-0.362, -0.044)**
Latitude	0.145	0.404	(-0.648, 0.939)
Longitude	**1.110**	**0.180**	**(0.759, 1.464)**
Floor surface (nest)	0.101	0.143	(-0.179, 0.382)
T^a Spring	0.040	0.092	(-0.140, 0.222)
T^a Winter	**-0.506**	**0.079**	**(-0.662, -0.349)**
T^a Spring x BT	**0.322**	**0.122**	**(0.083, 0.562)**
T^a Spring x GT	**-0.277**	**0.098**	**(-0.470, -0.084)**
T^a Winter x BT	**-0.445**	**0.120**	**(-0.682, -0.208)**
T^a Winter x GT	0.128	0.096	(-0.060, 0.318)
Altitude	**-0.480**	**0.213**	**(-0.899, -0.060)**
Material	**0.494**	**0.208**	**(0.084, 0.903)**
Urbanization	**-0.655**	**0.163**	**(-0.976, -0.334)**
Habitat (Deciduous)	0.339	0.246	(-0.144, -0.824)
Habitat (Evergreen)	-0.211	0.383	(-0.964, 0.541)
Habitat (Mixed)	0.196	0.142	(-0.082, 0.475)

*Effect sizes have been standardized to two SD following Gelman (2008). Reference levels were (no) urbanized for urbanization and (conifer) for habitat. Parameter estimates for predictors with confidence intervals not including zero are highlighted in bold. CI is confidence interval

Table 5 Summary results after model averaging of the effects of temperature anomaly in spring and winter and density of great and blue tit on clutch size of blue tit across Europe and North Africa. Estimates (SE) and 95% CI are reported. The model also included other potential predictors of clutch size of great tit. Sample size is 916 observations on yearly average laying date taken across 75 sites across Europe

Parameter	Estimate	SE	CI (95%)
Intercept	9.705	0.254	(9.205, 10.205)
Laying date of blue tit	**-0.954**	**0.107**	**(-1.165, -0.743)**
Density of blue tit (BT)	-0.143	0.097	(-0.335, 0.047)
Density of great tit (GT)	-0.109	0.080	(-0.267, -0.047)
Latitude	**1.560**	**0.467**	**(0.643, 2.478)**
Longitude	**0.491**	**0.234**	**(0.030, 0.951)**
Floor surface (nest)	-0.282	0.153	(-0.583, 0.017)
T^{a} Spring	-0.146	0.079	(-0.301, 0.008)
T^{a} Winter	**-0.159**	**0.067**	**(-0.291, -0.026)**
T^{a} Spring x BT	0.032	0.111	(-0.185, 0.250)
T^{a} Spring x GT	-0.136	0.086	(-0.306, 0.034)
T^{a} Winter x BT	0.027	0.100	(-0.169, 0.224)
T^{a} Winter x GT	0.106	0.093	(-0.077, 0.290)
Altitude	**-1.021**	**0.339**	**(-1.687, -0.355)**
Material	**0.608**	**0.261**	**(0.096, 1.121)**
Urbanization	-0.020	0.168	(-0.350, 0.309)
Habitat (Deciduous)	0.272	0.296	(-0.309, 0.854)
Habitat (Evergreen)	**-0.926**	**0.467**	**(-1.843, -0.010)**
Habitat (Mixed)	0.232	0.142	(-0.047, 0.513)

*Effect sizes have been standardized to two SD following Gelman (2008). Reference levels were (no) urbanized for urbanization and (conifer) for habitat. Parameter estimates for predictors with confidence intervals not including zero are highlighted in bold. CI is confidence interval