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## **Effects of climate change on intra- and interspecific competition in two species of hole-nesting birds**

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Running headline:

MØLLER ET AL.

Climate change affects intra- and interspecific competition and  
demographic variables

## **Abstract**

1. Although temperatures have increased considerably in recent decades due to climate change, the effects of increasing temperature on interactions among species are poorly known. We studied the effect of climate warming on the coexistence of two species of secondary hole nesting bird species, great tit *Parus major* and blue tit *Cyanistes caeruleus*, breeding in nest boxes in 75 study plots across Europe and North Africa.

2. Laying date advanced and clutch size became smaller with increasing temperature in both great and blue tit across study sites. There was an interaction between effect of temperature anomaly in spring and density of great and blue tits on laying date of great and blue tits. There was also an interaction effect between temperature anomaly in winter and density of great and blue tits on laying date of blue tits, but not on laying date of great tits.

3. We found an interaction between effect of temperature anomaly in spring and density of great tit on clutch size of great tit, and we found an interaction between effect of temperature anomaly in winter and density of great and blue tit on clutch size of great tit. In contrast, we did not find an interaction between effect of temperature anomaly and density on clutch size of blue tit. This implies that as temperature increased, laying date advanced steeply at high density sites.

4. For great tits clutch size was further reduced with increasing temperature during winter as density of great and blue tits increased and with increasing temperatures during spring as density of great tits increased.

5. Therefore, intraspecific and interspecific competition reduced clutch size in great tit with increasing temperatures, but it did not affect blue tits. This effect may be caused by an increase in temperature negatively affecting coexistence between blue and great tits.

#### KEYWORDS

blue tit, clutch size, *Cyanistes caeruleus*, great tit, interspecific competition, intraspecific competition, laying date, *Parus major*

## 1 | INTRODUCTION

Climate change is currently increasing temperatures, including increased elevated peak temperatures and increased variances in temperatures (Rind et al., 1989; Easterling et al., 2000). Such climate change is currently affecting organisms across the globe with consequences for their distribution, abundance and interactions (e. g. Stenseth et al., 2002; Parmesan & Yohe, 2003; Root et al., 2003; Møller et al., 2010).

Climate change has increasingly been documented to affect interspecific interactions such as those between hosts and parasites (e. g. Møller et al., 2011, 2013), interspecific competition (e. g. Beaugrand et al. 2003; Adler et al., 2006; Durant et al., 2012; Stenseth et al., 2015) and predator-prey interactions (e. g. Post et al., 1999). There are relatively few studies showing clear effects, and only few studies have investigated patterns across large temporal and spatial scales (Møller et al., 2011, 2013).

Climate change has been predicted to affect interspecific competition either through effects on the abundance of limiting resources, changes in the abundance of interacting species and changes in the distribution of species (Møller et al., 2010). Thus, a change in the abundance of one or more species may affect the abundance of others. As an example, Stenseth et al. (2015) showed from detailed analyses of four long-term datasets on great *Parus major* and blue tits *Cyanistes caeruleus* that there were direct density-dependent and density-independent processes (Stenseth et al.,

2016). There was evidence of changes in equilibrium densities in at least one of the four study populations. However, the study of such a small number of populations raises questions about the generality of these findings. Here we take a first step in this direction by investigating general patterns across large temporal and spatial scales by investigating a large number of populations at a continental scale.

Competition and coexistence effects may appear as effects of interspecific interactions on the abundance of the interacting parties with consequences for the disappearance of one or more of the species involved (Both et al., 2006). There are few studies of the impact of climate change on population size, preventing generalizations about such phenomena. Such studies raise the general question whether changes in abundance are due to competition, or whether additional factors are contributing to changes, such as shifts in abundance of food and other resources.

Intra- and interspecific competition are known to affect laying date and clutch size in hole nesting birds (Dhondt, 2012; Stenseth et al., 2015; Møller et al. 2018). However, some of these studies suggest that such effects of competition are just significant in specific plots or specific years, raising questions about the generality of these phenomena, but also the underlying causes for such specific mechanisms. Recently, Møller et al. (2018) published extensive analyses of effects of competition on laying date and clutch size in two species of tits across the European continent.

Here we expand these analyses by testing for the first time whether the effects of climate change during the last 50 years significantly influence the effects of winter and spring temperature on intra- and interspecific competition and in particular laying date and clutch size.

The objectives of this study were to test (1) whether laying date advanced and clutch size changed with increasing temperature, and whether this effect was modified by competition; (2) whether there was an interaction between effect of temperature anomaly and density on clutch size; and (3) whether intraspecific competition in blue or great tit changed as temperature increased. We did so by investigating a long-term dataset of 75 study sites for two species of secondary hole nesting birds, great tit *Parus major* and blue tit *Cyanistes caeruleus*, across Europe. Interspecific competition for food in the breeding season occurs when the smaller bird species consumes smaller instars of the same caterpillar species resulting in preemptive food consumption that differentially impairs the great tit, which is the inferior competitor (Dhondt, 2012). For resident tits, competition for access to nest boxes favors great tits when large-holed nest boxes are available. Great tits outcompete blue tits by excluding blue tits from boxes that are used as roost sites, even when boxes are superabundant (Dhondt, 2012). Tits and other hole nesting birds constitute model systems for the study of competition because experimental manipulation of abundance and distribution can be used as tools for studying mechanisms, the spatial and



temporal scales of interactions, and the outcomes of such interactions (Alatalo, 1985; Keddy, 1989; Dhondt, 2012).

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

We conducted an extensive study of laying date of first clutches and clutch size in two species of hole nesting birds in the Western Palearctic relying on collaboration between amateurs and professionals. We contacted participants in a previous exhaustive study of hole nesting birds (Lambrechts et al., 2010). Although the taxonomy of tits is currently under revision, we used two taxa of tits (great tit *Parus major* and blue tit *Cyanistes caeruleus*) with similar ecologies without considering that some populations in the Iberian Peninsula, the Canary Islands and North Africa may constitute separate species.

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 and location to standardize sampling procedures (cf. Nager & van Noordwijk, 1995). We assumed that the very small number of unidentified early repeat clutches that usually resulted 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 per study plot. Second or late clutches were excluded from analyses because they are usually smaller than first or early clutches, even for females not changing nest box within a given breeding season, and they show strong spatial and temporal variation (e.g. Kluijver, 1951; Lambrechts et al., 2008).

## 2.2 | Life-history traits and environmental factors

Information on latitude, longitude and altitude was provided by the authors or found in publications. For details, see the following publications (Vaugoyeau et al., 2016; Møller et al., 2014a, 2014b, 2018).

Tree species vary significantly in timing and amount of invertebrates available for raising offspring in tits. We broadly 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 dominated by a combination of the former tree vegetation classes (e.g. deciduous mixed with coniferous).

Scientists classified their study plots as either rural or urban with urban areas being characterized by city parks, gardens and similar habitats

in close proximity of humans, while forests, plantations and similar habitats were classified as rural.

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

We calculated the internal floor area (in cm<sup>2</sup>) 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 & Nilsson, 1985) and concrete scored as 0 (a mixture of cement and other materials; Lambrechts et al., 2010). Frequency distributions of the different variables are reported in Electronic Supplementary Material Tables S1-S2.

### 2.3 | 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 manuscript of 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). Specifically, we obtained data on 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 local study plot (cf. Nager & van Noordwijk, 1995). In total, we obtained information on 919 yearly mean estimated laying dates and 916 yearly mean estimates on clutch size in 75 study plots with both great and blue tits breeding during the period 1957-2012 (Møller *et al.*, 2014a, b). We chose study plots where 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. All data are available at DOI: doi:10.5061/dryad.p763611.

#### 2.4 | Environmental conditions

We used mean spring temperature anomalies during March-May, mean winter temperature anomalies during December-February and mean year temperature anomalies estimated as the temperature anomaly for every year with respect to the average temperature obtained for the time window 1980-2010 taken for each study plot. Temperature anomalies for each study plots were extracted from a 5 x 5 degree-grid where temperature anomalies were calculated averaging the anomalies for each meteorological station that is found within a grid point (<https://www.ncdc.noaa.gov/cag/>).

## 2.5 | Statistical analyses

To test our hypothesis about how the abundance of blue tits changes with respect to the abundance of great tits we evaluated all possible candidate models obtained from a generalized linear mixed model for which the response variable was the proportion of blue tits for a given year at a given study site. The response was modeled as a binomial with logit link function using the 'cbind' function of R. Specifically, cbind was the abundance of blue tit and total number). The total number was the sum of the abundance of great tits plus the abundance of blue tits. This model included as input variables latitude, longitude, altitude, temperature anomaly, urbanization (natural or urban) and habitat (conifer, deciduous, mixed or evergreen). In total, we included in this global model 7 predictor terms that resulted in  $2^7 = 128$  candidate models. The global model was a linear mixed effect model in which we included these predictors as fixed effects and year and study site as random effects (intercepts).

To test our hypotheses of how an increase in temperature interacts with the competitive or coexistence relationship between great and blue tits we evaluated all possible candidate models obtained from 16 generalized linear mixed models (4 response variables x 2 densities x 2 temperatures). 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 or global model. Each of these models included the density of great or blue tits and temperature anomaly of spring or winter. We did not include in the same model neither density of blue and great tit nor temperature anomaly in spring and winter because these variables were strongly positively correlated (density of great tit *vs* density of blue tit:  $r_s = 0.441$ ,  $P < 0.001$ ; temperature anomaly spring *vs* temperature anomaly winter:  $r_s = 0.497$ ,  $P < 0.001$ ). We expressly included the interaction term between temperature anomaly and density of great or blue tits to test the hypothesis that an increase in temperature could affect inter- or intraspecific competition between these two hole-nesting birds. We also included the previously listed confounding variables that have been shown to affect laying date or clutch size of great and blue tits, respectively. These input variables were latitude, longitude, altitude, nest material (wood or concrete), nest floor surface, urbanization (natural or urban) and habitat (conifer, deciduous, mixed or evergreen). In total, we included in each global model 10 predictor terms resulting in  $2^{10} = 1024$  candidate models. The global 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.

We first standardized the input variables entering the global model by scaling them after centering their mean by 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 and were on a comparable scale (Gelman, 2008; Grueber et al., 2011). 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 (i) that can be interpreted as the probability that it is the best model, given the data and set of candidate models (Burnham & Anderson, 2002). In all models the reference level of the fixed factor ‘habitat’ was ‘conifer’, for ‘urbanization’ it was ‘natural’, and for ‘material’ it was ‘concrete’. 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 library MuMIn (Bartón, 2009) and the library lme4 (Bates & Maechler, 2009) using R version 3.3.2 (R Development Core Team, 2006). 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 explain the response variable when the CI for the estimated parameter excluded zero (Grueber et al., 2011).

### 3 | RESULTS

#### 3.1 | Temporal trend in temperatures

Year temperature anomaly for January-December increased on average  $0.027^{\circ}\text{C} / \text{year}$  ( $F = 307.4$ ,  $df = 1, 462$ ,  $P < 0.0001$ , estimate (SE) =  $0.027$  (0.001)). Spring temperature anomaly for March-May increased on average  $0.033^{\circ}\text{C} / \text{year}$  ( $F = 202.60$ ,  $df = 1, 462$ ,  $P < 0.0001$ , estimate (SE) =  $0.033$  (0.002)). Winter temperature anomaly for December-February increased on average by  $0.011^{\circ}\text{C} / \text{year}$  ( $F = 12.06$ ,  $df = 1, 462$ ,  $P < 0.0006$ , 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 mean) included as a fixed effect. The inclusion of a random slope for year did not improve the models and therefore a common slope for year was assumed in these analyses. Thus, the increase of temperature was similar amongst study plots. (e.g., analyses were a model with and without a random slope for year were tested: Temperature (year): L-ratio=0.078,  $P=0.96$ ; Temperature (spring): L-ratio=0.000,  $P=1.0$ ; Temperature (winter): L-ratio=0.000,  $P=1.0$ )

### 3.2 | Inter- and intraspecific competition and response to climate change: timing of reproduction

The model of the analyses of laying date of great tits showed that across Europe great tits advanced breeding date as temperature increased, which is a well-known response to climate change in this species. The effect was



stronger for spring temperature compared to winter temperature as shown for the larger effect size of spring temperature (Table 1, Fig. 1).

Interestingly, we found a significant effect of the interaction term between temperature anomaly in spring and density of both great and blue tit on laying date of great tit. Thus, great tits laid their eggs earlier as temperature anomaly increased and laying date advanced steeply with temperature as density of both great and blue tits increased (e.g., for density of great tit; Fig. 3a).

The final model obtained from the analyses of laying date of blue tits showed that across Europe blue tits advanced laying date as temperature increased, which is a well-known response of climate change in this species. The effect was stronger for spring temperature compared to winter temperature, as shown for the larger effect size of spring temperature (Table 1, Fig. 1). Interestingly, we found a significant effect of the interaction term between temperatures anomaly in spring and winter and density in both great and blue tit on laying date of blue tit. Thus, blue tits laid their eggs earlier as temperature anomaly during both spring and winter increased and laying date advanced steeply with temperature as density of both great and blue tits increased (e.g. Fig. 3b for the interaction between density of blue tit and spring temperature on laying date of blue tit).

These effects were found while controlling for other confounding variables known to affect laying date, such as latitude, longitude, altitude, habitat, urbanization, nest floor surface and material (see Supplementary materials for the final models with all variables included).

### 3.3 | Inter- and intraspecific competition and response to climate change:

#### Clutch size

The final model obtained from the analysis of clutch size of great tits showed that across Europe great tit clutch size decreased as temperature increased. The effect was stronger for winter temperature compared to spring temperature as shown for the larger effect size of winter temperature (Table 2, Fig. 2). Interestingly, we found a significant effect of the interaction term between temperature anomaly in spring and density of great tit on clutch size of great tit. Specifically, great tits laid smaller clutches as temperature anomaly increased and clutches became smaller with temperature as density of great tits increased (Fig. 4a). However, the effect of the interaction term between temperature anomaly in spring and density of blue tit on clutch size of great tit was not significant as shown by the exclusion of zero in the confidence interval for this parameter. We found a significant effect of the interaction term between temperature anomaly in winter and density of great tit and of blue tits on clutch size of great tit (Fig. 4b). Thus, great tits laid smaller clutches as temperature

anomaly increased and clutches became smaller with temperature as density of both great and blue tits increased.

The final model obtained from the analysis of clutch size of blue tits showed that clutch size across Europe decreased as temperature increased. The effect of winter temperature was similar to the effect of spring temperature as shown for similar effect sizes of spring and winter temperature on clutch size of blue tits (Table 2, Fig. 2). We did not find a significant effect of any of the interaction terms between temperature (i.e., spring or winter) with density (i.e., great or blue tit) on clutch size of blue tits. Therefore, density of conspecifics or heterospecifics did not interact with changing environmental conditions for blue tits (i.e., temperature increase) on the mean number of blue tit eggs in a given breeding season across 75 study sites in Europe.

These effects were found while controlling for other confounding variables known to affect clutch size, such as laying date, latitude, longitude, altitude, habitat, urbanization, nest floor surface and nest material (see Supplementary materials for the final models with all variables included).

#### 4 | DISCUSSION

Across large spatial and temporal scales in Europe and North Africa we found that an increase in temperature anomaly due to climate warming

affected timing of breeding and clutch size of great and blue tit. This is not a novel finding since these effects of temperature on laying date and clutch size have previously been found in these species. What is novel though is that the strength of the effects of temperature anomaly on laying date and clutch size varied as shown by multiple significant interaction terms between density and temperature anomaly in both winter and spring. Furthermore, the generality of these findings is not obvious. This is the first study showing that the effect of temperature on laying date and clutch size is widespread across a large spatial and temporal scale in these two coexisting tits. We found that temperatures in spring and winter, and year, have increased during the study across study plots. As a response, great tits advanced laying as temperature in winter and spring increased. Surprisingly, we found that the observed increase in temperature was negatively related to clutch size in the two species of tits. According to how intra and inter-specific competition affected response to increasing temperatures, we found that laying date of great tit advanced steeply when spring temperature and density of conspecifics and heterospecifics increased. For blue tits, the same relationship between density and temperature was found also for winter temperature. Therefore, both species advanced the timing of breeding more with increasing densities of conspecific and heterospecific and temperatures. Interestingly, we found that clutch size of great tit is reduced more strongly when winter

temperature and density of conspecifics and heterospecifics increased and when spring temperature and density of conspecifics increased. This relationship was not detected for clutch size in blue tit. In this smaller species clutch size was not affected further when winter or spring temperature and density of conspecifics or heterospecifics increased.

We have shown that both species of tits advanced breeding date as a response to increasing temperatures. The response is stronger for spring than for winter temperature. Probably, spring temperature constitutes a clearer cue for individuals that they have to start breeding than would winter temperature. Although laying date advanced in response to climate change, clutch size decreased with increasing temperature as found for both species of tits. Therefore, it is possible that the advance in laying date would not suffice to match the emergence of caterpillar, the main food of these tit species (Perrins, 1965; Both et al., 2009). Therefore, a mismatch between emergence of food and timing of reproduction could also be occurring at large spatial and temporal scales across the breeding season, as already shown for specific European populations (e.g. Visser et al., 1998; Both et al., 2009). However, we should not forget that a reduction in clutch size with temperature could also be due to other causes. For example, an increase in winter temperature could increase adult survival in both species, specifically in blue tits, and this could affect the intensity of competition the subsequent spring which could reduce clutch size due to density-

dependent processes (e.g. Dhondt et al., 1992; Ferrer and Donazar, 1996).

However, the exact mechanisms still remain to be determined.

We would expect a significant interaction between density and temperature if intra- and interspecific competition was affected by climate change. We documented a significant effect of temperature anomaly interacting with density of blue and great tits on laying date of blue and great tits. Furthermore, we documented a significant effect of temperature anomaly interacting with density of blue and great tits on clutch size of great tits. In contrast, there was no interaction between temperature and density of great tits or blue tits on clutch size of blue tits. These findings suggest that the presence of conspecifics or heterospecifics could result in a further advancement in laying date in both great and blue tits. Possibly, an increase in density (i.e. intra- or interspecific competition) could affect the response to climate warming. If we look at competition alone this would delay laying date and reduce clutch size. However, in sites where density of conspecifics or heterospecifics is higher increasing temperatures resulted in a further advance in laying date. Possibly, the presence of conspecifics or heterospecifics could serve individuals as social cues for better responding to climate change. That would be the case when advanced laying date results more in synchrony between emergence of food and timing of breeding. However, the effect of the interaction between density and temperature on clutch size showed that an increase in intra- or interspecific

competition and temperature affected great, but not blue tits. Therefore, a more rapid advance in laying date with density and temperature was not an adaptive response in great tits, but it could be the case for blue tits since clutch size was not reduced in the latter species when temperature and density interacted to affect clutch size. The difference in response with respect to clutch size in great compared to blue tit could be related to the timing of reproduction being slightly different in the two species. Blue tits consumed earlier instars of caterpillar larvae that emerge earlier, and, therefore, the difference in response to climate change by the two species could affect small differences in timing of breeding.

In conclusion, studying the effects of increasing temperatures on timing of reproduction and on a measure of breeding success (i.e. clutch size) at large spatial and temporal scales, we found that great and blue tit responded to climate warming by advancing timing of reproduction. However, this advance in breeding date with increasing temperature did not prevent a reduction in clutch size due to increasing temperatures during the study period. In addition, the response to increasing temperature interacted with density by advancing laying date even more in great and in blue tits. This interaction reduced clutch size in great tit even more, while there was no similar effect in blue tits. Further studies are needed to examine in greater detail how intra- and interspecific relationships interact with

environmental conditions, such as temperature, on timing of breeding and on breeding success that ultimately will affect fitness and population sizes.

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## Data accessibility

Data are available from the Dryad Digital Repository upon acceptance.



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## Figure legends

**FIGURE 1.** Effects of temperature anomaly in spring and winter on laying date of great and blue tits. The lines ( $\pm 95\%$  CI) are the predicted values obtained from a linear mixed-effect model where latitude, longitude and altitude and nest floor surface are maintained on their mean values and habitat, urbanization and material at their reference values (i.e., conifer, natural habitat and material concrete).

**FIGURE 2.** Effects of temperature anomaly in spring and winter on clutch size of great and blue tit. The lines ( $\pm 95\%$  CI) are the predicted values obtained from a linear mixed-effect models were latitude, longitude and altitude and nest floor surface are maintained on their mean values and habitat, urbanization and material at their reference values (i.e., conifer, natural habitat and material concrete, respectively).

**FIGURE 3.** Effects of the interaction term of temperature anomaly in spring and density of great tits on laying date of great tits (a) and effects of the interaction term of temperature anomaly in spring and density of blue tits on laying date of blue tits (b). The lines 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 1024 candidate models.

**FIGURE 4.** Effects of the interaction term of temperature anomaly in spring and density of great tits on clutch size of great tits (a) and of the interaction term of temperature anomaly in winter and density of great tits on clutch size of great tits (b). The lines 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 1024 candidate models.



Figure 1

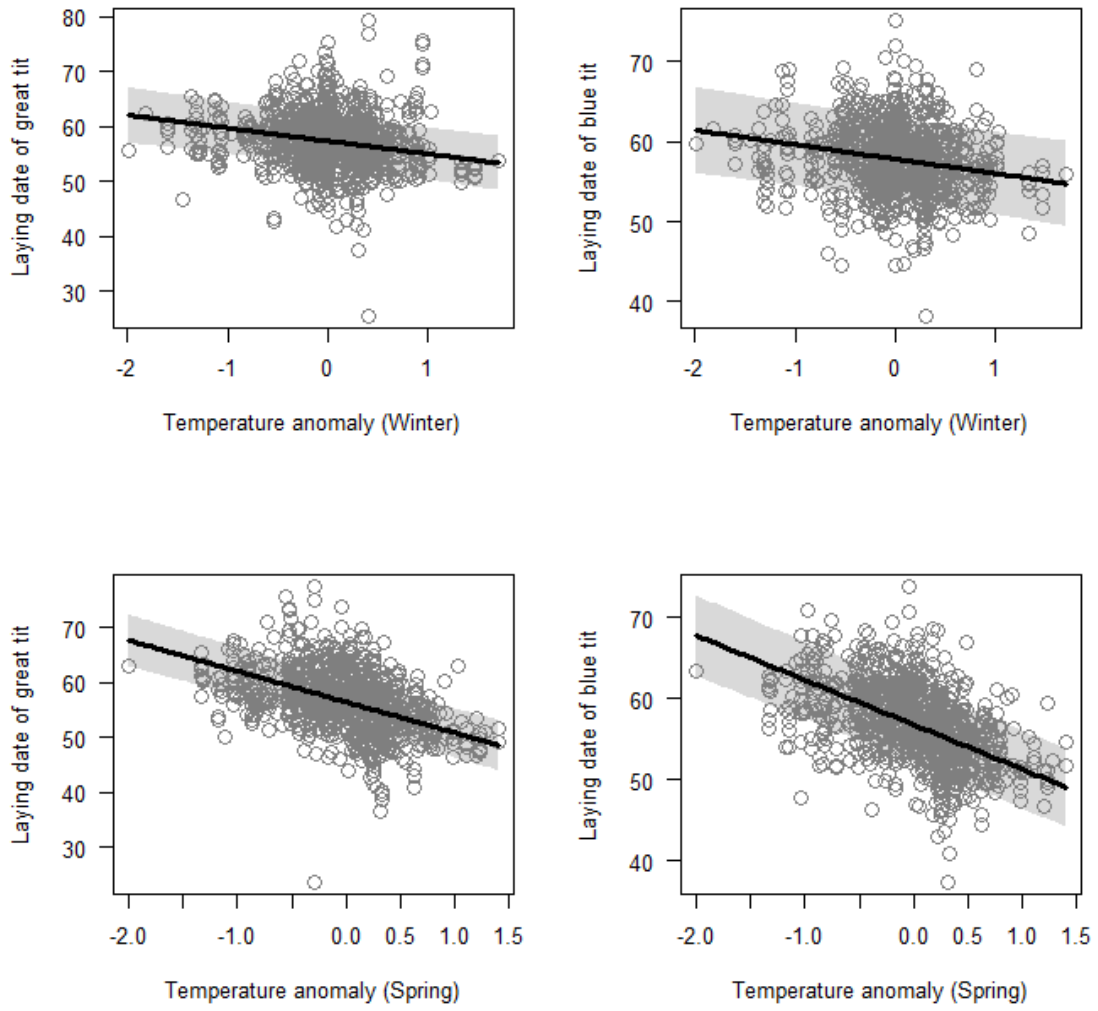


Figure 2

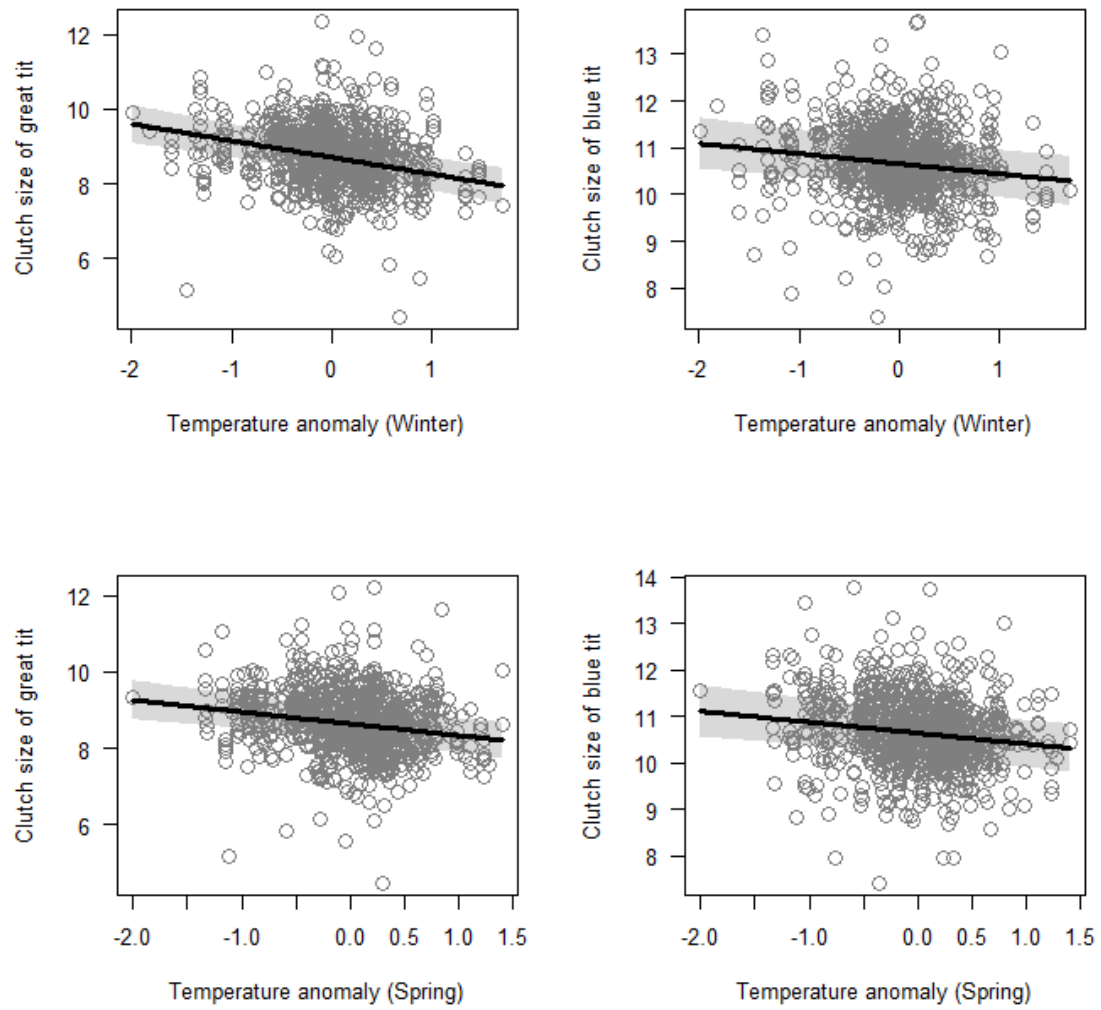


Figure 3 a.

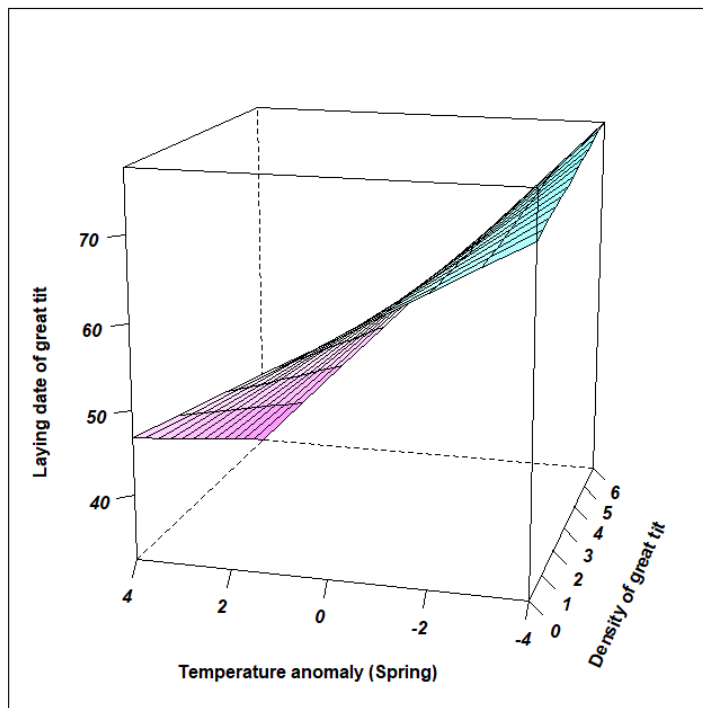


Figure 3b

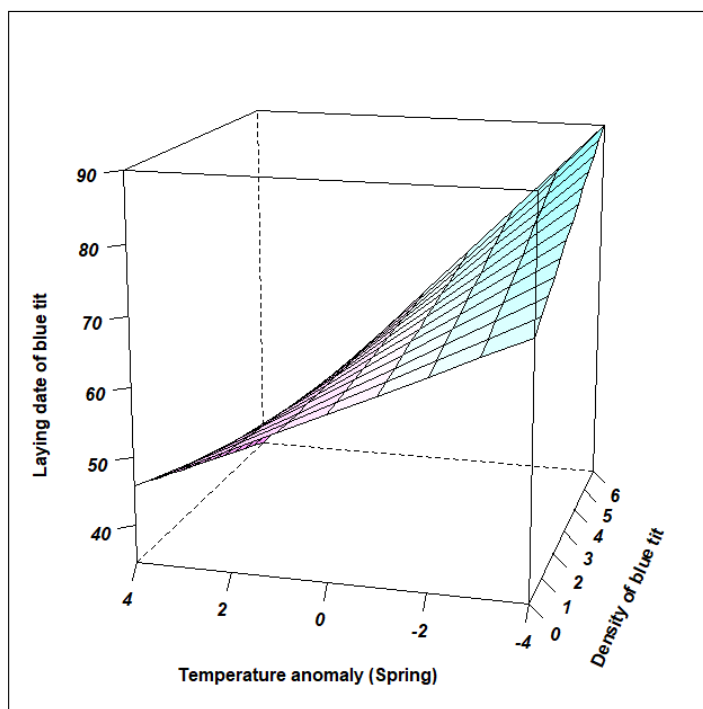


Figure 4a.

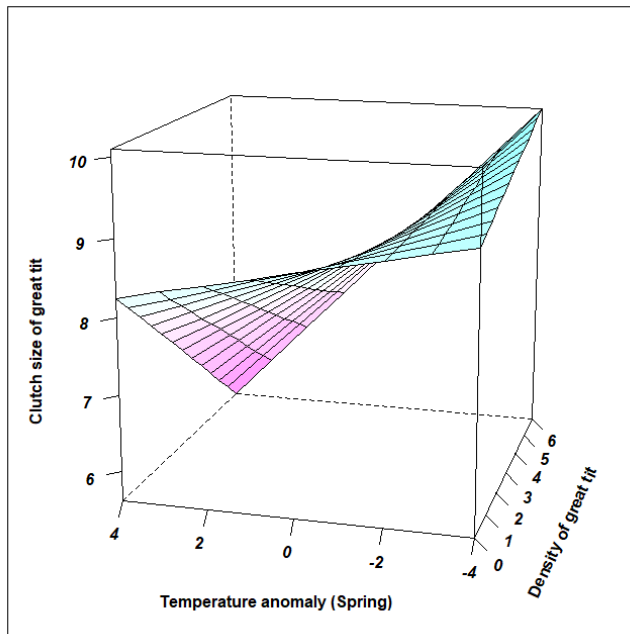
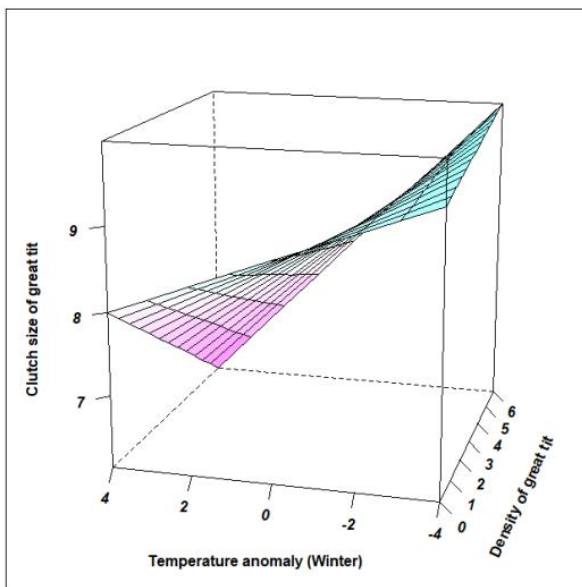


Figure 4b



**TABLE 1** Summary results after model averaging of the effects of temperature anomaly and density of great and blue tit on laying date of great tit in Europe. Significant temperature by density interactions are highlighted in grey colour. Estimates, SE and 95% CI are reported. The model also included other potential predictors of laying date of great tit (the final models with all predictors included in Supplementary materials).

Sample size is 919 observations of yearly average laying date at 75 sites across Europe

|                                      | Estimate      | SE           | 95% CI                   | Estimate                             | SE            | 95% CI                        |
|--------------------------------------|---------------|--------------|--------------------------|--------------------------------------|---------------|-------------------------------|
| <b>Laying date (GT)</b>              |               |              | <b>Laying date (GT)</b>  |                                      |               |                               |
| T <sup>a</sup> (Spring)              | <b>-5.240</b> | <b>0.568</b> | <b>(-6.355, -4.125)</b>  | T <sup>a</sup> (Spring)              | <b>-5.544</b> | <b>0.532 (-6.589, -4.500)</b> |
| Density (GT)                         | <b>-1.315</b> | <b>0.633</b> | <b>(-2.537, -0.158)</b>  | Density (BT)                         | 1.303         | 0.746 (-0.162, 2.768)         |
| T <sup>a</sup> (Spring)*Density (GT) | <b>-1.119</b> | <b>0.466</b> | <b>(-2.035, -0.203)</b>  | T <sup>a</sup> (Spring)*Density (BT) | <b>-2.048</b> | <b>0.643 (-3.312, -0.785)</b> |
| <b>Laying date (BT)</b>              |               |              | <b>Laying date (BT)</b>  |                                      |               |                               |
| T <sup>a</sup> (Winter)              | <b>-2.280</b> | <b>0.537</b> | <b>(-3.336, -1.224)</b>  | T <sup>a</sup> (Winter)              | <b>-2.450</b> | <b>0.547 (-3.526, -1.375)</b> |
| Density (GT)                         | <b>-1.154</b> | <b>0.711</b> | <b>(-2.502, -0.1269)</b> | Density (BT)                         | 1.009         | 0.833 (-0.249, 2.718)         |
| T <sup>a</sup> (Winter)*Density (GT) | -0.101        | 0.303        | (-1.331, 0.5806)         | T <sup>a</sup> (Winter)*Density (BT) | -0.736        | 0.833 (-2.677, 0.067)         |

**Laying date (BT)**

|                                      |               |              |                         |
|--------------------------------------|---------------|--------------|-------------------------|
| T <sup>a</sup> (Spring)              | <b>-4.810</b> | <b>0.466</b> | <b>(-5.726, -3.894)</b> |
| Density (GT)                         | <b>-1.289</b> | <b>0.514</b> | <b>(-2.299, -0.279)</b> |
| T <sup>a</sup> (Spring)*Density (GT) | <b>-1.928</b> | <b>0.393</b> | <b>(-2.700, -1.155)</b> |

|                                      |               |              |                         |
|--------------------------------------|---------------|--------------|-------------------------|
| T <sup>a</sup> (Winter)              | <b>-1.597</b> | <b>0.471</b> | <b>(-2.522, -0.672)</b> |
| Density (GT)                         | <b>-0.954</b> | <b>0.527</b> | <b>(-1.986, 0.048)</b>  |
| T <sup>a</sup> (Winter)*Density (GT) | <b>-0.909</b> | <b>0.496</b> | <b>(-1.821, -0.201)</b> |

**Laying date (BT)**

|                                      |               |              |                         |
|--------------------------------------|---------------|--------------|-------------------------|
| T <sup>a</sup> (Spring)              | <b>-5.344</b> | <b>0.447</b> | <b>(-6.222, -4.466)</b> |
| Density (BT)                         | <b>1.976</b>  | <b>0.638</b> | <b>(0.724, 3.228)</b>   |
| T <sup>a</sup> (Spring)*Density (BT) | <b>-3.071</b> | <b>0.539</b> | <b>(-4.129, -2.013)</b> |

|                                      |               |              |                          |
|--------------------------------------|---------------|--------------|--------------------------|
| T <sup>a</sup> (Winter)              | <b>-2.093</b> | <b>0.468</b> | <b>(-3.013, -1.1738)</b> |
| Density (BT)                         | <b>1.882</b>  | <b>0.648</b> | <b>(0.609, 3.155)</b>    |
| T <sup>a</sup> (Winter)*Density (BT) | <b>-1.953</b> | <b>0.589</b> | <b>(-3.109, -0.796)</b>  |

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**TABLE 2** Summary results after model averaging of the effects of temperature anomaly and density of great and blue tit on clutch size of great tit in Europe. Significant temperature by density interactions are highlighted in grey colour. Estimates, SE and 95% CI are reported. The model also included other potential predictors of clutch size (the final models with all predictors included in Supplementary materials). Sample size is 916 observations of yearly average laying dates in 75 sites across Europe

|                                      | Estimate      | SE           | 95% CI                  |                                      | Estimate      | SE           | 95% CI                  |
|--------------------------------------|---------------|--------------|-------------------------|--------------------------------------|---------------|--------------|-------------------------|
| <b>Clutch size (GT)</b>              |               |              |                         | <b>Clutch size (GT)</b>              |               |              |                         |
| T <sup>a</sup> (Spring)              | <b>-0.249</b> | <b>0.080</b> | <b>(-0.407, -0.092)</b> | T <sup>a</sup> (Spring)              | <b>-0.320</b> | <b>0.077</b> | <b>(-0.472, -0.169)</b> |
| Density (GT)                         | <b>-0.252</b> | <b>0.081</b> | <b>(-0.412, -0.092)</b> | Density (BT)                         | -0.080        | 0.103        | (-0.340, 0.056)         |
| T <sup>a</sup> (Spring)*Density (GT) | <b>-0.198</b> | <b>0.065</b> | <b>(-0.326, -0.070)</b> | T <sup>a</sup> (Spring)*Density (BT) | -0.004        | 0.036        | (-0.211, 0.148)         |
| T <sup>a</sup> (Winter)              | <b>-0.414</b> | <b>0.071</b> | <b>(-0.553, -0.274)</b> | T <sup>a</sup> (Winter)              | <b>-0.506</b> | <b>0.070</b> | <b>(-0.645, -0.366)</b> |
| Density (GT)                         | <b>-0.196</b> | <b>0.079</b> | <b>(-0.352, -0.041)</b> | Density (BT)                         | -0.103        | 0.098        | (-0.296, 0.089)         |

|                                      |               |                               |                                      |               |                               |
|--------------------------------------|---------------|-------------------------------|--------------------------------------|---------------|-------------------------------|
| T <sup>a</sup> (Winter)*Density (GT) | <b>-0.167</b> | <b>0.071 (-0.302, -0.043)</b> | T <sup>a</sup> (Winter)*Density (BT) | <b>-0.388</b> | <b>0.094 (-0.573, -0.202)</b> |
| <b>Clutch size (BT)</b>              |               |                               | <b>Clutch size (BT)</b>              |               |                               |
| T <sup>a</sup> (Spring)              | <b>-0.227</b> | <b>0.066 (-0.358, -0.096)</b> | T <sup>a</sup> (Spring)              | <b>-0.230</b> | <b>0.065 (-0.358, -0.102)</b> |
| Density (GT)                         | -0.072        | 0.083 (-0.269, 0.039)         | Density (BT)                         | -0.090        | 0.105 (-0.340, 0.039)         |
| T <sup>a</sup> (Spring)*Density (GT) | -0.023        | 0.050 (-0.204, 0.038)         | T <sup>a</sup> (Spring)*Density (BT) | 0.000         | 0.032 (-0.163, 0.175)         |
| <b>T<sup>a</sup> (Winter)</b>        | <b>-0.214</b> | <b>0.058 (-0.329, -0.099)</b> | <b>T<sup>a</sup> (Winter)</b>        | <b>-0.212</b> | <b>0.058 (-0.326, -0.098)</b> |
| Density (GT)                         | -0.048        | 0.072 (-0.248, 0.056)         | Density (BT)                         | -0.094        | 0.106 (-0.342, 0.036)         |
| T <sup>a</sup> (Winter)*Density (GT) | 0.000         | 0.021 (-0.121, 0.127)         | T <sup>a</sup> (Winter)*Density (BT) | 0.001         | 0.034 (-0.164, 0.189)         |

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