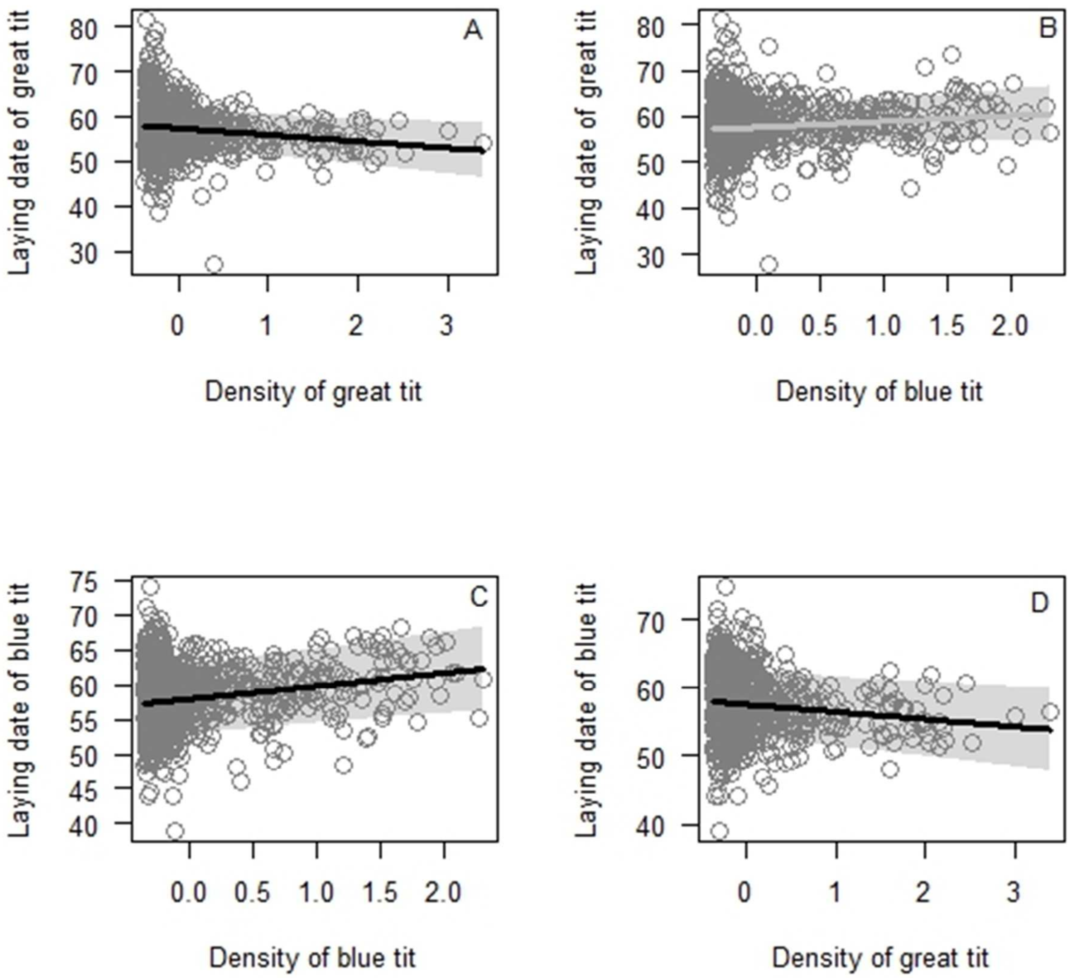

A
Laying date of great tit
80
70
60
50
40
30
0
1
2
3
Density of great tit
B
Laying date of great tit
80
70
60
50
40
30
0.0
0.5
1.0
1.5
2.0
Density of blue tit
C
Laying date of blue tit
75
70
65
60
55
50
45
40
0.0
0.5
1.0
1.5
2.0
Density of blue tit
D
Laying date of blue tit
70
60
50
40
0
1
2
3
Density of great tit

Effects of interspecific co-existence on laying date and clutch size in two closely related species of hole-nesting birds

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Running headline:

A. P. Møller et al.

Intra- and interspecific competition and demographic variables

Summary

1. Co-existence between great tits *Parus major* and blue tits *Cyanistes caeruleus*, but also other hole nesting taxa, constitutes a classic example of species co-occurrence resulting in potential interference and exploitation competition for food and for breeding and roosting sites. However, the spatial and temporal variation in co-existence and its consequences for competition remain poorly understood.

2. We used an extensive database on reproduction in nest boxes by great and blue tits based on 87 study plots across Europe and Northern Africa during 1957-2012 for a total of 19,075 great tit and 16,729 blue tit clutches to assess correlative evidence for a relationship between laying date and clutch size, respectively, and density consistent with effects of intraspecific and interspecific competition.

3. In an initial set of analyses, we statistically controlled for a suite of site specific variables. We found evidence for an effect of intraspecific competition on blue tit laying date (later laying at higher density) and clutch size (smaller clutch size at higher density), but no evidence of significant effects of intraspecific competition in great tits, nor effects of interspecific competition for either species.

4. To further control for site-specific variation caused by a range of potentially confounding variables, we compared means and variances in laying date and clutch size of great and blue tits among three categories of difference in density between great and blue tits. These comparisons revealed evidence, for both species, consistent with intraspecific competition and to a smaller extent with interspecific competition.

5. These findings suggest that competition associated with reproductive behaviour between blue and great tits is widespread, but also varies across large spatial and temporal scales.

Key-words: clutch size, density, interspecific competition, intraspecific competition, nest boxes, reaction norm, spatio-temporal variation.

Introduction

Numerous experimental studies have demonstrated that intraspecific and interspecific competition can reduce population size or decrease reproductive output (e.g. Schoener 1983; Gurevitch *et al.* 1992; Dhondt 2012). Competition, defined as the negative effects that one organism has upon another, may be due to interference over resources and/or to exploitation of resources that are limited in availability (Keddy 1989; Grover 1997). The limiting resources over which individuals compete vary considerably, as does the timing of competition during the annual cycle. However, factors other than competition such as compensation can also drive population dynamics (Houlahan *et al.* 2007; Ricklefs 2012). Because of such complexity, competition is not inevitable; indeed, a recent study of interspecific competition between two hole-nesting bird species in four European populations showed clear evidence of competition in only three of these populations (Stenseth *et al.* 2015). Similarly, in a review of density dependence of clutch size in titmice, Both (2000) only found a negative relationship in half of all study plots, again emphasizing that decreased reproduction is not a ubiquitous outcome.

Great tits *Parus major* and blue tits *Cyanistes caeruleus*, both secondary hole-nesting passerines, constitute a classic example of competition for food and cavities (review in Dhondt 2012). For example, Dhondt & Eyckerman (1980a) showed that high density of both species reduced reproductive output in great tits. In contrast to great tits, evidence for effects of both intraspecific and interspecific competition on reproduction are much weaker in blue tits. In both species, the intensity of competition was the strongest in poor quality habitats (Dhondt 2010). A field experiment based on the exclusion of great tits from nest boxes during winter resulted in an increase in the abundance of blue tits (Dhondt & Eyckerman 1980b), demonstrating that competition for roosting sites in winter can limit population size of the smaller blue tit in some habitats. In addition, observational monitoring of natural holes and experimental removal of access to tree cavities show that a shortage in nest sites can limit breeding population density in birds (Aitken & Martin 2008; Robles *et al.* 2011), even in cavity-rich environments (Robles *et al.* 2012), which in turn may lead to cascading effects via an increase in the intensity of interspecific competition (Aitken & Martin 2008).

Food availability is an underlying cause of limitation of population density in numerous organisms (Newton 1998; Ruffino *et al*. 2014). This has been shown clearly in food supplementation experiments: the addition of food often increases abundance, while food removal has the opposite effect (e.g. Minot 1978, 1981; Dhondt *et al*. 1992; Török & Tóth 1999; Siriwardena *et al*. 2007; Dhondt 2012). Likewise, extensive food provisioning in feeders by humans across broad spatial scales has caused dramatic increases in abundance of birds, and often also earlier timing of reproduction and increased reproductive success (review in Robb *et al.* 2008), especially in great tits (Tryjanowski *et al.* 2015). Another effect of urbanisation is that laying date advances in urban plots because of food and/or higher temperatures in urban areas (e.g. Dhondt *et al.* 1984; Wawrzyniak *et al.* 2015).

While interference competition mainly involves access to territories in spring and fall, and for cavities during the breeding season and in winter, exploitation competition is mainly over limiting food during the breeding season (Dhondt 1977) and in winter (Krebs 1971; Perdeck *et al*. 2000). If there is a change in timing or availability of food due to changing climate (Visser *et al.* 1998; Visser & Hollemann 2001; Stenseth *et al.* 2002; Parmesan & Yohe 2003; Adler *et al.* 2006; Visser 2008; Angert *et al.* 2009), then both density-dependent and density-independent processes should affect tit populations (Dhondt & Adriaensen 1999; Wilkin *et al*. 2006; Stenseth *et al.* 2015).

Intraspecific and interspecific competition among tits, but also other secondary hole nesting taxa, and the resources subject to competition, are highly variable across spatial and temporal scales (Alatalo 1984; Minot & Perrins 1986; Dhondt 2012). Therefore, there is a clear need for addressing questions about competition at such scales. Both great and blue tits have a large distribution, and, therefore, they are ideal for addressing questions about competition at large spatial and temporal scales.

The objective of this study was to assess the generality, at a large spatio-temporal scale, of effects of intraspecific and interspecific competition on laying date and clutch size of great and blue tits across Europe and Northern Africa using 35,800 clutches in nest boxes in areas where both species nest sympatrically. We predicted that (1) intraspecific competition, and to a lesser extent interspecific competition, would delay and increase the variance in laying dates and reduce clutch sizes. Furthermore, we predicted that (2) this effect should be more pronounced in blue than in great tits as interspecific competition increases given that blue tits are smaller than great tits.

(3) At any one site, differences in density across time and hence differences in competition between great and blue tits would be related to differences in laying date and clutch size. If interspecific competition occurs, we predict a reduction in mean and an increase in variance in clutch size in great tit and blue tit when density of heterospecifics is higher than the density of conspecifics and for intraspecific competition this reduction would occur when density of conspecifics is higher than the density of heterospecifics. For laying date we predicted for intraspecific competition a delay in mean laying date of great tits or blue tits when density of conspecifics outnumbered density of heterospecifics and the reverse for interspecific competition. A higher variance is a consequence of laying being delayed and clutch size reduced among individuals that suffer the most from competition with conspecifics or heterospecifics. This follows from the observation that at low density only high quality sites are occupied, while at high density poor quality sites (where the birds lay smaller clutches) are also occupied resulting in increased variances at

higher density (Solonen *et al.* 1991; Dhondt *et al.* 1992; Ferrer & Donázar 1996).

Materials and methods

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 87 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.

STATISTICAL ANALYSES

LMM of laying date and clutch size

The study sites differed in a number of features that were controlled statistically as covariates or factors in the analyses because our 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). The variables were latitude (°N) and longitude (°E), main habitat type (deciduous, coniferous, evergreen, or mixed), urbanisation (urbanised, or natural/semi-natural habitat), altitude at the centre of the study plot, nest floor surface as the internal base area within the nest box (in cm^2), and the material used to construct nest boxes (a binary variable classified as either wood or concrete). Further details of how these variables were obtained and quantified can be found in Lambrechts *et al*. (2010), Møller *et al*. (2014a, b) and Vaugoyeau *et al*. (2016).

We constructed eight linear mixed models (LMMs) with laying date and clutch size of great and blue tits as untransformed response variables and including all the above mentioned confounding variables into the models. The density of great tit or blue tit were also included in the fixed part of the model and its significance was tested by removing it from the saturated model testing for its effect using Likelihood Ratio Test (LRT). These eight models corresponded to laying date and clutch size of both species according to density of the species (= 2 variables x 2 species x 2 competition status (intraspecific/interspecific competition). Density of great tits and blue tits in the study plots was estimated as the number of occupied nest boxes / study area (ha) for each year and each species. The analyses of intraspecific and interspecific competition were restricted to those study plots where the duration of the study was at least five years, in order to be able to fit a random slope in the models of intraspecific competition. When testing for intraspecific competition (i.e. the effect of density of great tit in laying date and clutch size of great tit, or the effect of density of blue tit in laying date and clutch size of blue tit), we included study plot and year as two cross random intercepts to account for differences among sites and years, but also we estimate the variance in the slope of the relationship between density and laying date or clutch size amongst study plots (e.g. the slope of density of great tit on laying date or clutch size of great tit amongst study plots). The significance of the random slope in these models was also tested using Likelihood Ratio Tests (LRT), including only the intercept in the fixed part of the models (Crawley 2002). The random slope was removed from the models when $P > 0.05$. When testing for interspecific competition (i.e. the effect of density of great tit in laying date and clutch size of blue tit or the effect of density of great tit on laying date and clutch size of blue tit), study plot and year were included as two cross random intercepts to account for differences among sites and years. We did not include a random slope (e.g. the slope of the density of blue tit on laying date of great tit amongst study plots) because it might happen that in some study plots the number of observations could not match a model with and without the slope (e.g. when fitting a random slope for the density of blue tit on laying date of great tit we had 921 observations for the model excluding the random slope and 920 observations in the model including a random slope). Therefore, it was possible that in one out of five or more years of study one of the two species of tit was not recorded. This occurred very infrequently (e.g. only in one plot out of 75 for the above example), but it did not allow us to test for the significance of a random slope when testing for interspecific competition.

All eight analyses were weighted by sample size to account for differences in sampling effort among study plots (Garamszegi & Møller 2010). We calculated variance inflation factors (VIF) to identify problems of collinearity. All VIFs were smaller than 5, and in almost all cases smaller than 3, indicating that there were no problems of collinearity (McClave & Sincich 2003). We standardized regression predictors by centering (i.e. subtracting the mean and dividing by 2 SD). Therefore, numeric variables that take on more than two values were each rescaled to have a mean of 0 and a SD of 0.5 and binary variables were rescaled to have a mean of 0 and a difference of 1 between their two categories, while the factors with more than two categories remained unchanged (Gelman 2008).

Tests for differences in laying date and clutch size

We tested whether differences in clutch size between great and blue tits were related to differences in laying date between the two species and differences in density between great and blue tits, including their two-way interaction using standard least squares analyses, weighted by sample size. We included the interaction in order to test whether the difference in laying date had a stronger effect on difference in clutch size when the difference in density was larger. In addition, we tested whether differences in laying date were related to differences in density. In these analyses, we restricted the sample size to study plots with five or more years of study. Sample sizes differed slightly for different analyses due to missing values. Larger variances were the result of more heterogeneity in relationships between laying date or clutch size and density among study sites.

Effects of difference in density on effects of competition on laying date and clutch size

We used difference in log-transformed great tit density minus log-transformed blue tit density (henceforth density difference) as the predictor variable in the analyses to test for effects of competition on laying date and on clutch size (Table 1, Fig. 1). By doing so we controlled for any variable that would influence the breeding of the two tit species in a similar way at each site and year. When the density difference was negative, blue tits were more abundant than great tits. The relative strength of intraspecific compared to interspecific competition in blue tits will change from negative to positive density difference values (i.e. the relative strength of interspecific competition will increase), while the opposite is true for great tits.

Effects of categorized density differences on laying date and clutch size

We categorized density difference at three levels with similar number of data points: level 1: great tit density lower than blue tit density with log great tit density – log blue tit density being on average -0.58, SE = 0.02, range -1.78 to -0.12; level 2: great tit density similar to blue tit density with log great tit density – log blue tit density being on average 0.11, SE = 0.01, range -0.12 to 0.30; and level 3: great tit density higher than blue tit density with log great tit density –

log blue tit density being on average 0.66, SE = 0.02, range 0.30 to 1.76. These data were used in a Welch ANOVA for unequal variances by comparing means between the three groups. We also compared variances among these three categories of density difference using Levene's test.

Effects of spatial autocorrelation

We included latitude, latitude squared, longitude, longitude squared and the interaction between latitude and longitude in all models to control statistically for spatial autocorrelation (Lichtstein *et al.* 2002; Legendre 2003; Dorman *et al.* 2007; Diniz-Filho *et al.* 2008; Legendre & Legendre 2012). Analyses were made with JMP (SAS 2010) and the library lme4 (Bates & Maechler 2009) using R version 3.3.2 (R Development Core Team 2006).

Results

SUMMARY STATISTICS

The analyses of competition were based on a maximum of 978 plot by year estimates of laying date and clutch size varying due to differences in availability of data. We had data for a total of 87 plots where both species bred at least once. For great tits, mean laying date weighted by sample size was April 23 (SE = 0.36, N = 929) and mean clutch size was 8.61 eggs (SE = 0.04, N = 970). For blue tits, mean laying date was April 24 (SE = 0.41, N = 935) and mean clutch size was 9.93 eggs (SE = 0.06, N = 973).

EFFECTS OF INTRA- AND INTERSPECIFIC COMPETITION ON LAYING DATE AND CLUTCH SIZE

Laying date

Across study plots, great tit laying date was on average earlier when density of great tits was higher (Fig. 1A, Table 1). Laying date of great tits was marginally later at higher blue tit density (Fig. 1B; $P = 0.08$). This relationship was consistent among study plots as shown by the non-significant variance among study plots in the estimated slopes of the relationship between great tit density and great tit laying date for each study plot (variance explained = 13.71%, LRT = 2.33, d.f. = 2, $P = 0.31$). This is opposite to what is expected if intraspecific competition influences laying date and does not strongly support an effect of interspecific competition on great tit laying date.

Blue tit laying date was significantly later at higher conspecific density (Fig. 1C, Table 1) supporting the hypothesis that intraspecific competition influences laying date. There was a large and statistically significant variance amongst study plots in the estimated slopes between blue tit density and blue tit laying date (variance explained = 25.20%, LRT = 78.79, d.f. = 2, $P < 0001$) showing that the intensity of intraspecific competition varies strongly between study plots. Blue tit laying date was earlier when density of great tits was higher which is opposite to predictions if interspecific competition were to influence laying date (Fig. 1D).

Clutch size

Across study plots, great tit average clutch size did not vary significantly with conspecific density (Fig. 2A, 2B; Table 2). This analysis yielded a large and statistically significant variance in the estimated slopes amongst study plots (variance explained = 27.78%, LRT = 24.85, d.f. = 2, $P < 0.0001$) showing that the intensity of intraspecific competition varied strongly between study populations. We also found that great tit clutch size did not vary with blue tit density (Fig. 2B).

Blue tit average clutch size decreased with increasing conspecific density (Fig. 2C, Table 2) documenting an effect of intraspecific competition on clutch size across the range. Here we also found that the variance in the estimated slopes amongst study plots was large and statistically significant (blue tit: variance explained = 26.08%, LRT = 38.63, d.f. = 2, $P < 0.0001$; Table 2), indicating important differences in the intensity of intraspecific competition. Blue tit clutch size was independent of great tit density (Fig. 2C) showing no effect of interspecific competition on blue tit clutch size.

USING DIFFERENCES IN DENSITY TO DETECT COMPETITION

Mean laying date of blue and great tit was earlier at relative density level 2 (i.e. when great tit and blue tit numbers are similar) compared to levels 1 and 3. For great tit variance in laying date was also the lowest at relative density level 2 whereas for blue tit variance in laying date decreased progressively from relative density level 1 over level 2 to level 3 (Table 3). These results are consistent with both intraspecific and interspecific competition in great tit and for interspecific competition in blue tit.

Great tits laid their eggs later than blue tit (i.e. the difference in mean laying date between great tit and blue tit was positive) at relative density level 1, and these differences decreased progressively to relative density level 2 and level 3. Therefore, when great tits outnumbered blue tits (level 3) laying date of the two species became similar.

Mean clutch size of great tit and blue tit was the smallest at relative density level 1 (i.e. when blue tits outnumber great tits), while it was higher at relative density 2 and 3 (i.e., when either great tit and blue tit numbers are similar or great tits outnumber blue tits). Likewise, variance in clutch size for both great tit and blue tit decreased from relative density level 1 to levels 2 and 3 (Table 3). For great tits, these results are consistent with interspecific competition being more important than intraspecific competition, and for blue tits the reverse occurred with intraspecific competition being more important than interspecific competition.

The difference in clutch size between great tit and blue tit tended to become more negative (i.e. blue tit clutch size greater than great tit clutch size) from relative density level 1 to level 3. Therefore, when blue tits outnumbered great tits (level 1) the difference in clutch size between the two species was the smallest, and this difference became larger and favoured blue tits when great tits outnumbered blue tit (level 3). This is also consistent with intraspecific competition affecting blue tits (Table 3; Fig. 3).

Discussion and conclusions

This extensive study of spatial patterns in density-dependence of laying date and clutch size in two species of secondary hole-nesting birds revealed several novel observations. This claim is implicit in the comparison of the three categories of differences in log density of great tit minus log density of blue tits. Here we briefly discuss the broad conclusions that can be drawn from these results. The first novel observation was that intraspecific and interspecific competition are one and the same phenomenon. The second novel observation was that the slope of conspecific density on laying date in blue tits (but not great tits) differed among study plots. The third novel observation was heterogeneity among study plots in slopes of conspecific density on clutch size of great and blue tits. The Fourth novel observation was that changes in variance in laying date and clutch size provided tests for effects of density-dependence impacting laying date and clutch size indirectly via the range of habitats occupied.

In the analyses of laying date and clutch size depending on conspecific and heterospecific density we found evidence for an effect of intraspecific competition on blue tit laying date and blue tit clutch size. We did not find effects of intraspecific competition between great tit laying date and clutch size for great tits, nor effects of interspecific competition for either species. However, we did show differences between the two species, specifically that blue tits seemed to show stronger impacts of both intraspecific and interspecific competition, seemingly contradicting the second prediction. This difference among species may be due to differences in body size and hence differences in competitive ability in early spring when the smaller blue tit is at a selective advantage.

In order to further test our predictions, we also analysed patterns within study plots because such analyses are more powerful than within-plot analyses that automatically control for many potentially confounding variables showing the highest variation among plots. We investigated the relative impact of great and blue tit density on laying date and clutch size by testing the relation between the difference in density (density difference) of great and blue tits and laying date/clutch size. We started from the assumption that in coexisting species (and as found in previous work), intraspecific competition in tits is stronger than interspecific competition (Dhondt 2012). We found the earliest laying date at density difference level 2 (great tit density similar to blue tit density) for both great and blue tit. Thus, laying date was later for both species when either the density of conspecifics or heterospecific increased, consistent with laying date being affected by intra- and interspecific competition in both species. The variance in laying date was also the lowest at density level 2 for great tit further suggesting intra- and interspecific competition for great tits, whereas the variance was the largest at density level 1 for blue tits consistent with intraspecific competition, Furthermore, given the previous results, we expected that if intraspecific competition generally occurred across our 87 study plots, blue tit clutch size should be the smallest at density difference level 1, and the largest in level 2 (great tit density = blue tit density). Our results suggest that among blue tits intraspecific competition generally occurs, while interspecific competition may occur.

Laying date was the earliest at density level 2 for both great tit and blue tit. This latter result implies that, when analysing data across Europe and Northern Africa, controlling for differences in density is probably a more powerful approach than controlling for site-specific variation resulting from differences in latitude, longitude and elevation. The likely reason is that the density difference approach does not make assumptions regarding the shape of the relationships between the parameters of interest (laying date, clutch size) as, for example, latitude or elevation.

We can take this line of reasoning one step further by investigating the relationship between difference in laying date and difference in clutch size, on the one hand, and difference in density between great and blue tits on the other. Great tits laid their eggs later than blue tits at relative density level 1 (i.e., when blue tits outnumbered great tits). The difference in laying date of great tit in relation to blue tit tended to be more similar from density level 2 to level 3. Furthermore, the variance in difference in laying date differed significantly among categories of difference in density of great and blue tits, and the variance was significantly smaller when great tits were relatively abundant (density difference level 3). These outcomes are as expected for interspecific competition in great tits. The average difference in clutch size between great and blue tits was negatively correlated with the difference in density between great and blue tits, consistent with intraspecific and interspecific competition. The variance of the difference in clutch size between great and blue tits peaked when the difference in density was the smallest, consistent with intraspecific competition. At high density of great tit relative to blue tit, the difference in clutch size was smaller relative to clutch size of blue tit (Fig. 3). The variance in the difference in clutch size was the largest for levels of difference in density 1 and 2, consistent with intraspecific and interspecific competition.

Population density is often limited by food availability (Newton 1998; Ruffino *et al*. 2014), as shown by food supplementation often increasing abundance, while removal has the opposite effect (e.g. Minot 1978, 1981; Dhondt *et al*. 1992; Török & Tóth 1999; Siriwardena *et al*. 2007; Dhondt 2012). Likewise, food provisioning in feeders has caused dramatic increases in abundance of birds, earlier timing of reproduction and increased reproductive success (review in Robb *et al.* 2008; Tryjanowski *et al.* 2015). Tits often lay earlier in urban sites as a consequence of such provisioning (e.g. Dhondt *et al.* 1984; Wawrzyniak *et al.* 2015). Although we were unable to quantify the effects of food on laying date and clutch size in this study, we assume that food limitation at least partially affects density.

Because means and variances are generally positively correlated (Wright 1964), opposite results require a biological explanation. Here we have shown that means and variances are positively correlated for difference in laying date between great tit and blue tit, while that is not the case for difference in clutch size. This requires an explanation. We hypothesise that the habitat heterogeneity hypothesis predicts an increase in the variance in reproductive parameters because at low density only high quality sites are occupied, while at high density poor quality sites (where birds lay a smaller and later clutch) are occupied (Dhondt *et al.* 1992; Ferrer & Donázar 1996; Krüger *et al.* 2012). We suggest that at high density poor quality sites are occupied, while in reality at high densities both high quality and poor quality habitats are occupied, which would result in an increase in the variance in laying adte and clutch size. Habitat heterogeneity is the mechanism that predicts that at higher density variance in clutch size should increase (Solonen *et al.* 1991; Dhondt *et al*. 1992; Ferrer & Donázar 1996). The analyses of effects of density are consistent with these predictions.

The present study was based on nest boxes, and the population density of the number of occupied boxes per unit area does not apply to the fraction of the population breeding in natural holes. This situation does not differ from analyses of other nest box populations (e.g. Gustafsson 1987; Minot 1978, 1981; Dhondt *et al*. 1992; Török & Tóth 1999; Siriwardena *et al*. 2007; Dhondt 2012; Stenseth *et al.* 2015).

We analysed effects of competition in two congeneric secondary hole nesting birds. It is likely that the hole nesting community of birds and other animal taxa will have a similar or even stronger effect on the structure of the community of hole nesters. The present study predicts that similar analyses of laying date and clutch size in competing species such as other species of sympatric tits such as *Poecile palustris* and *P. montanus* and *Ficedula* flycatchers such as pied *F. hypoleuca* and collared flycatcher *F. albicollis* may allow quantification these effects of intra- and interspecific competition (Gustafsson 1987). Analyses of such effects may be particularly powerful in a climate change scenario where the interacting parties are differently impacted by temperature and precipitation while the effects of study plot remain constant.

In conclusion, we have documented that within-plot analyses of laying date and clutch size in great and blue tits across 87 sites with known common breeding records distributed across Europe and North Africa provide a powerful tool for quantifying the effects of intraspecific and interspecific competition. We conclude that a similar approach may potentially be adopted in analyses of intraspecific and interspecific interactions among other taxa.

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Data accessibility

Data available from the Dryad Digital Repository upon acceptance.

Author contribution

Conceived idea: APM. **Analysed data:** APM and JB. **Collected data:** APM, JB, AAD, FA, CB, JC, MC, BD, AD, ME, TE, AEG, AGG, LG, PH, SAH, SJ,

RJ, TL, BL, BM, TDM, RGN, JÅN, SGN, ACN, RP, VR, HR, TS, AS, AJVN and MML. **Wrote paper:** APM, AAD, JB. **Approved final manuscript:** APM, JB, AAD, FA, CB, JC, MC, BD, AD, ME, TE, AEG, AGG, LG, PH, SAH, SJ, RJ, TL, BL, BM, TDM, RGN, JÅN, SGN, ACN, RP, VR, HR, TS, AS, AJVN and MML.

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Legends to figures

Fig. 1. Laying date of great tit (1 = March 1st; A, B) and blue tit (C, D) in relation to density of great tit (number of occupied nest boxes per ha; A, C) and blue tit (B, D). The lines are the predicted values with 95% confidence intervals obtained from the linear mixed effect models while maintaining latitude, longitude and nest floor surface as their mean values. Main habitat type, urbanisation and nest box material as their reference values (i.e., conifer, concrete and no urbanization, respectively). Black lines show significant trends and grey lines non-significant trends.

Fig. 2. Clutch size of great tit (A, B) and blue tit (C, D) in relation to density of great tit (number of occupied nest boxes per ha; A, C) and blue tit (B, D). The lines are the predicted values with 95% confidence intervals obtained from the linear mixed effect models while maintaining latitude, longitude and nest floor surface as their mean values. Main habitat type, urbanisation and nest box material as their reference values (i.e., conifer, concrete and no urbanization, respectively). Black lines show significant trends and grey lines non-significant trends.

Fig. 3. Difference in clutch size between great tits (GT) and blue tits (BT) in each site/year in relation to the difference in $\log_{10}$ density (number of occupied nest boxes per ha) between great tits and blue tits in each site/year. The line shows the best fit ordinary least squares line with its 95% confidence band for illustrative purposes only. For statistical analysis, see Results.

Fig. 1

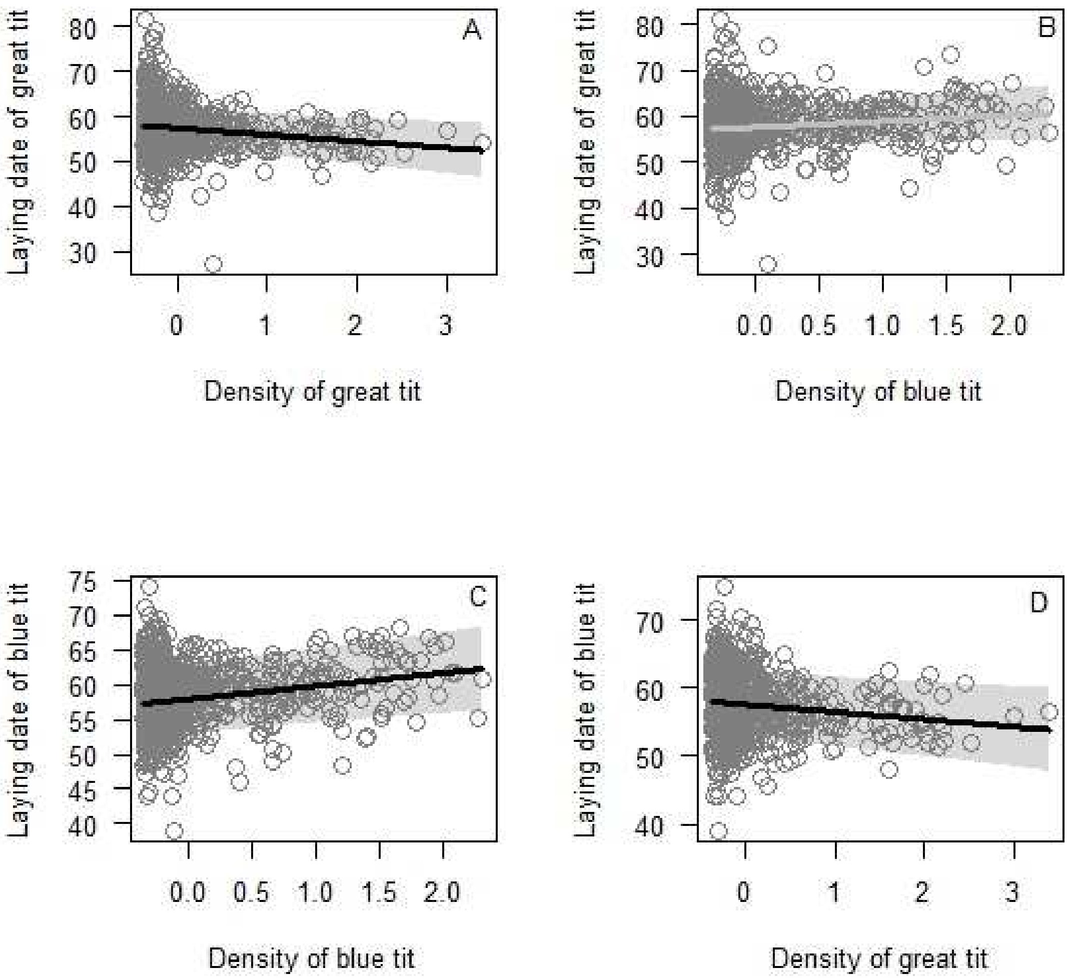
A
B
C
D
Laying date of great tit
Laying date of blue tit
Density of great tit
Density of blue tit

Fig. 2

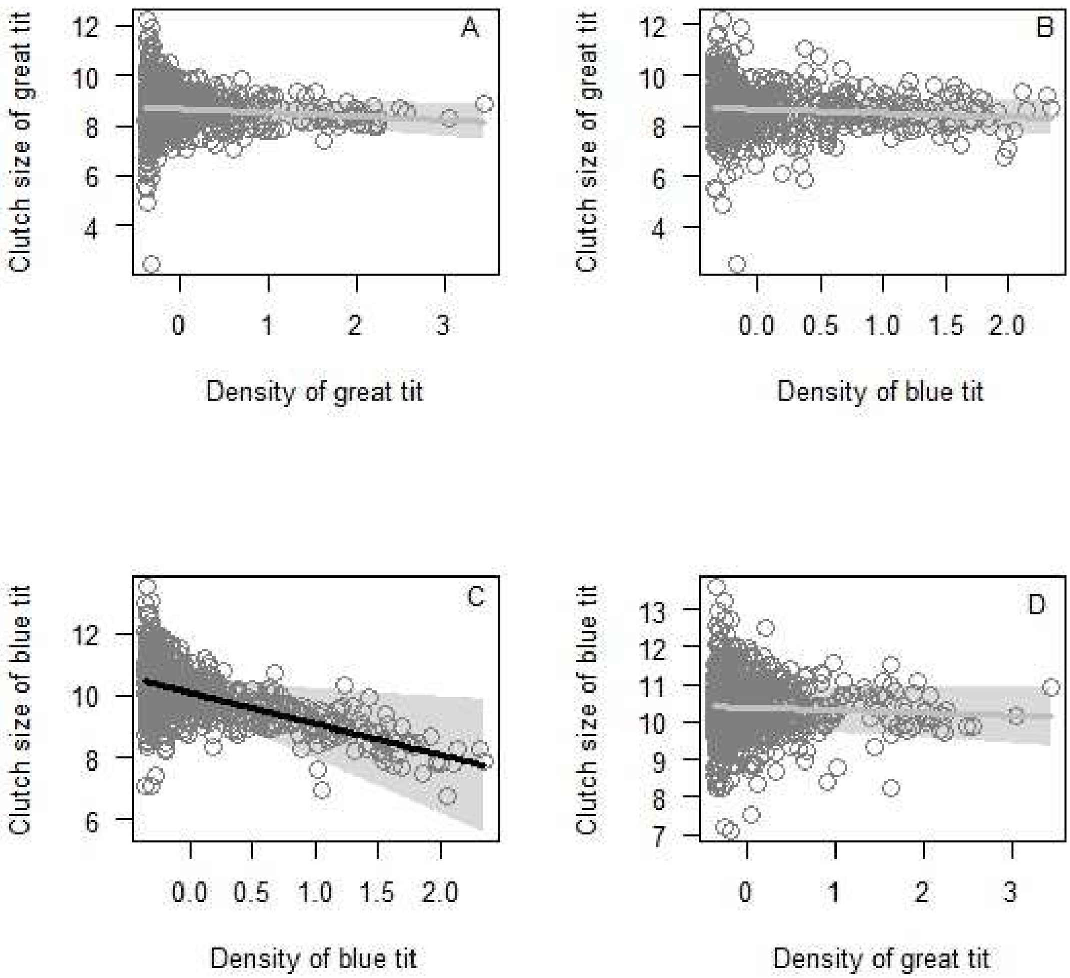
A
Clutch size of great tit
Density of great tit
B
Clutch size of great tit
Density of blue tit
C
Clutch size of blue tit
Density of blue tit
D
Clutch size of blue tit
Density of great tit

Fig. 3

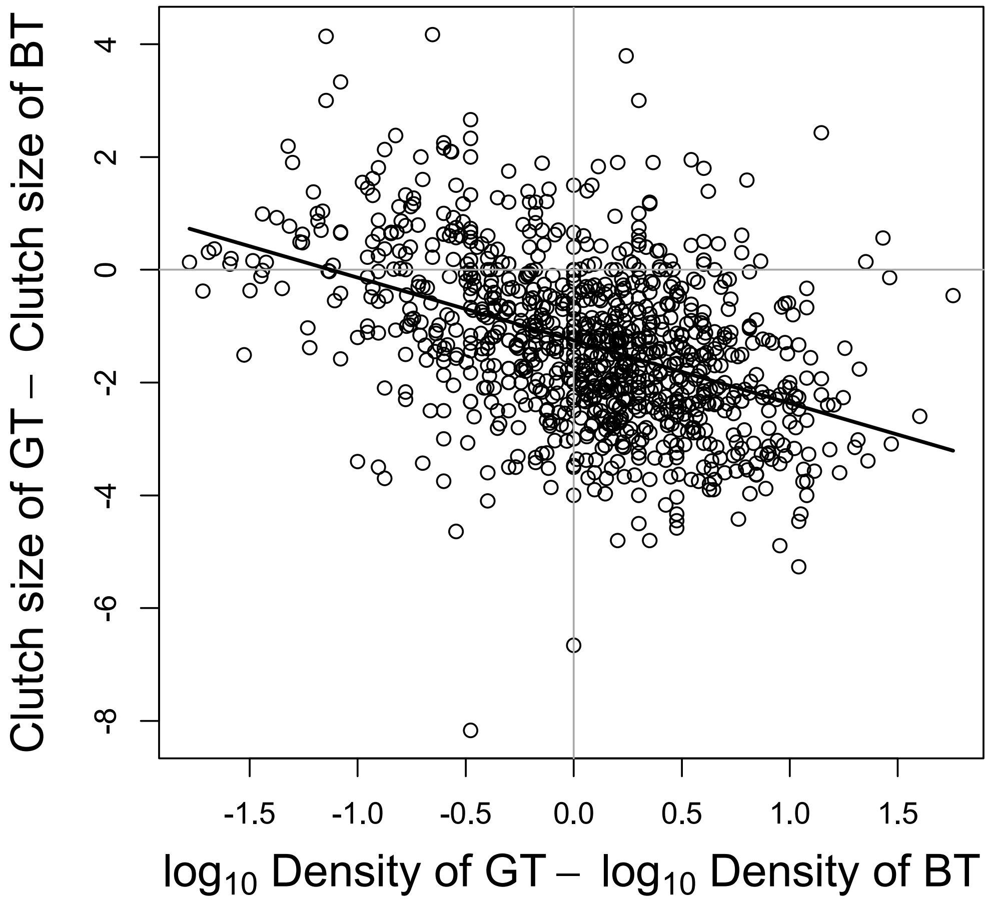
Clutch size of GT − Clutch size of BT
4
2
0
-2
-4
-6
-8
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
$\log_{10}$ Density of GT − $\log_{10}$ Density of BT

Table 1 Linear Mixed Models of laying date of great and blue tits in relation to density of great and blue tits after controlling statistically for latitude, latitude squared, longitude, longitude squared, longitude by latitude, main habitat type (fixed effect), urbanisation (fixed effect), nest box material, altitude and nest floor surface as fixed effects, and year and study site as random factors. Only the partial effects of density are shown here after controlling statistically for the variables listed above. The analyses were weighted by sample size. Effect sizes were Pearson's product-moment correlation coefficients. The analyses were based on 921 observations from 87 plots for great tit and on 930 observations from 87 sites for blue tits. The majority of sites (more than 99%) had at least five years of study or more.

Term	LRT	*P*	Estimate	SE	Effect size
Great tit laying date					
Density of great tits	6.13	0.01	-1.458	0.597	0.29
Density of blue tits	3.04	0.08	1.304	0.775	0.20
Blue tit laying date					
Density of great tits	4.34	0.04	-1.051	0.511	0.24
Density of blue tits	4.69	0.03	2.000	0.904	0.25

Table 2 Linear Mixed Models of clutch size of great and blue tits in relation to density of great and blue tits after controlling statistically for latitude, latitude squared, longitude, longitude squared, longitude by latitude, main habitat type, urbanisation, nest box material, altitude and nest floor surface as fixed terms, and study site and year as random factors. Only the partial effects of density are shown here after controlling statistically for the variables listed above. The analyses were weighted by sample size. Effect sizes were Pearson's product-moment correlation coefficients. The analyses were based on 966 observations from 87 sites for great tit and on 969 observations from 87 sites for blue tits. The majority of sites (more 99%) had at least five years of study or more.

Term	LRT	*P*	Estimate	SE	Effect size
Great tit clutch size					
Density of great tits	2.04	0.15	-0.120	0.080	0.15
Density of blue tits	2.36	0.12	-0.157	0.102	0.17
Blue tit clutch size					
Density of great tits	0.78	0.38	-0.073	0.079	0.10
Density of blue tits	6.41	0.01	-1.135	0.433	0.27

Table 3 Tests for differences in mean and variance in clutch size and laying date of great and blue tits with mean, variance and sample size for three similarly sized groups differing in population density (number of occupied nest boxes per ha) between blue tit and great tit. Welch ANOVA for means with unequal variances testing for homogeneity of means, while Levene's test analyses homogeneity of variances. The analyses were weighted by sample size.

		Great tit density < blue tit density			Great tit density = blue tit density			Great tit density > blue tit density			Welch ANOVA			Levene's test	
Difference in density (SE) N		-0.576 (0.020) 324			0.109 (0.007) 325			0.662 (0.015) 326							
	Mean	Variance	N	Mean	Variance	N	Mean	Variance	N	*F*	df	*P*	*F*	df	*P*
Laying date															
Great tit	55.5	134.2	305	53.4	89.6	311	56.9	111.5	308	46.0	2,7415.8	<0.0001	9.13	2,921	<0.0001
Blue tit	53.5	4896	308	47.6	1938	311	55.9	641	311	53.26	2,8157.6	<0.0001	34.73	2,927	<0.0001
Clutch size															
Great tit	8.27	2.58	321	8.83	1.24	323	8.74	1.21	326	22.23	2,7046.6	<0.0001	38.6	2,967	<0.0001
Blue tit	8.77	3.19	324	10.39	2.30	323	10.64	2.20	326	240.86	2,8671.2	<0.0001	24.06	2,970	<0.0001
Difference in laying date	2.22	890	304	1.71	745	311	0.97	462	308	6.53	2,21813	< 0.0001	11.81	2,920	<0.0001
Difference in clutch size	-0.50	2.16	321	-1.57	1.56	323	-1.90	1.76	326	146.18	2,22759	<0.0001	7.89	2,920	<0.0001