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

Anders Pape Møller[1], Javier Balbontín[2], André A. Dhondt[3], Vladimir Remeš[4], Frank Adriaensen[5], Clotilde Biard[6], Jordi Camprodon[7], Mariusz Cichoń[8], Blandine Doligez[9], Anna Dubiec[10], Marcel Eens[11], Tapio Eeva[12], Anne E. Goodenough[13], Andrew G. Gosler[14], Lars Gustafsson[15], Philipp Heeb[16], Shelley A. Hinsley[17], Staffan Jacob[18], Rimvydas Juškaitis[19], Toni Laaksonen[20], Bernard Leclercq[21], Bruno Massa[22], Tomasz D. Mazgajski[23], Ruedi G. Nager[24], Jan-Åke Nilsson[25], Sven G. Nilsson[26], Ana C. Norte[27], Rianne Pinxten[28], Hugo Robles[29], Tapio Solonen[30], Alberto Sorace[31], Arie J. van Noordwijk[32] and Marcel M. Lambrechts[33]

[1]Anders Pape Møller, Ecologie Systematique Evolution, CNRS, AgroParisTech, Université Paris-Saclay, F-91405 Orsay Cedex, France, anders.moller@u-psud.fr

[2]Javier Balbontín, Departamento de Zoología, Facultad de Biología, Edificio Verde, Avda. de Reina Mercedes s/n, E-41012 Sevilla, Spain, balbontin@us.es

[3] André A. Dhondt, Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA, aad4@cornell.edu

[4]Vladimir Remeš, Laboratory of Ornithology, Department of Zoology, Palacky University, CZ-77146 Olomouc, Czech Republic, vladimir.remes@upol.cz

[5]Frank Adriaensen, Evolutionary Ecology Group, University of Antwerp, Department of Biology, Campus CDE, B-2610 Antwerp, Belgium, frank.adriaensen@uantwerpen.be6[5] Clotilde Biard, IEES-Paris - Institut d'Ecologie et des Sciences de l'Environnement, Sorbonne universités, UPMC Univ Paris 06, UPEC,

[7]*Jordi Camprodon, Àrea de Biodiversitat, Grup de Biologia de la Conservació, Centre Tecnològic Forestal de Catalunya, Carretera de St. Llorenç de Morunys, km. 2, E-25280 Solsona, Spain, jordi.camprodon@ctfc.es*

[8]*Mariusz Cichoń, Jagiellonian Univ., Inst. Environm. Sci., Krakow, Poland, mariusz.cichon@uj.edu.pl*

[9]*Blandine Doligez, CNRS, Université Lyon 1, Université de Lyon, Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, 43 boulevard du 11 novembre 1918, F-69622 Villeurbanne Cedex, France, blandine.doligez@univ-lyon1.fr*

[10]*Anna Dubiec, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL-00-679 Warsaw, Poland, adubiec@miiz.waw.pl*

[11]*Marcel Eens, Campus Drie Eiken, Department of Biology, Behavioural Ecology & Ecophysiology Group, Building D, B-2610 Antwerp (Wilrijk), Belgium, marcel.eens@uantwerpen.be*

[12]*Tapio Eeva, Department of Biology, University of Turku, FI-20014 Turku, Finland, teeva@utu.fi*

[13]*Anne E. Goodenough, Department of Natural and Social Sciences, University of Gloucestershire, Glos GL50 4AZ, UK, aegoodenough@glos.ac.uk*

[14]*Andrew G. Gosler, Department of Zoology, Edward Grey Institute of Field Ornithology & Institute of Human Sciences, Oxford, South Parks Road, Oxford OX1 3PS, UK, andrew.gosler@zoo.ox.ac.uk*

[15]*Lars Gustafsson, Uppsala Univ., Department of Animal Ecology, Evolutionary Biolpgy Centre, SE-75236 Uppsala, Sweden, lars.gustafsson@ebc.uu.se*

[16]*Philipp Heeb, Laboratoire Évolution & Diversité Biologique, UPS Toulouse III, Bât 4R1, salle 122, 118 route de Narbonne, F-31062 Toulouse, France, heeb@cict.fr; philipp.heeb@univ-tlse3.fr*

[17]*Shelley H. Hinsley, CEH Wallingford, Maclean Building, Crowmarsh Gifford, Wallingford, OX10 8BB, sahi@ceh.ac.uk*

[18]Staffan Jacob, Station d'Ecologie Expérimentale du CNRS à Moulis, USR CNRS 2936, 2 route du CNRS, F-09200 Moulis, France, jacobstaffan@gmail.com

[19]Rimvydas Juškaitis, Institute of Ecology of Nature Research Centre, Akademijos 2, LT-08412 Vilnius, Lithuania, rjuskaitis@gmail.com

[20]Toni Laaksonen, Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland, tokrla@utu.fi

[21]Bernard Leclercq, 6 rue de la Croix St. Pierre, F-21410 Fleurey-sur-Ouche, France, bleclercoq@orange.fr

[22]Bruno Massa, Department of Agricultural, Food and Forest Sciences, Università di Palermo, Italy, bruno.massa@unipa.it

[23]Tomasz D. Mazgajski, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL-00-679, Warszawa, Poland, mazgaj@miiz.waw.pl

[24]Ruedi G. Nager, Institute of Biodiversity, Animal Health & Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK, Ruedi.Nager@glasgow.ac.uk

[25]Jan-Åke Nilsson, Department of Biology, Evolutionary Ecology, Lund University, SE-223 62 Lund, Sweden, Jan-Ake.Nilsson@biol.lu.se

[26]Sven G. Nilsson, Dept. of Biology, Biodiversity, Lund University, Ecology Building, SE-223 62 Lund, Sweden, sven.nilsson@biol.lu.se, sveng.nilsson@telia.com

[27]Ana C. Norte, MARE - Marine and Environmental Sciences Centre, Department of Life Sciences, Largo Marquês de Pombal, Faculty of Sciences and Technology, University of Coimbra, PT-3004-517 Coimbra, Portugal, acgnorte@ci.uc.pt

[28]Rianne Pinxten, Campus Drie Eiken, Department of Biology,Behavioural Ecology & Ecophysiology Group, Building D, B-2610 Antwerp (Wilrijk), Belgium, and Faculty of Social Sciences, Didactica Research Group, University of Antwerp, Belgium, annie.pinxten@uantwerpen.be

[29]Hugo Robles, Evolutionary Ecology Group (GIBE), Falculty of Sciences, University of A Coruña, Campus Zapateira, E-15008 A Coruña, Spain, and Evolutionary Ecology Group (EVECO), Department of Biology, University of Antwerp, Middelheimcampus, Groenenborgerlaan 171, B-2020 Antwerp, Belgium, Hugo.RoblesDiez@uantwerpen.be

[30]Tapio Solonen, Luontotutkimus Solonen Oy, Neitsytsaarentie 7b B 147, FI-00960 Helsinki, Finland, tapio.solonen@pp.inet.fi

[31]Alberto Sorace, ISPRA, Via V. Brancati 60, Rome, Italy, alberto.sorace@isprambiente.it

[32]Arie J. van Noordwijk, Netherlands Institute of Ecology (NIOO-KNAW), Doevendaalsesteg, 10, NL-6708 BP Wageningen, The Netherlands, a.vanNoordwijk@nioo.knaw.nl

[33]Marcel M. Lambrechts, Centre d'Ecologie Fonctionnelle et Evolutive, CEFE UMR 5175, Campus CNRS, 1919 route de Mende, F-34293 Montpellier Cedex 5, France, marcel.lambrechts@cefe.cnrs.fr

Word count: 7987

Address for correspondence (APM):
Tel: (+33) 1 69 15 56 88;
Fax: (+33) 1 69 15 56 96;
E-mail: anders.moller@u-psud.fr

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 for a total of more than 35,000 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 (latitude, longitude, elevation, nest box size and type, habitat, and others). 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 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). Density of tits in urban locations tends to be higher than in nearby rural plots because of higher food availability (Vaugoyeau *et al.* 2016). 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). 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. We relied on a unique long-term data base from 87 study plots using more than 35,000 breeding events in nest boxes in areas where both species nest sympatrically. Based on results from previous studies 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, (2) this effect should be more pronounced in great than in blue tits, due to the larger size of the former, and (3) at any one site, differences in density 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 outnumbers 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 made an attempt to obtain information on density, nest box size, clutch size, laying date and ecological variables from all studies 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). Briefly, we attempted to obtain 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 (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.

The study plots 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). These 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 nest base area (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).

STATISTICAL ANALYSES

We conducted eight LMMs with laying date and clutch size of great and blue tits as untransformed response variables. These 8 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 conditions (intraspecific/interspecific competition)). 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). Study plot and year were included as two cross random intercepts to account for differences among sites and years in the model testing for interspecific competition. In the models testing for intraspecific competition we included random intercepts for study plot and year. In addition, when analysing breeding variables for blue tits, the relationships between density and both laying date and clutch size were estimated for each individual plot and the estimate slopes from these relationships were entered as random factors. The same approach was used for great tits. The significance of the random slope in these models was 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 $P > 0.05$. In the models testing for interspecific competition a random slope could not be fitted in the models because data at the interspecific level did not match. 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. In addition, the other factors listed above describing site location and nestbox parameters were entered as fixed factors. All eight analyses were weighted by abundance to account for differences in sampling effort among study plots (Garamszegi & Møller 2010). We used the standardize function for standardizing regression predictors by centring (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 and the factors with more than two categories remained unchanged (Gelman 2008).

We also 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 in standard least squares analyses, again 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.

We used difference in log-transformed great tit density minus log-transformed blue tit density (henceforth density difference) as the predictor variable in analyses to test for effects of competition on laying date and on clutch size (Table 3, Fig. 3). 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.

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.

We included latitude, latitude squared, longitude, longitude squared and the interaction between latitude and longitude in the 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 and 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 was April 24 (SE = 0.35, N = 924) and mean clutch size was 8.61 eggs (SE = 0.04, N = 970). For blue tits, mean laying date was April 24 (SE = 0.34, N = 930) 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 tit 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. 1D, 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. 1C).

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. 2D, 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

We categorized density difference at three levels of similar number of study plots: 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 = 0.02, 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.

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) and 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.

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 level 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 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.

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).

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 3. Therefore, when great tits outnumbered blue tits (level 3) the laying date of the two species became similar.

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. The slope of conspecific density on laying date in blue tits (but not great tits) differed among study plots. Similar heterogeneity among study plots was found in slopes of conspecific density on clutch size of great and blue tits.

In the analyses of laying date and clutch size depending on conspecific and heterospecific density we controlled for a large number of possible effects on clutch size and on laying date (such as habitat type, degree of urbanization, latitude and longitude among others), but nevertheless only 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.

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.

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 bird abundance, while the removal of food 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). Density of tits in urban locations tends to be higher than in nearby rural locations (Vaugoyeau *et al*. 2016). Another effect of urbanisation is that in urban sites tit laying dates are earlier (e.g. Dhondt *et al.* 1984; Wawrzyniak *et al.* 2015). We could not quantify the effects of food on laying date and clutch size, but we assume that the effects of density are at least partially due to effects of food limitation.

Because means and variances are generally positively correlated (Wright 1964), opposite results require a biological explanation. 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 and Donázar 1996; Krüger *et al.* 2012). 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.

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 sympatric tits and flycatchers may allow quantification of the 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.

Acknowledgements

We would like to warmly thank the hundreds of collaborators and contributors who helped with study plot management, data collection, data management, administration, financial support, and scientific discussion. Listing their names individually would most probably provide a biased picture of all of their contributions. T. Eeva acknowledges funding by the Academy of Finland (project 265859).

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.

References

Adler, P.B., Hille Ris Lambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006) Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 12 793–12 798.

Aitken, K.E.H. & Martin, K. (2008) Resource selection plasticity and community responses to experimental reduction of a critical resource. *Ecology*, **89**, 971–980.

Alatalo, R.V. (1984) Evidence for interspecific competition among European tits *Parus* sp.: A review. *Annales Zoologici Fennici*, **19**, 309-317.

Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009) Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 11 641–11 645.

Bates, D. & Maechler, M. (2009) lme4: Linear mixed-effects models using S4 classes. R package, version 0.999375-31. Available at: http://CRAN.R-project.org/package=lme4.

Both, C. (2000) Density dependence of avian clutch size in resident and migrant species: Is there a constraint on the predictability of competitor density? *Journal of Avian Biology*, **31**, 412–417.

Crawley, J.M. (2002) *Statistical Computing. An Introduction to Data Analysis Using S-Plus*. Wiley, Chichester, UK.

Dhondt, A.A. (1977) Interspecific competition between great and blue tit. *Nature*, **268**, 521-523.

Dhondt, A.A. (2010) Effects of competition on great and blue tit reproduction: Intensity and importance in relation to habitat quality. *Journal of Animal Ecology*, **79**, 257-265.

Dhondt, A.A. (2012) *Interspecific competition in birds*. Oxford University Press, Oxford, UK.

Dhondt, A.A. & Adriaensen, F. (1999) Experiments on competition between Great and Blue Tit: Effects on Blue Tit reproductive success and population processes. *Ostrich*, **70**, 39-48.

Dhondt, A.A. & Eyckerman, R. (1980a) Competition and the regulation of numbers in great and blue tit. *Ardea*, **68**, 121-132.

Dhondt, A.A. & Eyckerman, R. (1980b) Competition between the great tit and the blue tit outside the breeding season in field experiments. *Ecology*, **61**, 1291-1296.

Dhondt, A.A., Eyckerman, R., Moermans, R. & Hublé, J. (1984) Habitat and laying date of great and blue tit *Parus major* and *Parus caeruleus*. *Ibis*, **126**, 388-397.

Dhondt, A.A., Kempenaers, B. & Adriaensen, F. (1992) Density-dependent clutch size caused by habitat heterogeneity. *Journal of Applied Ecology*, **61,** 643-648.

Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Bini, L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479–488.

Dorman, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distribution data: A review. *Ecography*, **30**, 609–628.

Ferrer, M. & Donázar, J.A. (1996) Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology*, **77**, 69-77.

Garamszegi, L.Z. & Møller, A.P. (2010) Effects of sample size and intraspecific variation in phylogenetic comparative studies: A meta-analytic review. *Biological Reviews*, **85**, 797-805.

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine,* **27**, 2865–2873.

Grover, J.P. (1997) *Resource Competition*. Chapman & Hall, London, UK.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992) A meta-analysis of competition in field experiments. *American Naturalist,* **140**, 539-572.

Gustafsson, L. (1987) Interspecific competition lowers fitness in collared flycatchers *Ficedula albicollis*: An experimental demonstration. *Ecology*, **68**, 291-296.

Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S., Fuhlendorf, S.D., Gaedke, U., Legendre, P., Magnuson, J.J., McArdle, B.H., Muldavin, E.H., Noble, D., Russell, R., Stevens, R.D., Willis, T.J., Woiwod, I.P. & Wondzell, S.M. (2007) Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3273–3277.

Keddy, P.A. (1989) *Competition*. Chapman and Hall, London, UK.

Krüger, O., Chakarov, N., Nielsen, J.T., Looft, V., Grünkorn, T., Struwe-Juhl, B. & Møller, A.P. (2012) Population regulation by habitat heterogeneity or individual adjustment? *Journal of Animal Ecology*, **81**, 330-340.

Lambrechts, M.M., Adriaensen, F., Ardia, D.R. *et al.* (2010) The design of artificial nest boxes for the study of secondary hole-nesting birds: A review of methodological inconsistencies and potential biases. *Acta Ornithologica*, **45**, 1-26.

Legendre, P. (1993) Spatial autocorrelation: Trouble or new paradigm? *Ecology*, **74**, 1659–1673.

Legendre, P. & Legendre, L. (2012) *Numerical ecology*. Elsevier, New York, NY.

Lichtstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecology*, **72**, 445–463.

McClave, J.T. & Sincich, T. (2003) *Statistics*. 9th Edition. Prentice-Hall, Englewood Cliffs, NJ.

Minot, E.O. (1978) Interspecific competition in tits. *Nature*, **275**, 463.

Minot, E.O. (1981) Effects of interspecific competition for food in blue tits (*Parus caeruleus*) and great tits (*Parus major*). *Journal of Animal Ecology*, **50**, 125-137.

Minot, E.O. & Perrins, C.M. (1986) Interspecific interference competition: Nest sites for blue and great tits. *Journal of Animal Ecology*, **55**, 331-350.

Møller, A.P. (1988) Parasites, predators and nest boxes: Facts and artefacts in nest box studies of birds? *Oikos*, **56**, 421-423.

Møller, A.P., Adriaensen, F., Artemyev, A., Bańbura, J. *et al.* (2014a) Clutch size in European secondary hole-nesting passerines in relation to nest-box floor area, habitat, geographic location and study year. *Methods in Ecology and Evolution*, **5**, 353-362.

Møller, A.P., Adriaensen, F., Artemyev, A., Bańbura, J. *et al.* (2014b) Variation in clutch size in relation to nest size in birds. *Ecology and Evolution*, **4**, 3583-3595.

Nager, R.G. & van Noordwijk, A.J. (1995) Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *American Naturalist*, **146**, 454–474.

Newton, I. (1998) *Population limitation in birds*. Academic, Amsterdam, Netherlands.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Perdeck, A.C., Visser, M.E. & Van Balen, J.H. (2000) Great Tit *Parus major* survival, and the beech-crop cycle. *Ardea*, **88**, 99–108.

R Core Team (2016) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R.E. (2012) Habitat-independent spatial structure in populations of some forest birds in eastern North America. *Journal of Animal Ecology*, **82**, 145–154.

Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S. (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, **6**, 476-484.

Robles, H., Ciudad, C. & Matthysen, E. (2011) Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: The role of traditional management practices. *Forest Ecology and Management*, **261**, 1428-1435.

Robles, H., Ciudad, C. & Matthysen, E. (2012) Responses to experimental reduction and increase of cavities by a secondary cavity-nesting bird community in cavity-rich Pyrenean oak forests. *Forest Ecology and Management*, **277**, 46-53.

Ruffino, L., Salo, P., Koivisto, E., Banks, B.P. & Korpimäki, E. (2014) Reproductive responses of birds to experimental food supplementation: A meta-analysis. *Frontiers in Zoology*, **11**, 80. doi:10.1186/s12983-014-0080-y

SAS (2012) *JMP version 10.0*. SAS Institute Inc., Cary, NC.

Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, 122, 240-285.

Siriwardena, G.M., Stevens, D.K., Anderson, G.Q.A., Vickery, J.A., Calbrade, N.A. & Dodd, S. (2007) The effect of supplementary winter seed food on breeding populations of farmland birds: Evidence from two large-scale experiments. *Journal of Applied Ecology*, **44**, 920-932.

Solonen, T., Tiainen, J., Korpimäki, E. & Saurola, P. (1991) Dynamics of Finnish Starling *Sturnus vulgaris* populations in recent decades. *Ornis Fennica*, **68**, 158-169.

Stenseth, N.C., Durant, J.M., Fowler, M.S., Matthysen, E., Adriaensen, F. et al. (2015) Testing for effects of climate change on competitive relationships and coexistence between two bird species. *Proceedings of the Royal Society of London B – Biological Sciences*, **282**, 20142929.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.

Tryjanowski, P., Morelli, F., Skórka, P., Goławski, A., Indykiewicz, P., Møller, A.P. & Zduniak, P. (2015) Who started first? Bird species visiting novel birdfeeders. *Scientific Reports*, **5**, 11858.

Török, J. & Tóth, L. (1999) Asymmetric competition between two tit species: A reciprocal removal experiment. *Journal of Animal Ecology*, **68**, 338-345.

Vaugoyeau, M., Adriaensen, F., Artemyev, A., Bańbura, J., Barba, E. *et al*. (2016) Interspecific variation in the relationship between clutch size, laying date and intensity of urbanisation in four species of hole-nesting birds. *Ecology and Evolution*, **6**, 16.

Visser, M.E. (2008) Keeping up with a warming world: Assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London B – Biological Sciences*, **275**, 649–659.

Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B – Biological Sciences*, **268**, 289–294.

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London B*, **265**, 1867–1870.

Visser, M.E., Adriaensen, F., van Balen, J.H. *et al*. (2003) Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society of London B – Biological Sciences*, **270**, 367-372.

Wilkin, T.A., Garant, D., Gosler, A.G. & Sheldon, B.C. (2006) Density effects on life-history traits in a wild population of the great tit *Parus major*: Analysis of long-term data with GIS techniques. *Journal of Animal Ecology,* **75**, 604-615.

Wright, S. (1964) *Evolution and the Genetics of Populations: Genetics and Biometric Foundations*. University of Chicago Press, Chicago, IL.

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

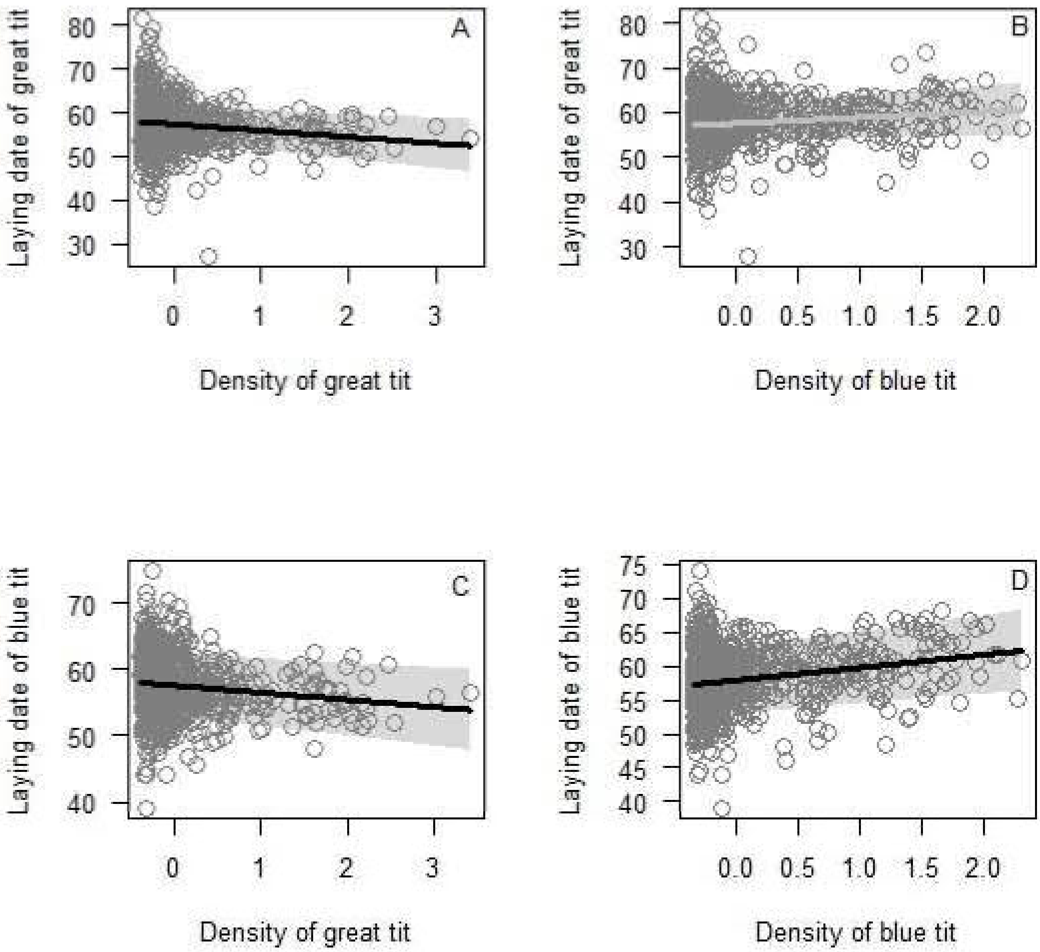
A
B
C
D
Laying date of great tit
Laying date of blue tit
Density of great tit
Density of blue tit
80
70
60
50
40
30
75
65
55
45
0
1
2
3
0.0
0.5
1.0
1.5
2.0

Fig. 2

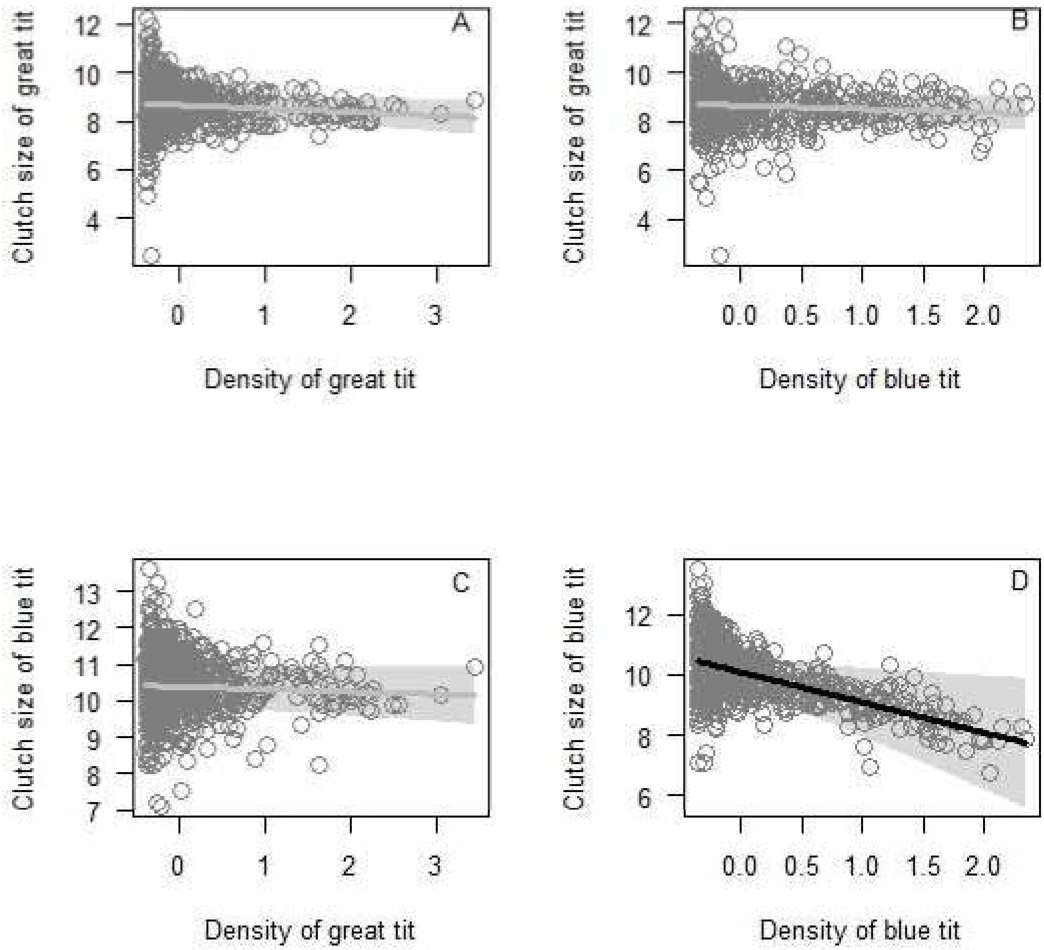
A
B
C
D
Clutch size of great tit
Clutch size of blue tit
Density of great tit
Density of blue tit
12
10
8
6
4
13
11
9
7
0
1
2
3
0.0
0.5
1.0
1.5
2.0

Fig. 3

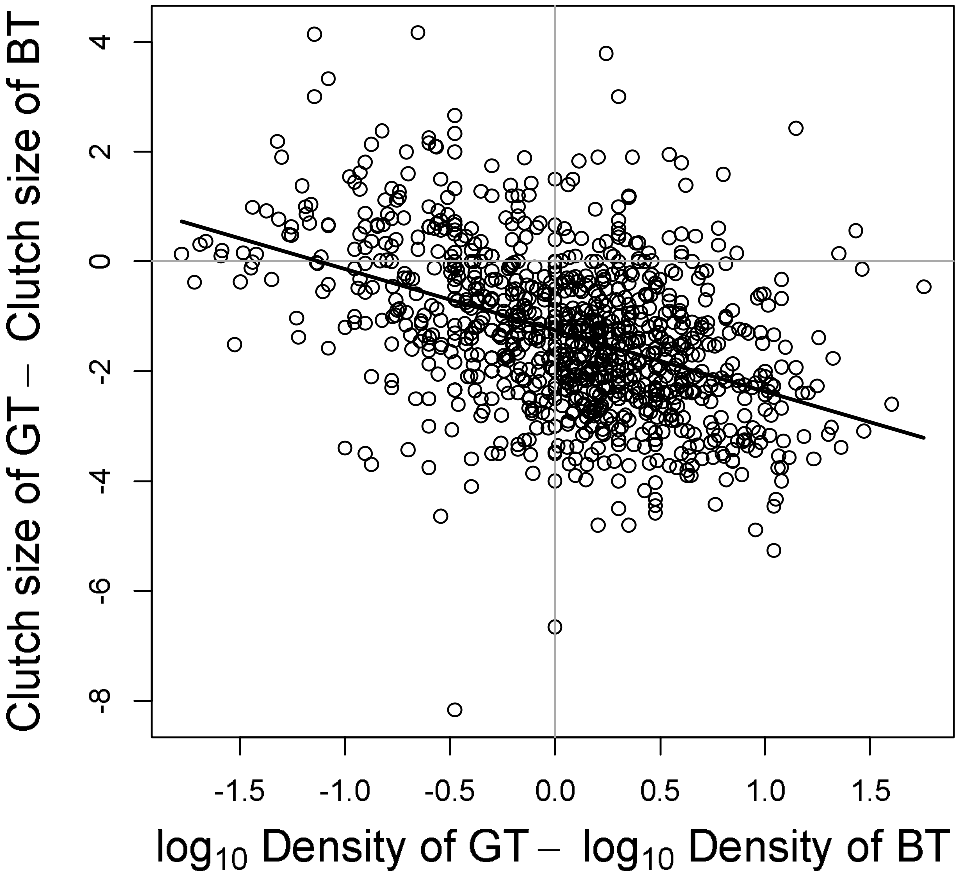
Clutch size of GT − Clutch size of BT
4
2
0
-2
-4
-6
-8
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
log10 Density of GT − log10 Density of BT

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 924 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