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Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size

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Abstract

Understanding species coexistence has long been a major goal of ecology. Coexistence theory for two competing species posits that intraspecific density dependence should be stronger than interspecific density dependence. Great tits and blue tits are two bird species that compete for food resources and nesting cavities. Based on long-term monitoring of these two competing species at sites across Europe, combining observational and manipulative approaches, we show that the strength of density regulation is similar for both species, and that individuals have contrasting abilities to compete depending on their age. For great tits, density regulation is driven mainly by intraspecific competition. In contrast, for blue tits, interspecific

51 competition contributes as much as intraspecific competition, consistent with asymmetric
52 competition between the two species. In addition, including age-specific effects of intra- and
53 interspecific competition in density-dependence models improves predictions of fluctuations
54 in population size by up to three times.
55

INTRODUCTION

Understanding species coexistence has long been a major goal in ecological studies (Ellner *et al.* 2019). Most species live in guilds or communities alongside other ecologically similar species, sometimes relying on common limiting resources. A major principle of coexistence theory for two competing species is that intraspecific density dependence should be stronger than interspecific density dependence (Chesson 2000). If interspecific competition is stronger than intraspecific competition, one species will ultimately be excluded (see e.g. Alatalo *et al.* 1985), which will change the composition of the entire ecological community (Kokkoris *et al.* 1999; Chesson 2000). A recent review showed that, in plant communities, intraspecific competition is indeed four to five times stronger than interspecific competition, providing the basis for the maintenance of diversity in natural communities (Adler *et al.* 2018). Assessing the relative contribution of inter- and intraspecific competition to density regulation is crucial to determine the chances of species persistence in a community.

Intraspecific density dependence causes a decrease of population growth rate with increasing density of the focal population (Royama 1992; Turchin 1995; Berryman *et al.* 2002; Lande *et al.* 2002; Brook & Bradshaw 2006). Classical analyses of density dependence are based on time series of population fluctuations, assuming that all individuals in the population have an equal competitive effect (Krebs 2002). Evidence is accumulating, however, that in age-structured populations, the strength of competitive effects vary along an individual's lifetime (see e.g. Coulson *et al.* 2001; Lande *et al.* 2002; de Roos & Persson 2013). For example, in a great tit (*Parus major*) population, the youngest birds have the strongest density-dependent effect on other individuals of the same age or older (Gamelon *et al.* 2016). Young birds constitute the critical age classes for density dependence (sensu Charlesworth 1972), in which the variation in the number of individuals most strongly affects density regulation. Until now, however, no field study has examined how age-specific

competitive effects influence the population growth rates of sympatric species (see Cameron *et al.* 2007 for laboratory settings). The question of how age-specific competitive effects influence the growth rates of sympatric species has rarely been addressed because the classical models of competition between two species A and B use linear combinations of their two densities. For instance, the well-known Lotka (1925) and Volterra (1926) competition model in continuous time measures the effect of species-specific densities N_A and N_B on species-specific population growth rates λ_A and λ_B , where K_A and K_B are the species-specific carrying capacities:

$$\log(\lambda_A) = r_A - \frac{r_A}{K_A} (N_A + \alpha_{AB} N_B),$$

$$\log(\lambda_B) = r_B - \frac{r_B}{K_B} (N_B + \alpha_{BA} N_A),$$

with α_{AB} and α_{BA} the competition coefficients corresponding to the per capita reduction in growth caused by each additional individual of the other species. However, such models are developed in the simple case of no age structure assuming the same ability for all individuals to compete. In the real world, this assumption is unrealistic, and it is thus important to test whether age structure can improve models of interspecific competition.

Great tits and blue tits (*Cyanistes caeruleus*) are hole-nesting bird species that compete for cavities and food. Competition intensity varies across Europe (Møller *et al.* 2018) and between habitats (Dhondt 2011). Long-term, individual-based monitoring of these two species have been performed across Europe and two complementary approaches have been adopted to understand how they compete. The first is observational, meaning that vital rates (e.g. survival, fecundity) and emergent population descriptors (e.g. population size) are estimated for these two sympatric species without changing the density of cavities (i.e., the number of nest boxes remains constant throughout the study). The second approach is manipulative and involves a change in the number or type of nest boxes over time (Torok & Tóth 1999; Dhondt

2011). Field experiments that manipulate density of one competitor and record the response of the other species have provided significant insight into the role of interspecific competition in the regulation of populations (see Connell 1983; Schoener 1983 for reviews).

Long-term studies of nestbox-breeding tits in the UK and in Belgium, consisting of both observational and manipulative approaches, provide an opportunity to explore how age classes of two competitive species affect each species' population growth rate. We adopted several approaches to address these issues. First, using an integrated population model (IPM) (see Schaub & Abadi 2011; Zipkin & Saunders 2018 for reviews), we estimated the age-specific numbers of the females of both species in all sites. This approach allows us to account for observation errors in population censuses, as well as uncertainty in the age of some individuals, which is crucial while investigating density dependence (Dennis *et al.* 2006; Lillegård *et al.* 2008; Abadi *et al.* 2012; Lebreton & Gimenez 2013; Schaub *et al.* 2013). Second, we compared the relative importance of intra- and interspecific competition for both species in geographically spread sites. Third, we examined how the number of individuals of both species in different age classes contributed to the observed variation in population growth rates of both species. One can hypothesize that including interspecific competition and age-specific contribution to density dependence in demographic analyses would improve predictions of population growth. We tested this hypothesis in all sites for both species by comparing predictions of population sizes from density-dependence models accounting or ignoring age structure and interspecific competition.

MATERIAL AND METHODS

Overview of different density-dependence models

(1) Classical approach

The classical approach to studying density dependence consists of assessing the extent to which population growth rate decreases with population size. The Ricker model is a simple and common way of representing density-dependent feedback in the per-unit-abundance growth rate (Ricker 1954; Dennis & Taper 1994). The Ricker model is the phenomenological relationship between population growth rate in year t ($\lambda_t = \frac{N_{t+1}}{N_t}$) and population size N_t . It takes the following form:

$$\log(\lambda_t) = \gamma_\lambda + \beta_N N_t + \text{res}_{\lambda_t} \quad (1)$$

where γ_λ is the intercept, β_N is the regression coefficient providing a measure of the strength of the density regulation, and res_{λ_t} are the residuals of the regression corresponding to the variation in λ not explained by population size.

(2) Age-specific contribution to density dependence

To determine how the different age classes contributed to the observed variation in population growth rate, the previous phenomenological relationship (Eqn. (1)) can be broken down by age-specific numbers $N_{i,t}$ (see Gamelon *et al.* 2016). In the case where four age classes are considered, Eqn. (1) becomes:

$$\log(\lambda_t) = \gamma_\lambda + \beta_{N_1} N_{1,t} + \beta_{N_2} N_{2,t} + \beta_{N_3} N_{3,t} + \beta_{N_4} N_{4,t} + \text{res}_{\lambda_t} \quad (2)$$

where β_{N_i} are the age-specific regression coefficients.

(3) Age-specific contribution to density dependence including interspecific competition

To determine how the number of individuals in the different age classes from species A and B contribute to the observed variation in population growth rate of species A ($\lambda_{A,t}$) and B ($\lambda_{B,t}$), we break down the previous phenomenological relationship (Eqn. (2)) by species-specific numbers $N_{iA,t}$ and $N_{iB,t}$. In the case where four age classes are considered, Eqn. (2) becomes:

$$\begin{aligned}
\log(\lambda_{A,t}) &= \gamma_{\lambda_A} + \beta_{N_{1,A}}(N_{1A,t} + \omega_A \times N_{1B,t}) + \beta_{N_{2,A}}(N_{2A,t} + \omega_A \times N_{2B,t}) + \\
&\quad \beta_{N_{3,A}}(N_{3A,t} + \omega_A \times N_{3B,t}) + \beta_{N_{4,A}}(N_{4A,t} + \omega_A \times N_{4B,t}) + res_{\lambda_{A,t}}, \\
\log(\lambda_{B,t}) &= \gamma_{\lambda_B} + \beta_{N_{1,B}}(N_{1B,t} + \omega_B \times N_{1A,t}) + \beta_{N_{2,B}}(N_{2B,t} + \omega_B \times N_{2A,t}) + \\
&\quad \beta_{N_{3,B}}(N_{3B,t} + \omega_B \times N_{3A,t}) + \beta_{N_{4,B}}(N_{4B,t} + \omega_B \times N_{4A,t}) + res_{\lambda_{B,t}}. \quad (3)
\end{aligned}$$

where $\beta_{N_{i,A}}$ and $\beta_{N_{i,B}}$ are the age-specific regression coefficients when interspecific competition is accounted for. In the first part of the equation, an ω_A value of 0 indicates that only the age-specific numbers of species A matter. In this scenario, only intraspecific competition explains variations in λ_A and interspecific competition has no impact on growth rate (as in Eqn. (2)). In contrast, an ω_A value of 1 indicates that an individual of species B has the same competitive effect on the population growth rate of species A as an individual of species A. Hence, ω_A (and ω_B) provides a measure of the relative importance of inter- vs. intraspecific competition on the total density regulation acting on λ_A (and λ_B). Noticeably, ω_A corresponds to α_{AB} in the Lotka-Volterra competition model and ω_B to α_{BA} . However, our model is more complex, since it includes density regulation acting among age classes. The strength of density regulation is given by the $\beta_{N_{i,A}}$ coefficients (with high $\beta_{N_{i,A}}$ indicating strong density regulation). If the required high-quality data is available, the above formula can easily be extended to more than two competing species and the competition coefficient ω_A can be made age-specific to relax the assumption of similar age differences in competitive strength for inter- and intraspecific competition.

Great tits and blue tits as a case study

Great tits and blue tits are two competing, short-lived birds abundant in European gardens and woodlands as year-round residents (Perrins & McCleery 1989). They are cavity-nesters and readily accept nest boxes as nesting sites, making it possible to monitor the entire breeding population. Nest boxes with a large entrance hole (32 mm) are suitable for both

species whereas nest boxes with a small entrance hole (26 mm) almost completely exclude great tits.

The data come from three long-term study sites near Antwerp (Boshoek and Peerdsbos) and Ghent in Belgium, and from eight sites (“rounds”) within Wytham Woods, near Oxford in the UK. In all sites, both great and blue tit populations were monitored. In the case of Wytham Woods, substantial differences (up to five fold) in nest box density between rounds as well as differences in vegetation structure, physical geography, etc. coupled with the large sample size, suggested that it would be appropriate to estimate effects at the level of the round (see e.g. Garant *et al.* 2005). Lumping the rounds into one single population would neglect such heterogeneity and ignore differences in population density as determined by nestbox density. Further, one might expect competition for sites to be more pronounced when boxes are at low density. Populations are open to immigration and emigration (Table 1, SI1). At all sites except Peerdsbos, the number of nest boxes remained constant during the study period (see Minot & Perrins 1986; Dhondt *et al.* 1990; Nour *et al.* 1998; Visser *et al.* 2003; Garant *et al.* 2005; Dhondt 2010; Matthysen *et al.* 2011 and Table 1 for further details on the study sites). In Peerdsbos, 33% of both large-holed and small-holed nest boxes were removed in 1997.

Demographic data

Nest boxes were visited during the breeding season and three types of demographic data were recorded:

(1) For each species, the total number of breeding females (C_t) was recorded. As most females start to breed at one year of age, the breeding population size is a good proxy for the total number of females in the population (Dhondt *et al.* 1990).

(2) All nestlings and mothers were fitted with a uniquely numbered leg-ring to allow identification. Additionally, mothers were aged (first-years versus adults [≥ 2 years]) based on plumage characteristics. We assumed that previously unringed mothers recruited into the population in the first year in which they were recorded breeding; some of these could not be aged due to left-census truncation (those recruited as adults). The breeding females of known age that are marked and monitored throughout their life provide capture-recapture (CR) data of known age females. We grouped the breeding birds of known age into four age classes: 1, corresponding to the first year of breeding (i.e., second calendar year of life); 2, corresponding to the second year of breeding; 3 corresponding to the third year of breeding; and 4, which groups breeding females aged 4 or more.

(3) Females locally ringed as nestlings were recorded as recruited to the breeding population if they were observed breeding in a subsequent year. This gave the number of females that successfully became a first-year breeding female in year $t+1$, termed the breeding recruitment for year t (J_t). This recruitment could be broken down by the age-class of the mother (see Dhondt 1989 for evidence of age-specific recruitment): first year breeder, second year, etc. This provided estimates of the number of recruits for mothers of age class i in year t ($J_{i,t}$). Also, we recorded the total number of breeding females of each age class i in year t ($B_{i,t}$).

Annual age-specific numbers of females using an IPM

Our analyses were performed on each study site separately (see Fig. 1 for a schematic of the different analytical steps). For each species, we integrated the recorded number of breeding females (C_t), CR data of females of known age, and data on reproductive success (i.e., $B_{i,t}$ and $J_{i,t}$) into an integrated population model (IPM) (Schaub & Abadi 2011). This framework provides estimates of all the vital rates (survival, fecundity), the true total number

of females N_t and the true age-specific numbers of females $N_{i,t}$ for each year t with improved precision and free of observation error (Besbeas *et al.* 2002; Abadi *et al.* 2010, 2012; Kéry & Schaub 2012). The joint analysis of these three datasets thus allowed us to account for observation error associated with the recorded number of counted breeding females (Lebreton & Gimenez 2013). It also allowed us to account for the incomplete information on age structure in the monitoring data (e.g. some females are of unknown age), for imperfect detection (e.g. recapture probability is not 1) and for demographic stochasticity (Lande *et al.* 2002).

Inference is based on the joint likelihood, corresponding to the multiplication of the likelihoods from the single datasets (CR data, data on reproductive success and population count) (Kéry & Schaub 2012). The likelihoods of the different datasets were specified as follows. For CR data of breeding females of known age, we used the Cormack-Jolly-Seber model (Lebreton *et al.* 1992) which allows estimation of annual survival between age class i and $i+1$ ($S_{i,t}$) and recapture (P_t) probabilities. For data on reproductive success, the observed number of daughters locally recruited per age class i ($J_{i,t}$) is Poisson distributed with $J_{i,t} \sim \text{Poisson}(B_{i,t} \times F_{i,t})$, where $F_{i,t}$ is the recruitment rate of females of age class i at year t . For the population count data, we used a state-space model (de Valpine & Hastings 2002) that consisted of a process model describing how the population size and structure changed over time as well as an observation model (Besbeas *et al.* 2002). We considered a pre-breeding age-structured model with the four pre-defined age classes. The true age-specific numbers of females $N_{i,t}$ corresponds to the sum of locally born females and immigrants. Assuming independence among the datasets, the likelihood of the IPM corresponds to the product of the likelihoods of the three different datasets, namely population counts, reproductive success data and CR data (Kéry & Schaub 2012). The assumption of independence is violated in our study because some of the breeding females may be found in the different datasets but, as

shown in a simulation study (Abadi *et al.* 2010), it is unlikely that it affects our parameter estimates and their precision with the kind of data we used here.

The model was fitted within a Bayesian framework. To assess convergence, we ran four independent chains with different starting values for a minimum of 100,000 MCMC iterations, with a burn-in of 50,000 iterations, thinning every 100th observation and resulting in 2,000 posterior samples. We used the Brooks and Gelman diagnostic $\hat{R}$ to assess the convergence of the simulations and used the rule $\hat{R} < 1.1$ to determine whether convergence was reached (Brooks & Gelman 1998). The analyses were implemented using JAGS version 3.4.0 (Plummer 2003) with package R2jags (Su & Yajima 2012). For a full description of the IPM, the priors used and the R code to fit the IPM, see an example on another great tit population (Gamelon *et al.* 2016).

To ensure that the priors for initial population numbers did not influence estimates of age-specific numbers during the first year of the study, we considered estimates provided by our IPM from the second year onwards (see SI2).

Age-specific contribution to density dependence including interspecific competition

As a derived parameter from the IPM, we computed the “observed” population growth rate of great tits (GT) in year t as $\lambda_{GT,t} = \frac{N_{GT,t+1}}{N_{GT,t}}$ for each posterior sample (2,000 in total) and recorded its posterior mean. To determine how the (posterior means of the) age-specific numbers of great tit N_{iGT} and blue tit N_{iBT} females contributed to the observed variation in λ_{GT} , we applied Eqn. (3) with species A corresponding to great tit and species B to blue tit (BT). As $N_{GT,t}$, $N_{iGT,t}$ and $N_{iBT,t}$ were estimated in the IPM model, sampling variance and observation errors were accounted for. This approach thus precludes spurious detection of density dependence (see Freckleton *et al.* 2006; Schaub *et al.* 2013; Gamelon *et al.* 2016 for a similar approach). To determine the value of ω_{GT} (i.e., the relative importance of inter- and

intraspecific competition in the dynamics of great tits) that provides the best fit of Eqn. (3) to the data, we calculated the Akaike Information Criterion (AIC) (Burnham & Anderson 2002) of Eqn. (3) for ω_{GT} ranging from 0 to 1 in increments of 0.005. The model with the lowest AIC was considered as the best one, and its corresponding value of ω_{GT} was recorded. We did not consider competitive exclusion as a possible scenario and thus prevented interspecific competition from exceeding intraspecific competition in our analyses by restricting the competition coefficients ω to values less than unity. By not allowing parameter values above unity, the parameters are tested in a region in accordance with biological a priori and the accuracy in the estimation is improved. We reported the estimates of the regression coefficients $\beta_{Ni,GT}$ from the best model retained, which indicate how the number of females of both species in age class N_i contributed to the observed variations in λ_{GT} .

For each site, we applied the same approach on blue tits to determine how the age-specific numbers of great tit (N_{iGT}) and blue tit (N_{iBT}) females contributed to the observed variation in blue tit population growth rate, $\lambda_{BT,t}$.

Implications for the dynamics of age-structured populations

For each population, from the estimates of ω_{BT} , $\beta_{Ni,BT}$ and $\gamma_{\lambda,BT}$ and the true age-specific numbers of females $N_{iGT,t}$ and $N_{iBT,t}$ during the study periods, we calculated the expected population growth rate $\lambda_{BT,expected1}$ (from Eqn. (3)). We compared it to the observed annual growth rate λ_{BT} during this period (i.e., estimated with the IPM) through a simple linear regression.

Second, Eqn. (2) was fitted, meaning that interspecific competition was ignored. From these new estimates of $\beta_{Ni,BT}$ and γ_{λ} and from true age-specific numbers of blue tit females $N_{iBT,t}$ between 1997 and 2016, we calculated the expected growth rate $\lambda_{BT,expected2}$. This was then compared to the observed growth rate λ_{BT} with a linear regression.

Finally, Eqn. (1) was fitted, meaning that both interspecific competition and age-specific contribution to density dependence were ignored. From these annual estimates of $\beta_{N_{BT}}, \gamma_{\lambda}'$ and from true total number of blue tits $N_{BT,t}$ between 1997 and 2016, we calculated $\lambda_{BT,expected3}$ and compared it to the observed growth rate λ_{BT} .

Analyses were performed with R software, version 3.4.3 (R Development Core Team 2017).

RESULTS

IPM

Age-specific numbers of females $N_{iGT,t}$ and $N_{iBT,t}$ varied over time, for both great tits and blue tits in all sites (SI2). Survival and fecundity rates also fluctuated through years, and generally differed among age classes (SI3,4). The recapture probability varied over years and was generally high in all sites for both species (SI5).

Relative importance of inter- vs. intraspecific competition

For each site and each species, we estimated the value of ω_{GT} and ω_{BT} that provided the best fit of the model described in Eqn. (3) (Fig. 2). At eight out of 10 sites (excluding the manipulative experiment at Peerdsbos), ω_{GT} equals 0 (Fig. 2). This indicates small contribution of interspecific competition to the changes in population size of great tits, i.e. blue tits have little effect on the growth rate of the great tit population, λ_{GT} . At the two other sites, ω_{GT} equals 0.39, indicating that two to three blue tits have the same competitive effect as one great tit.

For blue tits, at seven out of 10 sites, accounting for interspecific competition (with $\omega_{BT}>0$) in Eqn. (3) better explains variation in population growth rate λ_{BT} than ignoring interspecific competition (with $\omega_{BT}=0$). Thus, the number of great tits present at a site affects λ_{BT} . The relative importance of inter- vs. intraspecific competition ω_{BT} even reached unity for

some sites (Fig. 2), indicating that one great tit has the same competitive effect as one blue tit. At the three other sites, ω_{BT} equals 0, indicating that the number of great tits has no effect on λ_{BT} .

Effects of age-class numbers on population growth rate

Negative β_{N_i} values indicate that higher number of females in age class N_i translates to lower population growth rate. The β_{N_i} values were negative, positive, or not significant depending on the species, the study sites and the age class (Fig. 3). Thus, the different age classes did not contribute equally to the strength of density dependence. While in some sites, age 1 and 2 had the strongest negative effect on λ (e.g. at Common Piece, Fig. 3), older age classes contributed the most to density regulation in other areas (e.g. in the blue tit population at Singing Way). The effects of age-class numbers on λ have the same order of magnitude for both species (Fig. 3) indicating that they experience similar strength of density dependence.

Change in the number of nest boxes over time

In Peerdsbos, the removal of some nest boxes during the study period provides an opportunity to explore the effect of a change in nest box number on the relative contribution of inter- and intraspecific competition to the population dynamics. Prior to the removal in 1997, the effects of interspecific competition were close to intraspecific competition in both species ($\omega_{GT}=0.730$ and $\omega_{BT}=0.87$, Fig. 2). One great tit had almost the same competitive effect as one blue tit on λ_{GT} and one blue tit had the same competitive effect as one great tit on λ_{BT} . In the second period (i.e., after 1997), the relative importance of interspecific competition dropped for great tits ($\omega_{GT}=0.055$) and increased for blue tits ($\omega_{BT}=1$). Thus, interspecific competition becomes negligible on λ_{GT} whereas on λ_{BT} , one blue tit tended to have the same competitive effect as one great tit.

The removal of some nest boxes was associated with a two-fold increase of the strength of density regulation for great tits (Fig. 3). Together with a low ω_{GT} reported during the second period, these results indicate that great tits play a major role in their own regulation. However, the strength of density regulation was not stronger in the second period for blue tits (Fig. 3). Together with a high ω_{BT} , this means that blue tits were mainly limited by great tits in the second period, although with the same intensity as in the first period.

Implications for the dynamics of age-structured populations

After the removal in 1997 in Peerdsbos, great tits contributed greatly to the strong density dependence acting on the dynamics of the blue tit population ($\omega_{BT}=1$). This population is a relevant case study for exploring how including interspecific competition in demographic analyses might help to predict variations in population growth rate λ_{BT} . The posterior means of λ_{BT} (on a log-scale) estimated through the IPM varied between -0.56 and 0.48, indicating that the population decreased and increased over time (Fig. 4, grey lines). These fluctuations were caused by the combined effect of both density-dependent and -independent factors (such as climate variations). The expected growth $\lambda_{BT,expected1}$ predicted by our density-dependent model accounting for age-specific contribution to density dependence and interspecific competition (Eqn. (3)) matched well with the observed variations in λ_{BT} (Fig. 4A, blue line). This model explains 56% of the variance in λ_{BT} . However, $\lambda_{BT,expected2}$ predicted by a density-dependent model accounting for age-specific contribution to density dependence but ignoring interspecific competition (Eqn. (2)) provided a poorer fit (Fig. 4B, blue line), explaining only 36% of the variance in observed λ_{BT} . The classical approach (Eqn. (1)) assuming equal contribution of all ages to density dependence and ignoring interspecific competition provided an even poorer fit (Fig. 4C, blue line), explaining only 24% of the variance in observed λ_{BT} .

The blue tit population at Peerdsbos is not an exception with regards to improved predictions of fluctuations in population size when both age structure and interspecific competition are accounted for. Accounting for age and interspecific competition in demographic analyses substantially improves our predictions of variations in growth rate for most of the blue tit populations, by up to three times (Fig. 5). For great tit populations, while accounting for age-specific contribution to density dependence improves the model fit (Fig. 5, comparison between Eqn. (1) and Eqn. (2)), accounting for interspecific competition has rather little effect on the predictive power of the density-dependence model (Fig. 5, comparison between Eqn. (2) and Eqn. (3)).

DISCUSSION

Fluctuations in size of natural populations are due to temporal variation in climate (see e.g. Sæther *et al.* 2000, 2004; Coulson *et al.* 2001; Stenseth *et al.* 2003; Berryman & Lima 2006) and density dependence (Royama 1992; Turchin 1995). The relative importance of environmental stochastic and deterministic (i.e. density-dependent) factors in affecting population growth rates has long been debated (Andrewartha & Birch 1954; Nicholson 1957; Turchin 1995; Coulson *et al.* 2004) but it is now accepted that both play an important role (Leirs *et al.* 1997; Coulson *et al.* 2001; Boyce *et al.* 2006). Several studies of tits have shown that both climate variation and density dependence induce spatio-temporal variation in population dynamics (Sæther *et al.* 2003; Grøtan *et al.* 2009). Accordingly, in our study, density dependence was present in all populations (negative β parameters, Fig. 3) and account for up to 92% of the recorded variation in population growth (see e.g. the blue tit population at Great Wood, Fig. 5). Within a population, both intra- and interspecific competition contributed to the density regulation. These contributions were age-dependent. Our findings question the assumptions commonly made when estimating the strength of density

dependence (Krebs 2002), that *i*) interspecific competition is negligible; and *ii*) all individuals in the population have an equal competitive effect. Relaxing these assumptions greatly improves predictions of fluctuations in population size in age-structured populations. Variation in population growth rates is better predicted when interspecific competition and age-specific contribution to density dependence are accounted for. In populations limited by intra- and interspecific competition such as blue tit populations, we strongly recommend the use of a scalar function describing how several age classes of competitive species affect the population growth rate negatively.

Contribution of inter- and intraspecific competition to changes in population size

Classical models of competition between two species such as Lotka (1925) and Volterra (1926) use linear combinations of the two densities and ignore age structure. Here, we provide a straightforward method to estimate the relative importance of intra- vs. interspecific competition in age-structured populations. When close to 0, the competition coefficient (here called ω) indicates that only intraspecific competition explains variations in population growth rate λ , whereas close to 1, it indicates a similar contribution of intra- and interspecific competition to observed variations in λ . A value above unity would indicate that interspecific competition is higher than intraspecific competition, and that the coexistence between the two species only results from immigration. A proper evaluation of this hypothesis would require a spatially-explicit competition model.

Based on long-term monitoring of two competing species, we found that the relative contribution of interspecific competition to density dependence (ω values) is species-specific, with interspecific competition being more important in blue tits than in great tits. This indicates asymmetric competition, in accordance with previous studies that have shown that when great tit population density is high, great tits direct high levels of aggression against

blue tits during competition for food or breeding sites (Dhondt 2011). The increased relative importance of interspecific competition ω_{BT} for the blue tit population at Peerdsbos after the removal of some nest boxes probably results from interspecific competition for roosting sites in winter, as shown in multiple experiments (Dhondt 2011). Great tits can even exclude most blue tits if all nest boxes are suitable for both species, through higher rates of dispersal in blue tits (Dhondt 2011). Conversely, great tit population growth was only slightly sensitive to blue tit population density and was mainly limited by intraspecific competition. Intraspecific competition is common in great tits and well documented (Both *et al.* 1999). An experimental study showed that competition among conspecifics in great tit could lead to higher juvenile dispersal (Kluyver 1971). Similarly, there is compelling evidence that at high density, great tits occupy lower quality territories, leading to reduced clutch size (Perrins 1979; Dhondt *et al.* 1992). In contrast to the situation for blue tits, our analyses suggest that density regulation in great tit populations mainly operates through intraspecific competition.

Age-specific contribution to density regulation

We found that the strength of density regulation (β parameters) is comparable for great and blue tits. However, individuals differ in their contribution to density dependence dependent on their age. Previous work that focused on a single great tit population (Gamelon *et al.* 2016) provided support for the important role of the youngest age classes in density regulation. Our current findings suggest that, even if young females consistently contribute to density regulation, older individuals also play an important role, in one-third of the populations. Although it is beyond the scope of this study, the fact that some ages appear to be important in driving density regulation at some sites but not others is deserving of further study, and could be attributable to variation in local environmental conditions.

Conclusion

We studied the population dynamics of two co-occurring and ecologically competing bird species in the UK and Belgium. The two species exhibit similar strength of density regulation, and individuals of different ages play contrasting roles in that regulation. While in blue tits, interspecific competition can be as important as intraspecific competition in determining this regulation, great tit populations show little sensitivity to the local density of blue tits. Beyond the interspecific differences, we detected among-site differences in the strength of density regulation (β parameters) and the relative importance of interspecific competition (ω values). Variation in ecological conditions (e.g. availability of food resources, cavities) could explain such discrepancies. While we focused on pairwise interactions, more complex interactions with other competitors present in some of the areas may affect the growth rates of great tit and blue tit populations. Expanding our approach to more than two competitor populations offers exciting avenues of research (Levine *et al.* 2017).

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Table 1 Eleven sites included in the study where intra- and interspecific density dependence were investigated. Displayed are the study sites (in Belgium and the UK), the study period during which demographic data were collected on great tits and blue tits, and the number of marked great tit (N_{GT}) and blue tit (N_{BT}) females as part of capture-recapture programs. The number of nest boxes provided to tits was reduced at Peerdsbos in 1997 and remained constant in the other sites.

	Study sites	Study period	Monitored females
1	Boshoek	1994-2016	$N_{GT}=1634$; $N_{BT}=1348$
2	Ghent	1994-2011	$N_{GT}=399$; $N_{BT}=136$
3 / 4	Peerdsbos	1980-1996 / 1997-2016	$N_{GT}=805$; $N_{BT}=778$
5	Bean Wood	2001-2016	$N_{GT}=379$; $N_{BT}=372$
6	Broad Oak	2003-2016	$N_{GT}=636$; $N_{BT}=682$
7	Common Piece	2003-2016	$N_{GT}=357$; $N_{BT}=361$
8	Extra	2008-2016	$N_{GT}=930$; $N_{BT}=536$
9	Great Wood	2008-2016	$N_{GT}=597$; $N_{BT}=436$
10	Marley	2001-2016	$N_{GT}=553$; $N_{BT}=455$
11	Marley Plantation	2001-2016	$N_{GT}=479$; $N_{BT}=305$
12	Singing Way	2001-2016	$N_{GT}=514$; $N_{BT}=319$

Figure 1 Schematic of the different analytical steps to investigate intra- and interspecific density dependence. In each study site, demographic data including capture-recapture (CR) data are collected on great tits (GT, yellow) and blue tits (BT, blue). In each site, data are analyzed within an Integrated Population Model (IPM) and time series of population size (N_t), population growth rate λ_t , age-specific survival rates ($S_{i,t}$), fecundity rates ($F_{i,t}$) and numbers ($N_{i,t}$) are obtained for each species in each location. Outside the IPMs, these parameters then feed density-dependence models ignoring (Eqns. 1 & 2) or accounting (Eqn. 3) for interspecific competition. In this latter case, β_{N_i} corresponding to the age-specific contribution to density dependence and ω , the relative importance of inter- vs. intraspecific competition, are estimated for both species at a given location.

Figure 2 Boxplot showing the relative importance of inter- vs. intraspecific competition on the total density regulation acting on great tit's population growth rate ω_{GT} (in yellow) and on blue tit's population growth rate ω_{BT} (in blue) across sites. Values equal to 0 indicate no interspecific competition and values equal to 1 indicate a similar competitive effect of great tit and blue tit. Numbers refer to the study sites (see correspondence in Table 1).

Figure 3 Columns show the effects of the number of breeding females N_i in age class i of both species on great tit population growth rates λ_{GT} (log-transformed) (in yellow) and on blue tit population growth rates λ_{BT} (log-transformed) (in blue) in the eleven study sites (in rows). Displayed are the means of the regression coefficients β_{N_i} and their associated standard errors. Negative values indicate that higher number of females in the age class N_i translates to lower population growth rate. The boxplots summarize the effects of the number of breeding females N_i in age class i of both species on λ_{GT} and λ_{BT} across sites.

Figure 4 Blue tit population growth rate (λ_{BT} , on a log-scale) at Peerdsbos between 1997 and 2016. Grey lines correspond to the observed growth rate λ_{BT} (i.e., estimated through the IPM) with its 95% confidence interval. Blue lines (and their 95% confidence intervals) correspond to **A**) growth rate $\lambda_{BT,expected1}$ predicted by a density-dependent model accounting for age-specific contribution to density dependence and both intra- and interspecific competition (Eqn. (3)); **B**) growth rate $\lambda_{BT,expected2}$ predicted by the same model as that in A) but ignoring interspecific competition (Eqn. (2)); **C**) growth rate $\lambda_{BT,expected3}$ predicted by the same model as that in B) but assuming equal contribution of all ages to density dependence (i.e., classical approach, Eqn. (1)).

Figure 5 Coefficient of determination (R^2) between observed population growth rates and predicted ones from Eqn. (3) (i.e. by a density-dependent model accounting for age-specific contribution to density dependence and both intra- and interspecific competition), Eqn. (2) (i.e. ignoring interspecific competition but accounting for age-specific contribution) and Eqn. (1) (i.e. classical approach) for great tit (in yellow, one color per site) and blue tit populations (in blue, one color per site). Numbers refer to the study sites (see correspondence in Table 1).