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► To cite this version:

Marlène Gamelon, Stefan J G Vriend, Steinar Engen, Frank Adriaensen, André A Dhondt, et al.. Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size. *Ecology Letters*, 2019, 22 (5), pp.797 - 806. 10.1111/ele.13237 . hal-03282103

HAL Id: hal-03282103

<https://hal.science/hal-03282103>

Submitted on 9 Aug 2021

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

3

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25 **Running title:** Intra- and interspecific regulation in tits

26 **Keywords:** competitive interactions; *Cyanistes caeruleus*; density dependence; density
27 regulation; *Parus major*; population growth rate

28

29 **Type of article:** Letter

30 **Number of words in the abstract:** 146/150

31 **Number of words in the main text:** 5000/5000

32 **Number of references:** 69

33 **Number of figures:** 5

34 **Number of tables:** 1

35 **Authorship:** F.A., E.M., A.A.D., and B.C.S. contributed to data collection; F.A., S.R.E. and
36 S.J.G.V. prepared the datasets; M.G., S.E., F.A., E.M., B.C.S. and B.E.S. conceived the study;
37 M.G. conducted the analyses and wrote the manuscript and all authors contributed to
38 revisions on later manuscript versions.

39 **Data accessibility:** The data and the R scripts supporting the results are archived in Dryad
40 doi:10.5061/dryad.45873cg

41

42 **Abstract**

43 Understanding species coexistence has long been a major goal of ecology. Coexistence theory
44 for two competing species posits that intraspecific density dependence should be stronger than
45 interspecific density dependence. Great tits and blue tits are two bird species that compete for
46 food resources and nesting cavities. Based on long-term monitoring of these two competing
47 species at sites across Europe, combining observational and manipulative approaches, we
48 show that the strength of density regulation is similar for both species, and that individuals
49 have contrasting abilities to compete depending on their age. For great tits, density regulation
50 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

56 INTRODUCTION

57 Understanding species coexistence has long been a major goal in ecological studies
58 (Ellner *et al.* 2019). Most species live in guilds or communities alongside other ecologically
59 similar species, sometimes relying on common limiting resources. A major principle of
60 coexistence theory for two competing species is that intraspecific density dependence should
61 be stronger than interspecific density dependence (Chesson 2000). If interspecific competition
62 is stronger than intraspecific competition, one species will ultimately be excluded (see e.g.
63 Alatalo *et al.* 1985), which will change the composition of the entire ecological community
64 (Kokkoris *et al.* 1999; Chesson 2000). A recent review showed that, in plant communities,
65 intraspecific competition is indeed four to five times stronger than interspecific competition,
66 providing the basis for the maintenance of diversity in natural communities (Adler *et al.*
67 2018). Assessing the relative contribution of inter- and intraspecific competition to density
68 regulation is crucial to determine the chances of species persistence in a community.

69 Intraspecific density dependence causes a decrease of population growth rate with
70 increasing density of the focal population (Royama 1992; Turchin 1995; Berryman *et al.*
71 2002; Lande *et al.* 2002; Brook & Bradshaw 2006). Classical analyses of density dependence
72 are based on time series of population fluctuations, assuming that all individuals in the
73 population have an equal competitive effect (Krebs 2002). Evidence is accumulating,
74 however, that in age-structured populations, the strength of competitive effects vary along an
75 individual's lifetime (see e.g. Coulson *et al.* 2001; Lande *et al.* 2002; de Roos & Persson
76 2013). For example, in a great tit (*Parus major*) population, the youngest birds have the
77 strongest density-dependent effect on other individuals of the same age or older (Gamelon *et*
78 *al.* 2016). Young birds constitute the critical age classes for density dependence (sensu
79 Charlesworth 1972), in which the variation in the number of individuals most strongly affects
80 density regulation. Until now, however, no field study has examined how age-specific

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

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

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

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

103 2011). Field experiments that manipulate density of one competitor and record the response of
104 the other species have provided significant insight into the role of interspecific competition in
105 the regulation of populations (see Connell 1983; Schoener 1983 for reviews).

106 Long-term studies of nestbox-breeding tits in the UK and in Belgium, consisting of
107 both observational and manipulative approaches, provide an opportunity to explore how age
108 classes of two competitive species affect each species' population growth rate. We adopted
109 several approaches to address these issues. First, using an integrated population model (IPM)
110 (see Schaub & Abadi 2011; Zipkin & Saunders 2018 for reviews), we estimated the age-
111 specific numbers of the females of both species in all sites. This approach allows us to
112 account for observation errors in population censuses, as well as uncertainty in the age of
113 some individuals, which is crucial while investigating density dependence (Dennis *et al.*
114 2006; Lillegård *et al.* 2008; Abadi *et al.* 2012; Lebreton & Gimenez 2013; Schaub *et al.*
115 2013). Second, we compared the relative importance of intra- and interspecific competition
116 for both species in geographically spread sites. Third, we examined how the number of
117 individuals of both species in different age classes contributed to the observed variation in
118 population growth rates of both species. One can hypothesize that including interspecific
119 competition and age-specific contribution to density dependence in demographic analyses
120 would improve predictions of population growth. We tested this hypothesis in all sites for
121 both species by comparing predictions of population sizes from density-dependence models
122 accounting or ignoring age structure and interspecific competition.

123

124 **MATERIAL AND METHODS**

125 **Overview of different density-dependence models**

126 **(1) Classical approach**

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

$$133 \quad \log(\lambda_t) = \gamma_{\lambda'} + \beta_N N_t + res_{\lambda_t'} \quad (1)$$

134 where $\gamma_{\lambda'}$ is the intercept, β_N is the regression coefficient providing a measure of the strength
 135 of the density regulation, and $res_{\lambda_t'}$ are the residuals of the regression corresponding to the
 136 variation in λ not explained by population size.

137

138 **(2) Age-specific contribution to density dependence**

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

$$143 \quad \log(\lambda_t) = \gamma_{\lambda} + \beta_{N_1} N_{1,t} + \beta_{N_2} N_{2,t} + \beta_{N_3} N_{3,t} + \beta_{N_4} N_{4,t} + res_{\lambda_t} \quad (2)$$

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

145

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

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

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

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

171

172 **Great tits and blue tits as a case study**

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

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

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

194

195 **Demographic data**

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

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

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

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

219

220 **Annual age-specific numbers of females using an IPM**

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

226 of females N_t and the true age-specific numbers of females $N_{i,t}$ for each year t with improved
227 precision and free of observation error (Besbeas *et al.* 2002; Abadi *et al.* 2010, 2012; Kéry &
228 Schaub 2012). The joint analysis of these three datasets thus allowed us to account for
229 observation error associated with the recorded number of counted breeding females (Lebreton
230 & Gimenez 2013). It also allowed us to account for the incomplete information on age
231 structure in the monitoring data (e.g. some females are of unknown age), for imperfect
232 detection (e.g. recapture probability is not 1) and for demographic stochasticity (Lande *et al.*
233 2002).

234 Inference is based on the joint likelihood, corresponding to the multiplication of the
235 likelihoods from the single datasets (CR data, data on reproductive success and population
236 count) (Kéry & Schaub 2012). The likelihoods of the different datasets were specified as
237 follows. For CR data of breeding females of known age, we used the Cormack-Jolly-Seber
238 model (Lebreton *et al.* 1992) which allows estimation of annual survival between age class i
239 and $i+1$ ($S_{i,t}$) and recapture (P_t) probabilities. For data on reproductive success, the observed
240 number of daughters locally recruited per age class i ($J_{i,t}$) is Poisson distributed with
241 $J_{i,t} \sim \text{Poisson}(B_{i,t} \times F_{i,t})$, where $F_{i,t}$ is the recruitment rate of females of age class i at year t .
242 For the population count data, we used a state-space model (de Valpine & Hastings 2002) that
243 consisted of a process model describing how the population size and structure changed over
244 time as well as an observation model (Besbeas *et al.* 2002). We considered a pre-breeding
245 age-structured model with the four pre-defined age classes. The true age-specific numbers of
246 females $N_{i,t}$ corresponds to the sum of locally born females and immigrants. Assuming
247 independence among the datasets, the likelihood of the IPM corresponds to the product of the
248 likelihoods of the three different datasets, namely population counts, reproductive success
249 data and CR data (Kéry & Schaub 2012). The assumption of independence is violated in our
250 study because some of the breeding females may be found in the different datasets but, as

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

253 The model was fitted within a Bayesian framework. To assess convergence, we ran
254 four independent chains with different starting values for a minimum of 100,000 MCMC
255 iterations, with a burn-in of 50,000 iterations, thinning every 100th observation and resulting
256 in 2,000 posterior samples. We used the Brooks and Gelman diagnostic \hat{R} to assess the
257 convergence of the simulations and used the rule $\hat{R} < 1.1$ to determine whether convergence
258 was reached (Brooks & Gelman 1998). The analyses were implemented using JAGS version
259 3.4.0 (Plummer 2003) with package R2jags (Su & Yajima 2012). For a full description of the
260 IPM, the priors used and the R code to fit the IPM, see an example on another great tit
261 population (Gamelon *et al.* 2016).

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

265

266 **Age-specific contribution to density dependence including interspecific competition**

267 As a derived parameter from the IPM, we computed the “observed” population growth
268 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)
269 and recorded its posterior mean. To determine how the (posterior means of the) age-specific
270 numbers of great tit N_{iGT} and blue tit N_{iBT} females contributed to the observed variation in λ_{GT} ,
271 we applied Eqn. (3) with species A corresponding to great tit and species B to blue tit (BT).
272 As $N_{GT,t}$, $N_{iGT,t}$ and $N_{iBT,t}$ were estimated in the IPM model, sampling variance and observation
273 errors were accounted for. This approach thus precludes spurious detection of density
274 dependence (see Freckleton *et al.* 2006; Schaub *et al.* 2013; Gamelon *et al.* 2016 for a similar
275 approach). To determine the value of ω_{GT} (i.e., the relative importance of inter- and

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

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

290

291 **Implications for the dynamics of age-structured populations**

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

297 Second, Eqn. (2) was fitted, meaning that interspecific competition was ignored. From
298 these new estimates of $\beta_{Ni,BT}$ and γ_{λ} and from true age-specific numbers of blue tit females
299 $N_{iBT,t}$ between 1997 and 2016, we calculated the expected growth rate $\lambda_{BT,expected2}$. This was
300 then compared to the observed growth rate λ_{BT} with a linear regression.

301 Finally, Eqn. (1) was fitted, meaning that both interspecific competition and age-
302 specific contribution to density dependence were ignored. From these annual estimates of
303 $\beta_{N_{BT}}, \gamma\lambda'$ and from true total number of blue tits $N_{BT,t}$ between 1997 and 2016, we calculated
304 $\lambda_{BT,expected3}$ and compared it to the observed growth rate λ_{BT} .

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

306

307 **RESULTS**

308 **IPM**

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

313

314 **Relative importance of inter- vs. intraspecific competition**

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

322 For blue tits, at seven out of 10 sites, accounting for interspecific competition (with
323 $\omega_{BT}>0$) in Eqn. (3) better explains variation in population growth rate λ_{BT} than ignoring
324 interspecific competition (with $\omega_{BT}=0$). Thus, the number of great tits present at a site affects
325 λ_{BT} . The relative importance of inter- vs. intraspecific competition ω_{BT} even reached unity for

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

329

330 **Effects of age-class numbers on population growth rate**

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

339

340 **Change in the number of nest boxes over time**

341 In Peerdsbos, the removal of some nest boxes during the study period provides an
342 opportunity to explore the effect of a change in nest box number on the relative contribution
343 of inter- and intraspecific competition to the population dynamics. Prior to the removal in
344 1997, the effects of interspecific competition were close to intraspecific competition in both
345 species ($\omega_{GT}=0.730$ and $\omega_{BT}=0.87$, Fig. 2). One great tit had almost the same competitive
346 effect as one blue tit on λ_{GT} and one blue tit had the same competitive effect as one great tit on
347 λ_{BT} . In the second period (i.e., after 1997), the relative importance of interspecific competition
348 dropped for great tits ($\omega_{GT}=0.055$) and increased for blue tits ($\omega_{BT}=1$). Thus, interspecific
349 competition becomes negligible on λ_{GT} whereas on λ_{BT} , one blue tit tended to have the same
350 competitive effect as one great tit.

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

357

358 **Implications for the dynamics of age-structured populations**

359 After the removal in 1997 in Peerdsbos, great tits contributed greatly to the strong
360 density dependence acting on the dynamics of the blue tit population ($\omega_{BT}=1$). This population
361 is a relevant case study for exploring how including interspecific competition in demographic
362 analyses might help to predict variations in population growth rate λ_{BT} . The posterior means
363 of λ_{BT} (on a log-scale) estimated through the IPM varied between -0.56 and 0.48, indicating
364 that the population decreased and increased over time (Fig. 4, grey lines). These fluctuations
365 were caused by the combined effect of both density-dependent and -independent factors (such
366 as climate variations). The expected growth $\lambda_{BT,expected1}$ predicted by our density-dependent
367 model accounting for age-specific contribution to density dependence and interspecific
368 competition (Eqn. (3)) matched well with the observed variations in λ_{BT} (Fig. 4A, blue line).
369 This model explains 56% of the variance in λ_{BT} . However, $\lambda_{BT,expected2}$ predicted by a density-
370 dependent model accounting for age-specific contribution to density dependence but ignoring
371 interspecific competition (Eqn. (2)) provided a poorer fit (Fig. 4B, blue line), explaining only
372 36% of the variance in observed λ_{BT} . The classical approach (Eqn. (1)) assuming equal
373 contribution of all ages to density dependence and ignoring interspecific competition provided
374 an even poorer fit (Fig. 4C, blue line), explaining only 24% of the variance in observed λ_{BT} .

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

384

385 **DISCUSSION**

386 Fluctuations in size of natural populations are due to temporal variation in climate (see
387 e.g. Sæther *et al.* 2000, 2004; Coulson *et al.* 2001; Stenseth *et al.* 2003; Berryman & Lima
388 2006) and density dependence (Royama 1992; Turchin 1995). The relative importance of
389 environmental stochastic and deterministic (i.e. density-dependent) factors in affecting
390 population growth rates has long been debated (Andrewartha & Birch 1954; Nicholson 1957;
391 Turchin 1995; Coulson *et al.* 2004) but it is now accepted that both play an important role
392 (Leirs *et al.* 1997; Coulson *et al.* 2001; Boyce *et al.* 2006). Several studies of tits have shown
393 that both climate variation and density dependence induce spatio-temporal variation in
394 population dynamics (Sæther *et al.* 2003; Grøtan *et al.* 2009). Accordingly, in our study,
395 density dependence was present in all populations (negative β parameters, Fig. 3) and account
396 for up to 92% of the recorded variation in population growth (see e.g. the blue tit population
397 at Great Wood, Fig. 5). Within a population, both intra- and interspecific competition
398 contributed to the density regulation. These contributions were age-dependent. Our findings
399 question the assumptions commonly made when estimating the strength of density

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

408

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

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

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

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

438

439 **Age-specific contribution to density regulation**

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

449

450 **Conclusion**

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

463

464 **Acknowledgments**

465 We warmly thank two anonymous referees and the Editor for their helpful comments on
466 previous drafts of this paper. We are grateful to all those who have collected data. We also
467 warmly thank Marcel E. Visser for stimulating discussions. This work was supported by the
468 Research Council of Norway through its Centres of Excellence funding scheme (project
469 number 223257).

470

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628

629 **Table 1** Eleven sites included in the study where intra- and interspecific density dependence
630 were investigated. Displayed are the study sites (in Belgium and the UK), the study period
631 during which demographic data were collected on great tits and blue tits, and the number of
632 marked great tit (N_{GT}) and blue tit (N_{BT}) females as part of capture-recapture programs. The
633 number of nest boxes provided to tits was reduced at Peerdsbos in 1997 and remained
634 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	$N_{GT}=514$; $N_{BT}=319$

635

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

646

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

652

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

660

661 **Figure 4** Blue tit population growth rate (λ_{BT} , on a log-scale) at Peerdsbos between 1997 and
662 2016. Grey lines correspond to the observed growth rate λ_{BT} (i.e., estimated through the IPM)
663 with its 95% confidence interval. Blue lines (and their 95% confidence intervals) correspond
664 to **A**) growth rate $\lambda_{BT,expected1}$ predicted by a density-dependent model accounting for age-
665 specific contribution to density dependence and both intra- and interspecific competition
666 (Eqn. (3)); **B**) growth rate $\lambda_{BT,expected2}$ predicted by the same model as that in A) but ignoring
667 interspecific competition (Eqn. (2)); **C**) growth rate $\lambda_{BT,expected3}$ predicted by the same model as
668 that in B) but assuming equal contribution of all ages to density dependence (i.e., classical
669 approach, Eqn. (1)).

670

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

677