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Density dependence in an age-structured population of great tits: identifying the critical age classes

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1 **Density dependence in an age-structured population of great tits:**
2 **identifying the critical age classes**

3

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14

15 **Running head:** Critical age classes in great tit

16 **Abstract.** Classical approaches for the analyses of density dependence assume that all the
17 individuals in a population equally respond and equally contribute to density dependence.
18 However, in age-structured populations, individuals of different ages may differ in their
19 responses to changes in population size and how they contribute to density dependence
20 affecting the growth rate of the whole population. Here, we apply the concept of critical age
21 classes, i.e., a specific scalar function that describes how one or a combination of several age
22 classes affect the demographic rates negatively, in order to examine how total density
23 dependence acting on the population growth rate depends on the age-specific population
24 sizes. In a 38-year dataset of an age-structured great tit (*Parus major*) population, we find
25 that the age classes including the youngest breeding females were the critical age classes for
26 density regulation. These age classes correspond to new breeders that attempt to take a
27 territory and that have the strongest competitive effect on other breeding females. They
28 strongly affected population growth rate and reduced recruitment and survival rates of all
29 breeding females. We also show that depending on their age class, females may differently
30 respond to varying density. In particular, the negative effect of the number of breeding
31 females was stronger on recruitment rate of the youngest breeding females. These findings
32 question the classical assumptions that all the individuals of a population can be treated as
33 having an equal contribution to density regulation and that the effect of the number of
34 individuals is age independent. Our results improve our understanding of density regulation
35 in natural populations.

36

37 **Key words:** age-structured population, Bayesian, density dependence, density regulation,
38 integrated population model, *Parus major*, recruitment, survival

39

40 INTRODUCTION

41 Fluctuations in population size are dependent on the combined effects of density-
42 independent (stochastic) and density-dependent (deterministic) factors (Lande et al. 2003).
43 Density dependence operates through a negative feedback between the population growth
44 rate and the population size at one or more time steps (Royama 1992, Turchin 1995,
45 Berryman et al. 2002, Lande et al. 2002, Brook and Bradshaw 2006). In many cases, density
46 dependence results in regulation of the population fluctuations around a mean population
47 size, the carrying capacity (Sinclair 1989). Consequently, that affects many important
48 characteristics of the population dynamics that have implications for the management of
49 populations. For example, the form of the density regulation affects the sustainable rate of
50 harvest of exploited populations (Sæther et al. 1996, Hilborn and Walters 2003) and
51 persistence time of populations vulnerable to extinction (Lande et al. 2003).

52 Estimates of the strength of density dependence in population dynamics have
53 traditionally been based on time-series analyses of population counts (Royama 1992, Turchin
54 1995, Lande et al. 2003, Coulson et al. 2008). Thus, the potential negative effect of density
55 on population growth rate is estimated by a phenomenological relationship between
56 population growth rate and total population size. Such a phenomenological relationship at the
57 level of the population is based on the assumption that all individuals irrespective of their age
58 are exchangeable in terms of i) responses to varying density and ii) in their competitive effect
59 on other individuals (Krebs 2002). If the age structure fluctuates temporally and the above
60 assumptions do not hold, such time-series analyses of population counts will lead to biased
61 estimates of the density-dependent component of the population dynamics.

62 The assumptions of equal responses and equal contribution of all ages to density
63 dependence are often violated in age-structured populations. Indeed, there is now compelling
64 evidence that individuals of different ages can differ in their response to density-dependent

65 factors. For instance, in their review on large mammals and herbivores, Bonenfant et al.
66 (2009) highlighted that density-dependent responses of survival and fecundity rates are
67 common and strongly age-dependent. Similarly, an increase in population density strongly
68 affects specifically adult survival in the red-backed shrikes (*Lanius collurio*) and has virtually
69 very little effect on juvenile survival (Abadi et al. 2012). But interestingly, in age-structured
70 populations subject to density dependence, the influence of an individual on other ones may
71 also depend on its age and consequently individuals may differently contribute to density
72 dependence. For instance, in long-lived territorial birds in which adults breed in the same
73 territory for several years and new breeders are dependent on occupying vacant territories, the
74 number of adults, specifically, negatively impacts the number of new recruits in the
75 population (Sæther et al. 2002). Surprisingly, to our knowledge, such an age-specific
76 contribution to density dependence has been poorly explored in terrestrial systems.

77 Nearly forty years ago, an important contribution to the analysis of density-
78 dependence in age-structured populations was provided by Charlesworth (1972), who
79 introduced the concept of the *critical age class*. This denotes the age class or combination of
80 age classes in which the variation in the number of individuals most strongly affects the
81 density regulation. However, this concept has had little influence on empirical analyses of
82 population dynamics (e.g., Beddington 1974). Hence, whether all age classes or only the size
83 of some specific age classes contributes to density-dependent effects in age-structured
84 populations remains an open question. This is most likely due to the difficulty of censusing
85 and determining the age of all the individuals in a population. Thanks to recent
86 methodological advances, accounting for observation errors in population census while
87 investigating density dependence is now possible (Dennis et al. 2006, Lillegård et al. 2008,
88 Abadi et al. 2012, Lebreton and Gimenez 2013, Schaub et al. 2013).

89 Here, we fill this gap by identifying the critical age classes (sensu Charlesworth 1972,
90 1973) for density dependence that mostly affect the population growth rate and its
91 components caused by variation in survival and fecundity in an age-structured population.
92 The great tit (*Parus major*) population in Hoge Veluwe National Park (the Netherlands) has
93 highly fluctuated in size during the last 40 years (Reed et al. 2013a) and there is evidence
94 based on time-series analyses of strong density dependence in the dynamics of this
95 population (Both 1998b, Grøtan et al. 2009, Reed et al. 2013b, 2013a). First, using a
96 Bayesian integrated population model (IPM) (see Schaub and Abadi 2011 for a review), we
97 estimated age-specific demographic rates and age-specific numbers, including observation
98 error in records of individuals as well as uncertainty in the age of some monitored birds.
99 Then, by relaxing the assumption of equal contribution of all birds to the density dependence,
100 we examined how the different age classes contributed to the observed variation in
101 demographic rates and determined which age classes contribute the most to the total density
102 dependence acting on the growth rate of our population.

103

104 MATERIAL AND METHODS

105 *Study species and study area*

106 The data analyzed come from a long-term study of a great tit population at Hoge
107 Veluwe National Park in the Netherlands (52°02'N, 5°51'E), a mixed pine-deciduous wood
108 of 171 ha (see Reed et al. 2013b for further details on the study area and procedure for data
109 collection). The great tit is a 18-20 g small passerine bird species abundant in European
110 gardens and woodlands and not migratory (Perrins and McCleery 1989). It is a short-lived
111 species; the oldest breeding female recorded in our population was 7 years of age. This hole-
112 nester accepts nest boxes for breeding, allowing monitoring of the whole population as long
113 as more nest boxes than required are provided. Females usually start reproduce in the second

114 calendar year of life (Perrins 1979). They produce one clutch of up to 18 eggs laid each year,
115 although double-clutching may be sometimes observed (Husby et al. 2009). A common
116 measure of breeding success is the number of recruits, corresponding to the number of young
117 which survive long enough to breed in the nest boxes (Perrins and McCleery 1989). In the
118 study area, very few females bred in natural cavities and most of them bred in nest boxes
119 (Grøtan et al. 2009). More nest boxes than required were provided to ensure that the
120 availability of nest boxes did not influence population density (Reed et al. 2013b). We
121 focused on the years between 1973 and 2012 when the study area remained the same size and
122 the number of nest boxes was approximately constant (Reed et al. 2013b). As the study area
123 is surrounded by a matrix of potential suitable habitats for great tits, the population is open to
124 immigration and emigration (Reed et al. 2013b).

125

126 *Demographic data*

127 Three types of demographic data were available for this population: capture-recapture
128 (CR) data, total number of breeding females at year t , and number of recruits produced by
129 breeding females. During the breeding season (April to June) each year, nest boxes were
130 visited at least once a week. All young were ringed on day seven post-hatching. The ringed
131 mothers were identified and the unringed mothers were given a ring allowing future
132 identifications. These unringed mothers (1955 females during the study period) were assumed
133 to have immigrated into the population the current year. It was possible to exactly age most
134 of these immigrants (1686 females), resulting in a total of only 269 breeding females of
135 unknown age over the course of the study period. Overall, CR data were available for 2691
136 breeding females of known age (1005 locally fledged females plus 1686 females that fledged
137 elsewhere but immigrated to the study area to breed).

138 The second type of demographic data available was an estimate of the total number of
139 counted breeding females each year t (C_t) on the study site. Rates of non-breeding are very
140 low in our study population (Bauchau and Van Noordwijk 1995), thus breeding population
141 size is a good proxy for the total number of females of age 1+ in the population. We will refer
142 to C_t as the population count with the understanding that this is a population count of
143 breeding females only. To calculate the population count for a given year, we summed the
144 number of breeding females of known age, the number of breeding females of unknown age
145 and an estimate of the number of breeding females not caught (and thus not identified nor
146 aged) because they have deserted their clutches early in the breeding attempt (Reed et al.
147 2013b). The number of females of the latter type could be estimated by the number of
148 clutches found without a mother. We assumed that any clutch found without an identified
149 mother corresponded to a breeding female that was present but not captured. There were 536
150 clutches without an identified mother in the study period.

151 The last type of data was age-class specific counts of breeding females and the age-
152 class specific contribution to recruitment. Based on the life history of great tits, we used four
153 age classes of breeding females with age class 1 corresponding to the first year of breeding
154 (second calendar year of life), age class 2 to the second year of breeding and third calendar
155 year of life, age class 3 to the third year of breeding and fourth calendar year of life and age
156 class 4 to older breeding females. Female fledglings were ringed on day seven and were
157 recorded as recruited to the breeding population if they were caught as a breeding female in a
158 subsequent year (Both et al. 1999). This gave us the observed number of local female
159 fledglings in year t that successfully became a first year breeding female in year $t+1$. This we
160 termed the breeding recruitment for year t (J_t). This recruitment could be broken down by the
161 age-class of the mother: first year breeder, second year, etc. This provided estimates of the
162 number of recruits by mothers of age class i in year t ($J_{i,t}$). In addition, we recorded the total

163 number of breeding females of each age class i in year t ($B_{i,t}$). In total, 824 daughters of
164 known age mothers locally recruited during the study period.

165

166 *Annual age-specific demographic rates and true age-specific numbers*

167 We aimed to estimate annual age-specific survival and recruitment rates as well as the
168 true (as opposed to observed) annual age-specific numbers of females. Our observed annual
169 number of breeding females of different age classes contains a number of sources of
170 observation error. There were females for which the age class was unknown (some
171 immigrants). Although the recapture probability was high on the study site (Reed et al.
172 2013b), not all females were recaptured, resulting in errors and uncertainty in the number of
173 females in the different age classes. This also leads to errors and uncertainty in the estimates
174 of survival and recruitment. In addition, there was a possibility of double counts. For instance
175 if one female produced two clutches but was only identified in one of them because she has
176 deserted one of the clutches. Lastly, there was the possibility that some clutches were missed
177 because females bred in natural cavities.

178 To account for these issues, we analyzed simultaneously CR data of known age
179 females, data on the reproductive success of breeding females of known age ($J_{i,t}$ and $B_{i,t}$), and
180 the population count C_t using an IPM. Briefly, an IPM (Schaub and Abadi 2011) is the joint
181 analysis of different datasets like for instance CR data and census data. This joint analysis of
182 these different sources of data increases the precision of the estimates of the shared
183 parameters. Inference is based on the joint likelihood, corresponding to the multiplication of
184 the likelihoods from the single datasets (CR data, data on reproductive success and
185 population count) (Kéry and Schaub 2012). The likelihoods of the different datasets were
186 specified as follows in the IPM. For CR data of breeding females of known age, we used the

187 Cormack-Jolly-Seber model (Lebreton et al. 1992) which allows estimation of annual
 188 survival between age class i and $i+1$ ($S_{i,t}$) and recapture (P_t) probabilities.

189 For data on reproductive success, we assumed that the observed number of daughters
 190 locally recruited per age class i ($J_{i,t}$) is Poisson distributed with $J_{i,t} \sim \text{Poisson}(B_{i,t} \times F_{i,t})$,
 191 where $B_{i,t}$ is the observed number of breeding females of age class i and $F_{i,t}$ is the
 192 recruitment rate of females of age class i at year t . $F_{i,t}$ is the term we are estimating and is the
 193 contribution of mothers of age class i to recruitment into the age class 1 breeding class next
 194 year. Considering the contribution of mothers of age class i to recruitment to the age class 1
 195 breeding females next year instead of the clutch size or the number of fledglings produced
 196 allowed emigration and mortality in the first year of life to be included in the recruitment
 197 estimate.

198 For the population count data, we used a state-space model (de Valpine and Hastings
 199 2002) which consisted of a process model describing how the population size and structure
 200 changed over time as well as an observation model (Besbeas et al. 2002). In details, for the
 201 process model, we considered a pre-breeding age-structured model with the four pre-defined
 202 age classes and assumed that reproduction starts in the second calendar year of life when
 203 females enter their first year breeding and our age class 1 (Perrins 1979). The total number of
 204 breeding females of age class i in year t was denoted $N_{i,t}$. $N_{i,t}$ was defined as $N_{i,t} = n_{i,t} +$
 205 $I_{i,t} + A_{i,t}$, where $n_{i,t}$ is the number of local females in each age class i in year t , $I_{i,t}$ is the
 206 number of immigrants of age class i but for which it was impossible to give an exact age and
 207 $A_{i,t}$ is the number of known age immigrants of age class i . To account for demographic
 208 stochasticity, especially important in small populations (Lande et al. 2003), we used Poisson
 209 and binomial processes to describe the number of local breeding females in each age class
 210 ($n_{i,t}$): $n_{1,t+1} \sim \text{Poisson}(N_{1,t} \times F_{1,t} + N_{2,t} \times F_{2,t} + N_{3,t} \times F_{3,t} + N_{4,t} \times F_{4,t})$,

211 $n_{2,t+1} \sim \text{Bin}(N_{1,t}, S_{1,t})$, $n_{3,t+1} \sim \text{Bin}(N_{2,t}, S_{2,t})$ and $n_{4,t+1} \sim \text{Bin}(N_{3,t}, S_{3,t}) +$

212 Bin $(N_{4,t}, S_{4,t})$. For the immigrant females $I_{i,t}$ for which it was impossible to give an exact
213 age, we considered that each year t , a proportion of them are females of age class i . This
214 allowed taking into account uncertainty on the age of these immigrant females without
215 making any explicit assumption about their exact age. Since virtually all individuals breed in
216 the nest boxes, we assumed that all new immigrants were observed. Note that females were
217 classified as immigrants only in their year of arrival into the study population and then join
218 the local population. The true number of breeding females in the population at year t ($N_{tot,t}$) is
219 then $\sum_{i=1}^4 N_{i,t}$. The observation model describes the link between the population counts C_t and
220 the true number of breeding females in the population ($N_{tot,t}$). We assumed that:
221 $C_t \sim N(N_{tot,t}, \sigma_C^2)$ truncated to positive values with σ_C^2 which incorporates observation errors
222 of the counts. The observation model accounts for both count errors (females unobserved or
223 double-counted) and lack of fit of the state equations to the true dynamics of the population
224 (Schaub and Abadi 2011).

225 Assuming independence among the datasets, the likelihood of the IPM is given by the
226 product of the likelihoods of the three different datasets, namely population counts C_t ,
227 reproductive ($J_{b,t}$ and $B_{b,t}$) data and CR data (Kéry and Schaub 2012). It is noteworthy that
228 most of the breeding females may be found in the three different datasets, in particular the
229 breeding females of known age. Thus, the assumption of independence is violated in our
230 study. However, a recent simulation study of IPM performance has shown that the violation
231 of the assumption of independence does not have a strong impact on the performance of the
232 estimators and highlighted a gain in precision and accuracy when all three datasets
233 (population counts, reproductive success and CR data) are analyzed simultaneously into an
234 IPM (Abadi et al. 2010). There is no goodness-of-fit test available for the IPM (Schaub and
235 Abadi 2011). However, we could test the CR model outside of the IPM using U-CARE
236 (Choquet et al. 2009). We found no lack of fit (global test: $\chi^2(77)=51.981, P=0.987$).

237 We were interested in estimating annual age-specific survival and recruitment rates
238 while allowing correlated variability among these demographic rates. We used a hierarchical
239 formulation of the IPM to get the best possible annual estimates of the demographic rates, not
240 inflated by sampling variation (Kéry and Schaub 2012). In this formulation, the annual
241 estimates are thought to originate from a random process with a common mean and a
242 constant temporal variance (see e.g., Schaub et al. 2012, 2013 for a similar approach).
243 Recruitment was specified on the log-scale $\log(F_{i,t}) = \mu_{F_i} + \varepsilon_{F_{i,t}}$, where μ_{F_i} is the mean
244 contribution of mothers of age class i to recruitment next year and $\varepsilon_{F_{i,t}}$ is the age-specific
245 temporal residual. The logit link was used for survival so that $\text{logit}(S_{i,t}) = \mu_{S_i} + \varepsilon_{S_{i,t}}$. ε is
246 the matrix including the temporal residuals of the eight demographic rates (i.e., one temporal
247 residual for recruitment rate $\varepsilon_{F_{i,t}}$ and one temporal residual for survival rate $\varepsilon_{S_{i,t}}$ per age
248 class i). These residuals were treated as a realization from a multivariate normal distribution
249 $\varepsilon \sim MVN(0, \Sigma)$ with Σ the variance-covariance matrix allowing correlated variability. The
250 recapture probability, assumed to be age-independent, was modeled with random time
251 variation as well $\text{logit}(P_t) = \mu_P + \varepsilon_{P_t}$.

252 The IPM was fit within the Bayesian framework, and non-informative priors
253 (Appendix S1) were specified for all the parameters allowing the inference to be dominated
254 by information in the data and not by the information in the priors. Markov chain Monte
255 Carlo (MCMC) simulation was used for parameter estimation. To assess convergence, we ran
256 four independent chains with different starting values for 100,000 MCMC iterations, with a
257 burn-in of 50,000 iterations thinning every 100th observation resulting in 2,000 posterior
258 samples. We used the Brooks and Gelman diagnostic \hat{R} to assess the convergence of the
259 simulations and used the rule $\hat{R} < 1.02$ to determine whether convergence has been reached
260 (Brooks and Gelman 1998). The analyses were implemented using JAGS version 3.4.0
261 (Plummer 2003) called from R version 3.1.1 (R Development Core Team 2011) with package

262 R2jags (Su, YS and Yajima, M 2012). The JAGS code for fitting the IPM is available in
 263 Appendix S2. To ensure that the priors for initial population sizes do not influence estimates
 264 of demographic rates and age-specific numbers the first year of the study (i.e., in 1973), only
 265 the years between 1974 and 2012 were used in the analyses.

266

267 *The effects of age-class numbers on age-specific demographic rates*

268 The IPM was used to estimate age-specific demographic and age-specific true
 269 numbers. Once these were estimated, linear regressions were used to examine how the
 270 different age classes contributed to the observed variation in age-specific demographic rates.

271 The following regression models were used:

$$272 \quad \log(F_{i,t}) = \gamma_{F_i} + \beta_{F_i,N_1}N_{1,t} + \beta_{F_i,N_2}N_{2,t} + \beta_{F_i,N_3}N_{3,t} + \beta_{F_i,N_4}N_{4,t} + res_{F_{i,t}} \quad (1)$$

273 and

$$274 \quad \text{logit}(S_{i,t}) = \gamma_{S_i} + \beta_{S_i,N_1}N_{1,t} + \beta_{S_i,N_2}N_{2,t} + \beta_{S_i,N_3}N_{3,t} + \beta_{S_i,N_4}N_{4,t} + res_{S_{i,t}} \quad (2)$$

275 where γ are the intercepts, β are the regression coefficients and res are the residuals of the
 276 regressions corresponding to the variation in demographic rates not explained by age-specific
 277 numbers. These regressions were fit for each posterior sample (2,000 in total). As $F_{i,t}$, $S_{i,t}$ and
 278 $N_{j,t}$ in Eqn. 1 and 2 are estimated in the IPM model, they are not contaminated with sampling
 279 variance and observation errors and thus this approach does not lead to spurious detection of
 280 density dependence (Freckleton et al. 2006, see Schaub et al. 2013 for a similar approach).

281 Because we were interested in the effect of each age class on survival and recruitment rates,
 282 the regression coefficients β_{F_i,N_j} and β_{S_i,N_j} were calculated for each posterior sample. Then,
 283 from these 2,000 estimates of β_{F_i,N_j} and β_{S_i,N_j} , the 95% credible intervals (CRI) and the
 284 probability for the coefficients to be lower than zero (i.e., $P(\beta < 0)$) were computed. For
 285 instance, a high probability $P(\beta_{F_1,N_2} < 0)$ would indicate a high probability for a negative effect
 286 of the number of females in age class 2 on recruitment rates of age class 1. Note that we

287 looked for possible multicollinearity among explanatory variables which can lead to high
 288 standard errors and difficulties in interpreting parameter estimates in regressions (Graham
 289 2003) by computing the posterior modes of pairwise correlation coefficients between $N_{i,t}$ and
 290 $N_{j,t}$. They varied from 0.010, 95% CRI [-0.174; 0.193] to 0.294, 95% CRI [0.027; 0.524].
 291 Since collinearity was low, all age-specific numbers $N_{i,t}$ were included in the regression
 292 model as explanatory variables (Eqn. 1 and 2) (Price et al. 2009, 2010).

293

294 *The effects of age-class numbers on population growth rate*

295 As derived parameter from the IPM, we computed the population growth rate λ in
 296 year t as $\lambda_t = \frac{N_{tot,t+1}}{N_{tot,t}}$ for each posterior sample. To determine how the number of females in
 297 the different age classes contributed to the observed variation in population growth rate, we
 298 explored the phenomenological relationship between population growth rate (λ_t on a log-
 299 scale) and age-specific true numbers $N_{j,t}$. Hence:

$$300 \quad \log(\lambda_t) = \gamma_\lambda + \beta_{\lambda,N_1}N_{1,t} + \beta_{\lambda,N_2}N_{2,t} + \beta_{\lambda,N_3}N_{3,t} + \beta_{\lambda,N_4}N_{4,t} + res_{\lambda_t} \quad (3)$$

301 where γ_λ is the intercept, β_{λ,N_j} are the regression coefficients and res_{λ_t} are the residuals of
 302 the regression corresponding to the variation in population growth rate not explained by age-
 303 specific numbers.

304 We also investigated the phenomenological relationship between population growth
 305 rate and true total number of breeding females. We used a Ricker density-dependence model,
 306 which is a simple way of representing density-dependent feedback in the per-unit-abundance
 307 growth rate (Ricker 1954, Dennis and Taper 1994):

$$308 \quad \log(\lambda_t) = \gamma_{\lambda'} + \beta_{\lambda,N_{tot}}N_{tot,t} + res_{\lambda_t'} \quad (4)$$

309 where $\gamma_{\lambda'}$ is the intercept, $\beta_{\lambda,N_{tot}}$ is the regression coefficient and $res_{\lambda_t'}$ are the residuals of
 310 the regression corresponding to the variation in population growth rate not explained by the

311 total number of breeding females. As previously done for recruitment rates (Eqn.1) and
312 survival rates (Eqn. 2), these regressions (Eqn. 3 and 4) were fit for each posterior sample
313 (2,000 in total). The regression coefficients β_{λ, N_j} and $\beta_{\lambda, N_{tot}}$ were calculated for each
314 posterior sample. Then, CRI and the probability for the coefficients to be lower than zero
315 (i.e., $P(\beta < 0)$) were computed.

316 All these analyses were performed with R software (R Development Core Team
317 2011) using the `lm()` function for the linear regressions.

318

319 RESULTS

320 *Age-specific numbers*

321 Our parameter estimates are presented as the mean of the posterior distribution with
322 their associated 95% CRI. The estimated total number of breeding females fluctuated
323 between 60.67, 95% CRI [49.00; 73.00] and 201.61, 95% CRI [185.00; 218.00] over the
324 study period. The mean population growth rate (calculated as $\exp(\frac{\sum_t \log(\lambda_t)}{38})$) was estimated
325 to be 1.003, 95% CRI [0.999; 1.006]. The mean of the posterior was close to 1 and the CRI
326 included 1 reflecting that the population fluctuated around a mean population size over the
327 course of the study period. The age-specific numbers showed large temporal fluctuations
328 (Fig. 1A). Correspondingly, the coefficients of variation of the number of breeding females
329 over the study period were estimated to 0.363, 95% CRI [0.334; 0.391] for age class 1, to
330 0.375, 95% CRI [0.318; 0.435] for age class 2, to 0.464, 95% CRI [0.384; 0.547] for age
331 class 3 and to 0.499, 95% CRI [0.383; 0.626] for age class 4. On average, the breeding
332 population was composed of 52.1%, 95% CRI [50.8%; 53.6%] of females from age class 1,
333 25.1%, 95% CRI [24.0%; 26.3%] of age class 2, 13.5%, 95% CRI [12.5%; 14.4%] of age
334 class 3 and 9.3%, 95% CRI [8.0%; 10.7%] of older females.

335

336 *Age-specific demographic rates*

337 The mean recapture probability was estimated to be 93.9%, 95% CRI [91.8%; 95.5%]
 338 indicating a high recapture rate. The estimated demographic rates in all age classes exhibited
 339 large temporal variation (Appendix S3). Age class 2 had the highest estimated mean survival
 340 and the probability that age class 2 survival was greater than the survival for all other age
 341 classes ($P(\widehat{S}_2 > \widehat{S}_i)$ for $i = 1, 3$ or 4) was 97.8%. Age class 4 had the lowest estimated mean
 342 survival and the probability that age class 4 survival was lower than all other age classes'
 343 survival ($P(\widehat{S}_4 < \widehat{S}_i)$ for $i = 1, 2$ or 3) was 100%. Age class 3 had a lower estimated mean
 344 survival than age class 1 and the probability that age class 3 survival was lower than age class
 345 1 survival ($P(\widehat{S}_3 < \widehat{S}_1)$) was 91.2%. Age class 2 had again the highest estimated mean
 346 recruitment rate and the probability that age class 2 recruitment was greater than all other age
 347 classes' recruitment ($P(\widehat{F}_2 > \widehat{F}_i)$ for $i = 1, 3$ or 4) was 70.6%. Age class 1 had the lowest
 348 estimated mean recruitment rate and the probability that age class 1 recruitment was lower
 349 than recruitment for all other age classes ($P(\widehat{F}_1 < \widehat{F}_i)$ for $i = 2, 3$ or 4) was 88.7%. Age class 3
 350 had a higher estimated mean recruitment than age class 4 and the probability that age class 3
 351 recruitment was higher than age class 4 recruitment ($P(\widehat{F}_3 > \widehat{F}_4)$) was 62.6%. Therefore,
 352 estimated mean survival and recruitment rates decreased from age class 2 onwards indicating
 353 senescence in both survival and recruitment rates in this great tit population (Fig. 1B).

354

355 *The effects of age-class numbers on age-specific demographic rates*

356 The β_{N_i} values indicated how the number of females in age class N_i contributed to the
 357 observed variation in age-specific demographic rates. Thus, negative β_{N_i} values indicate that
 358 higher number of females in the age class N_i translates to lower survival and/or recruitment.
 359 The mean of the posterior β_{N_1} was always negative and the CRI did not include zero (Table 1,

360 first column) reflecting that the number of females in age class 1 affected survival and
361 recruitment rates of all age classes. Thus, the higher the number of females in age class 1, the
362 lower the recruitment rates (Fig. 2A) and the lower the survival rates (Fig. 3A) for all age
363 classes. The probability that this negative effect of age class 1 on survival and recruitment
364 rates was stronger than the effects of age class 2, age class 3 or age class 4 ($P(\beta_{N_1} < \beta_{N_i})$ for
365 $i = 2, 3$ or 4) was greater than 58.1% indicating that the per capita effect on density
366 dependence is the largest for age class 1. Moreover, age class 1 being the biggest age class,
367 age class 1 was the age class contributing the most to the observed variation in survival and
368 recruitment rates.

369 The mean of the posterior β_{N_2} was always negative for recruitment rates and the CRI
370 did not include zero (Table 1, second column) reflecting that the number of females in age
371 class 2 affected recruitment rates of all age classes. Thus, the higher the number of females in
372 age class 2, the lower the recruitment rates (Fig. 2B) for all age classes. The probability that
373 this negative effect of age class 2 on recruitment rates was stronger than the effects of age
374 class 3 or age class 4 ($P(\beta_{F,N_2} < \beta_{F,N_i})$ for $i = 3$ or 4) was greater than 66.8% indicating that,
375 after age class 1, the per capita effect on density dependence is the largest for age class 2.
376 Moreover, age class 2 being the second largest age class, age class 2 was the second age class
377 contributing the most to the observed variation in recruitment rates. The mean of the posterior
378 β_{N_2} was also always negative for survival rates however the CRI included zero in all cases
379 (Table 1, second column). This reflects the pattern seen in Fig. 3B. There is a slight negative
380 effect of age class 2 females on survival, but the pattern relationship is quite weak.

381 The mean of the posterior β_{N_3} was always negative but the CRI included zero in all
382 cases (Table 1, third column). This reflects the patterns seen in Fig. 2C and 3C. There is no
383 effect of the number of females in age class 3 on recruitment rates and survival rates of all
384 age classes.

385 The mean of the posterior β_{N_4} was always positive and CRI included zero (Table 1,
 386 fourth column). This indicates that the number of females in age class 4 had no effect on
 387 recruitment rates (Fig. 2D) and survival rates (Fig. 3D) of all age classes.

388

389 *The age-specific demographic responses to age-class numbers*

390 The number of females in age class 1 affected recruitment rates of all age classes with
 391 different intensities. The probability that the negative effect of the number of females in age
 392 class 1 was stronger on recruitment rate of age class 1 than on recruitment for all other age
 393 classes ($P(\beta_{F_1,N_1} < \beta_{F_i,N_1})$ for $i = 2, 3$ or 4) was greater than 75.6% (Table 1, Fig. 2A). In
 394 contrast, the number of females in age class 1 affected survival of all age classes with similar
 395 intensity except age class 3 was less intensively affected. Indeed, the probability that the
 396 negative effect of the number of females in age class 1 was lower on survival rate of age class
 397 3 than on survival for all other age classes ($P(\beta_{S_i,N_1} < \beta_{S_3,N_1})$ for $i = 1, 2$ or 4) was greater
 398 than 75.2% (Table 1, Fig. 3A). The number of females in age class 2 affected recruitment
 399 rates of all age classes with different intensities. The probability that the negative effect of the
 400 number of females in age class 2 was stronger on recruitment rate of age class 1 than on
 401 recruitment for all other age classes ($P(\beta_{F_1,N_2} < \beta_{F_i,N_2})$ for $i = 2, 3$ or 4) was greater than
 402 62.1% (Table 1, Fig. 2B).

403

404 *The effects of age-class numbers on population growth rate*

405 The mean of the posterior $\beta_{\lambda,N_{tot}}$ was estimated to be -0.009, 95% CRI [-0.010; -
 406 0.008] and the probability that $\beta_{\lambda,N_{tot}}$ was negative equaled to 1 (Fig. 4). Splitting the
 407 contribution of N_{tot} into the age-specific contribution N_i , we found that the mean of the
 408 posterior β_{λ,N_1} was estimated to be -0.011, 95% CRI [-0.012; -0.009] and the probability that

409 β_{λ,N_1} was negative equaled to 1, reflecting that the number of females in age class 1 affected
410 the population growth rate (Fig. 4). The mean of the posterior β_{λ,N_2} was estimated to be -
411 0.008, 95% CRI [-0.013; -0.004] and the probability that β_{λ,N_2} was negative equaled to 1,
412 reflecting that the number of females in age class 2 affected the population growth rate too
413 (Fig. 4). The mean of the posterior β_{λ,N_3} was estimated to be -0.005, 95% [-0.013; 0.002] and
414 the probability that β_{λ,N_3} was negative equaled to 90.9%. The posterior mean of age class 3's
415 effect on λ was much closer to 0 (no effect) than for age class 1 or age class 2 and the
416 posterior distribution was much more diffuse for age class 3 (Fig. 4). Finally, the mean of the
417 posterior β_{λ,N_4} was estimated to be -0.002, 95% CRI [-0.016; 0.011] and the probability that
418 β_{λ,N_4} was negative equaled to 60.2%. The posterior mean of age class 4's effect on λ was
419 close to 0 (no effect) and the posterior distribution was extremely diffuse (Fig. 4).

420

421 DISCUSSION

422 We found that age-specific numbers of females have different effects on demographic
423 rates and also on population growth rate of this great tit population. In particular, the number
424 of females in age class 1, corresponding to females in their first year of breeding, strongly
425 affected survival and recruitment of all age classes and also the population growth rate.
426 Moreover, we showed that age classes differently respond to an increase in the number of
427 breeding females. These findings question the assumption that all adult individuals can be
428 treated as having an equal contribution to density regulation and that the effect of the number
429 of individuals is age independent. This assumption is commonly made when investigating the
430 strength and effects of density dependence on populations.

431 Natural populations are regulated by both stochastic and deterministic (i.e., density-
432 dependent) factors (Lack 1954), this great tit population is no exception. Indeed, Grøtan et al.

433 (2009) have recently shown that environmental stochastic effects, such as the amount of
434 seeds of beeches present in the winter and the spring temperature, could influence the
435 dynamics of the population of great tits in the Hoge Veluwe National Park. We showed here
436 that the population is also strongly affected by the number of breeding females present in the
437 population (Fig. 4). These results are in line with previous studies on this population (Both
438 1998a, Both et al. 1999, 2000, Reed et al. 2013a) that found strong density dependence. We
439 found clear evidence for both density-dependent survival and recruitment into the breeding
440 population. Until now, investigations of density-dependent survival in birds have remained
441 scarce in the literature (but see e.g., Both et al. 1999, Reed et al. 2013b). In his recent book,
442 Dhondt (2011) pointed out that a large number of studies explored to what extent
443 reproduction decreases with density “*while very few studies attempted to determine if [...]*
444 *survival also decrease[s]*”.

445 In addition to its effect on survival, competition has been shown to be the underlying
446 mechanism leading to density-dependent fecundity (see e.g., Both 1998a for an experimental
447 study). More specifically, we have highlighted a decrease of the number of daughters
448 produced that will recruit into the local population, when the number of breeding females
449 increases. Such a decrease of the number of recruits may correspond to effects of the number
450 of females at different life history stages. For instance, competition for food before and
451 during egg laying can alter the amount of energy allocated to reproduction (Lack 1966, Both
452 et al. 2000) leading to density-dependent reduction of clutch size as it has previously been
453 reported in this population (Both 1998b). Moreover, variation in population size can also
454 directly affect nestlings survival by decreasing rates of chick feeding (Sillett and Holmes
455 2002) or by decreasing the probability that an individual recruits into the local population
456 (Drent 1984). In support of that, it has been shown that survival in the first year of life is
457 strongly density-dependent in that great tit population (Both et al. 1999, Reed et al. 2013b)

458 and recent work has even highlighted that the number of new recruits a given year was
459 unrelated to the number of fledglings produced the previous year because of increased
460 competition for limited resources in their first year of life (Reed et al. 2013a). All these
461 effects of the number of females on the clutch size, and/or later on the number of nestlings
462 and/or later on the number of females that will effectively remain in the local population to
463 breed, explained the negative effect of the number of females on the number of recruits we
464 found at the end.

465 If survival and recruitment decrease for all age classes with increasing population
466 size, the intensity of such a decrease is age-specific. In particular, the negative effect of the
467 number of females was stronger on recruitment rate of age class 1 than on recruitment for all
468 other age classes. As the great tit is characterized with high breeding territory fidelity, these
469 findings suggest that when the number of breeding females increases in the population, strong
470 intraspecific competition occurs leading to a reduction of recruitment rates particularly
471 important for the youngest age class. This age-specific demographic response to an increase
472 of the population size has also been found in a variety of taxa. For instance, in Soay sheep
473 (*Ovis aries*), survival of lambs and old females was affected by density, whereas survival of
474 prime adults and yearlings was not associated with density (Coulson et al. 2001). More
475 generally, it has been shown that in large herbivores, the negative effect of population size is
476 stronger on juvenile survival than on adult survival (Gaillard et al. 1998). In contrast, in the
477 red-backed shrikes, density effects were stronger on adult survival than on juvenile survival
478 (Abadi et al. 2012).

479 In addition to investigating which age classes were affected by an increase of
480 population size, we explored here the effect of the age-specific numbers on demographic
481 rates and population growth rate. Indeed, we explored the "per capita" effects on density
482 dependence, i.e., the density-dependent effect of an individual of a given age class on another

483 individual. We showed that an increase in the number of females in age class 1, specifically,
484 had a negative effect on survival and recruitment rates of all ages (Table 1). Moreover, an
485 increase in the number of females in age class 2 had a negative effect on recruitment rates of
486 all age classes (Table 1). Such findings may be explained in light of great tit life history.
487 These age classes bring together new breeders attempting to take a territory. In such a short-
488 lived species with high breeding territory fidelity, these age classes have the strongest
489 competitive effect on other breeding females. Looking at the effect of the number of females
490 on the population growth rate (λ), we decomposed the effect of total number of breeding
491 females into the effects of age-specific numbers (Fig. 4). Unsurprisingly, the number of
492 females in age class 1 affected λ the most, followed by the number of females in age class 2.
493 Thus, these age classes may be defined as the critical age classes (sensu Charlesworth 1972,
494 1973) for that population.

495 It is noteworthy that the critical age classes constitute here the highest proportion of
496 the population. From age class 2 onwards, survival rates start to decrease with ages (Fig. 1B)
497 explaining why only 22.8% of the breeding population corresponds to females of age class 3
498 and older. This decline of survival with increasing ages provides additional support for
499 actuarial senescence in this short-lived species, as recently shown in another great tit
500 population (Bouwhuis et al. 2012). Interestingly, likely due to a decline in brood size and
501 fledgling number produced by the oldest breeding females (Bouwhuis et al. 2009),
502 recruitment rates also decrease from age 2 onwards (Fig. 1B). Therefore, we highlighted that
503 the senescent age classes 3 and 4 were not the critical age classes. These findings also point
504 out the critical role of the youngest age classes in the demography of our population.

505

506 *Conclusions*

507 According to Charlesworth (1973): “*In any particular case, this density regulation*
508 *must occur in response to the number of individuals in a specific group of ages, which I shall*
509 *call the "critical age group." The critical age group might, for example, be composed of all*
510 *individuals of reproductive age, or of newborn individuals, depending on the biology of the*
511 *population.*” From this pioneering definition of the critical age class, we explored how the
512 different age classes contributed to the observed variation in age-specific demographic rates
513 and population growth rate in a great tit population. We highlighted that the youngest age
514 classes were the critical age classes. We also found age-specific demographic responses to an
515 increase of the number of breeding females in the population. We thus found clear empirical
516 evidence that the assumption of equal responses and equal contribution of all age classes to
517 density dependence may be violated *in natura*.

518

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526

527 LITERATURE CITED

- 528 Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010. An assessment of integrated population
529 models: bias, accuracy, and violation of the assumption of independence. *Ecology* 91:7–14.
- 530 Abadi, F., O. Gimenez, H. Jakober, W. Stauber, R. Arlettaz, and M. Schaub. 2012. Estimating the
531 strength of density dependence in the presence of observation errors using integrated population
532 models. *Ecological Modelling* 242:1–9.

- 533 Bauchau, V., and A. J. Van Noordwijk. 1995. Comparison of survival estimates obtained from three
534 different methods of recapture in the same population of the great tit. *Journal of Applied Statistics*
535 22:1031–1038.
- 536 Beddington, J. R. 1974. Age distribution and the stability of simple discrete time population models.
537 *Journal of Theoretical Biology* 47:65–74.
- 538 Berryman, A. A., M. Lima Arce, and B. A. Hawkins. 2002. Population regulation, emergent
539 properties, and a requiem for density dependence. *Oikos* 99:600–606.
- 540 Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-
541 recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*
542 58:540–547.
- 543 Bonenfant, C., J. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P.
544 Blanchard, N. Pettolelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009. Chapter 5 Empirical
545 Evidence of Density-Dependence in Populations of Large Herbivores. Pages 313–357 in H. Caswell,
546 editor. *Advances in Ecological Research*. Academic Press.
- 547 Both, C. 1998a. Experimental evidence for density dependence of reproduction in great tits. *Journal of*
548 *Animal Ecology* 67:667–674.
- 549 Both, C. 1998b. Density dependence of clutch size: habitat heterogeneity or individual adjustment?
550 *Journal of Animal Ecology* 67:659–666.
- 551 Both, C., J. M. Tinbergen, and M. E. Visser. 2000. Adaptive density dependence of avian clutch size.
552 *Ecology* 81:3391–3403.
- 553 Both, C., M. E. Visser, and N. Verboven. 1999. Density-dependent recruitment rates in great tits: the
554 importance of being heavier. *Proceedings of the Royal Society B: Biological Sciences* 266:465.
- 555 Bouwhuis, S., R. Choquet, B. C. Sheldon, and S. Verhulst. 2012. The forms and fitness cost of
556 senescence: age-specific recapture, survival, reproduction, and reproductive value in a wild bird
557 population. *The American Naturalist* 179:E15–27.
- 558 Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective
559 disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings.*
560 *Biological Sciences / The Royal Society* 276:2769–2777.
- 561 Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in
562 abundance time series of 1198 species. *Ecology* 87:1445–1451.
- 563 Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative
564 simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- 565 Charlesworth, B. 1972. Selection in populations with overlapping generations. III. Conditions for
566 genetic equilibrium. *Theoretical Population Biology* 3:377–395.
- 567 Charlesworth, B. 1973. Selection in Populations with Overlapping Generations. V. Natural Selection
568 and Life Histories. *The American Naturalist* 107:303–311.
- 569 Choquet, R., J.-D. Lebreton, O. Gimenez, A.-M. Reboulet, and R. Pradel. 2009. U-CARE: Utilities

- 570 for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* 32:1071–
571 1074.
- 572 Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock,
573 M. J. Crawley, and B. T. Grenfell. 2001. Age, Sex, Density, Winter Weather, and Population Crashes
574 in Soay Sheep. *Science* 292:1528–1531.
- 575 Coulson, T., T. H. G. Ezard, F. Pelletier, G. Tavecchia, N. C. Stenseth, D. Z. Childs, J. G. Pilkington,
576 J. M. Pemberton, L. E. B. Kruuk, T. H. Clutton-Brock, and M. J. Crawley. 2008. Estimating the
577 functional form for the density dependence from life history data. *Ecology* 89:1661–1674.
- 578 Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating density
579 dependence, process noise, and observation error. *Ecological Monographs* 76:323–341.
- 580 Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural
581 populations: estimation and testing. *Ecological monographs* 64:205–224.
- 582 Dhondt, A. A. 2011. *Interspecific Competition in Birds*. Oxford University Press.
- 583 Drent, P. J. 1984. Mortality and dispersal in summer and its consequences for the density of great tits
584 *Parus major* at the onset of autumn. *Ardea* 72:127–162.
- 585 Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. Census error and the
586 detection of density dependence. *Journal of Animal Ecology* 75:837–851.
- 587 Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores:
588 variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- 589 Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology*
590 84:2809–2815.
- 591 Grøtan, V., B.-E. Sæther, S. Engen, J. H. Van Balen, A. C. Perdeck, and M. E. Visser. 2009. Spatial
592 and temporal variation in the relative contribution of density dependence, climate variation and
593 migration to fluctuations in the size of great tit populations. *Journal of Animal Ecology* 78:447–459.
- 594 Hilborn, R., and C. J. Walters. 2003. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and*
595 *Uncertainty*. Springer Science & Business Media.
- 596 Husby, A., L. E. B. Kruuk, and M. E. Visser. 2009. Decline in the frequency and benefits of multiple
597 brooding in great tits as a consequence of a changing environment. *Proceedings of the Royal Society*
598 *B: Biological Sciences* 276:1845–1854.
- 599 Kéry, M., and M. Schaub. 2012. *Bayesian Population Analysis using WinBUGS: A hierarchical*
600 *perspective*. Academic Press, Boston.
- 601 Krebs, C. J. 2002. Two complementary paradigms for analysing population dynamics. *Philosophical*
602 *Transactions of the Royal Society B: Biological Sciences* 357:1211–1219.
- 603 Lack, D. 1966. *Population studies of birds*. Clarendon P., Oxford.
- 604 Lack, D. L. 1954. *The natural regulation of animal numbers*. Clarendon Press.
- 605 Lande, R., S. Engen, and B.-E. Saether. 2003. *Stochastic Population Dynamics in Ecology and*

- 606 Conservation. Oxford University Press, Oxford ; New York.
- 607 Lande, R., S. Engen, B.-E. Saether, F. Filli, E. Matthysen, and H. Weimerskirch. 2002. Estimating
608 density dependence from population time series using demographic theory and life-history data. *The*
609 *American Naturalist* 159:321–337.
- 610 Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing
611 biological hypotheses using marked animals: a unified approach with case studies. *Ecological*
612 *monographs* 62:67–118.
- 613 Lebreton, J.-D., and O. Gimenez. 2013. Detecting and estimating density dependence in wildlife
614 populations. *The Journal of Wildlife Management* 77:12–23.
- 615 Lillegård, M., S. Engen, B.-E. Sæther, V. Grøtan, and M. C. Drever. 2008. Estimation of population
616 parameters from aerial counts of north american mallards: a cautionary tale. *Ecological Applications*
617 18:197–207.
- 618 Perrins, C. 1979. *British Tits*. First Edition edition. Collins, London.
- 619 Perrins, C. M., and R. H. McCleery. 1989. Laying Dates and Clutch Size in the Great Tit. *The Wilson*
620 *Bulletin* 101:236–253.
- 621 Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs
622 Sampling. Pages 20–22 *Proceedings of the 3rd International Workshop on Distributed Statistical*
623 *Computing*. Hornik K, Leisch F, Zeileis A, Vienna, Austria.
- 624 Price, B., A. S. Kutt, and C. A. McAlpine. 2010. The importance of fine-scale savanna heterogeneity
625 for reptiles and small mammals. *Biological Conservation* 143:2504–2513.
- 626 Price, B., C. A. McAlpine, A. S. Kutt, S. R. Phinn, D. V. Pullar, and J. A. Ludwig. 2009. Continuum
627 or discrete patch landscape models for savanna birds? Towards a pluralistic approach. *Ecography*
628 32:745–756.
- 629 R Development Core Team. 2011. *R: A language and environment for statistical computing*.
- 630 Reed, T. E., V. Grøtan, S. Jenouvrier, B.-E. Sæther, and M. E. Visser. 2013a. Population growth in a
631 wild bird is buffered against phenological mismatch. *Science* 340:488–491.
- 632 Reed, T. E., S. Jenouvrier, and M. E. Visser. 2013b. Phenological mismatch strongly affects
633 individual fitness but not population demography in a woodland passerine. *The Journal of Animal*
634 *Ecology* 82:131–144.
- 635 Ricker, W. E. 1954. Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*
636 11:559–623.
- 637 Royama, T. 1992. *Analytical Population Dynamics*. Springer Science & Business Media.
- 638 Sæther, B.-E., S. Engen, and R. Lande. 1996. Density-Dependence and Optimal Harvesting of
639 Fluctuating Populations. *Oikos* 76:40–46.
- 640 Sæther, B.-E., S. Engen, and E. Matthysen. 2002. Demographic Characteristics and Population
641 Dynamical Patterns of Solitary Birds. *Science* 295:2070–2073.

- 642 Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper
643 insights into population dynamics. *Journal of Ornithology* 152:227–237.
- 644 Schaub, M., H. Jakober, and W. Stauber. 2013. Strong contribution of immigration to local population
645 regulation: evidence from a migratory passerine. *Ecology* 94:1828–1838.
- 646 Schaub, M., T. S. Reichlin, F. Abadi, M. Kéry, L. Jenni, and R. Arlettaz. 2012. The demographic
647 drivers of local population dynamics in two rare migratory birds. *Oecologia* 168:97–108.
- 648 Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its
649 annual cycle. *Journal of Animal Ecology* 71:296–308.
- 650 Sinclair, A. R. E. 1989. Population regulation of animals. Pages 197–241 *Ecological concepts*.
651 Oxford: Blackwell Scientific. J. M. Cherrett.
- 652 Su, YS, and Yajima, M. 2012. R2jags: A Package for Running jags from R. R package version 0.03-
653 08.
- 654 Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 *Population*
655 *Dynamics*. Academic Press. N. Cappucino & P.W. Price, New York.
- 656 de Valpine, P. de, and A. Hastings. 2002. Fitting population models incorporating process noise and
657 observation error. *Ecological Monographs* 72:57–76.
- 658

659 **Table 1.** Effects of the number of breeding females N_j in age class j on recruitment rates F_i (log-transformed) (contribution of mothers of age
660 class i to age class 1 breeding females) and on survival rates S_i (logit-transformed) of age class i . Displayed are the means of the posterior
661 distributions of the regression coefficients β and their associated 95% CRI. In parentheses are the posterior probability that the coefficients are
662 less than zero $P(\beta < 0)$ (among the 2,000 posterior samples).

Demographic rates of age class i (responses)	Number of breeding females of age class j (covariates)			
	N_1	N_2	N_3	N_4
	β_{N_1}	β_{N_2}	β_{N_3}	β_{N_4}
$\log(F_1)$	-0.023[-0.029;-0.018](1.000)	-0.018[-0.032;-0.005](0.995)	-0.003[-0.028;0.021](0.609)	0.012[-0.029;0.050](0.259)
$\log(F_2)$	-0.017[-0.023;-0.012](1.000)	-0.016[-0.029;-0.004](0.995)	-0.005[-0.028;0.016](0.693)	0.009[-0.024;0.043](0.271)
$\log(F_3)$	-0.019[-0.027;-0.013](1.000)	-0.016[-0.031;-0.003](0.992)	-0.001[-0.026;0.023](0.530)	0.009[-0.029;0.046](0.296)
$\log(F_4)$	-0.020[-0.029;-0.012](1.000)	-0.016[-0.033;-0.001](0.981)	-0.010[-0.040;0.018](0.746)	0.010[-0.034;0.055](0.298)
$\text{logit}(S_1)$	-0.011[-0.014;-0.007](1.000)	-0.003[-0.012;0.006](0.752)	-0.006[-0.022;0.009](0.767)	0.002[-0.022;0.026](0.437)
$\text{logit}(S_2)$	-0.010[-0.015;-0.005](1.000)	-0.003[-0.014;0.007](0.742)	-0.001[-0.019;0.016](0.547)	0.005[-0.020;0.033](0.358)
$\text{logit}(S_3)$	-0.007[-0.013;-0.002](0.998)	-0.001[-0.010;0.009](0.596)	-0.002[-0.017;0.013](0.618)	0.003[-0.019;0.026](0.400)
$\text{logit}(S_4)$	-0.011[-0.022;-0.002](0.995)	-0.003[-0.019;0.014](0.692)	-0.002[-0.027;0.021](0.575)	0.004[-0.027;0.040](0.397)

663 **Figure legends**

664 **Figure 1. (A)** Posterior means of the age-specific numbers of breeding females N_i estimated
665 from the IPM between 1974 and 2012 in the great tit population of Hoge Veluwe National
666 Park, the Netherlands. **(B)** Posterior means of the age-specific mean survival (in black) and
667 recruitment (in grey) rates between 1974 and 2012 and their associated 95 % CRI.

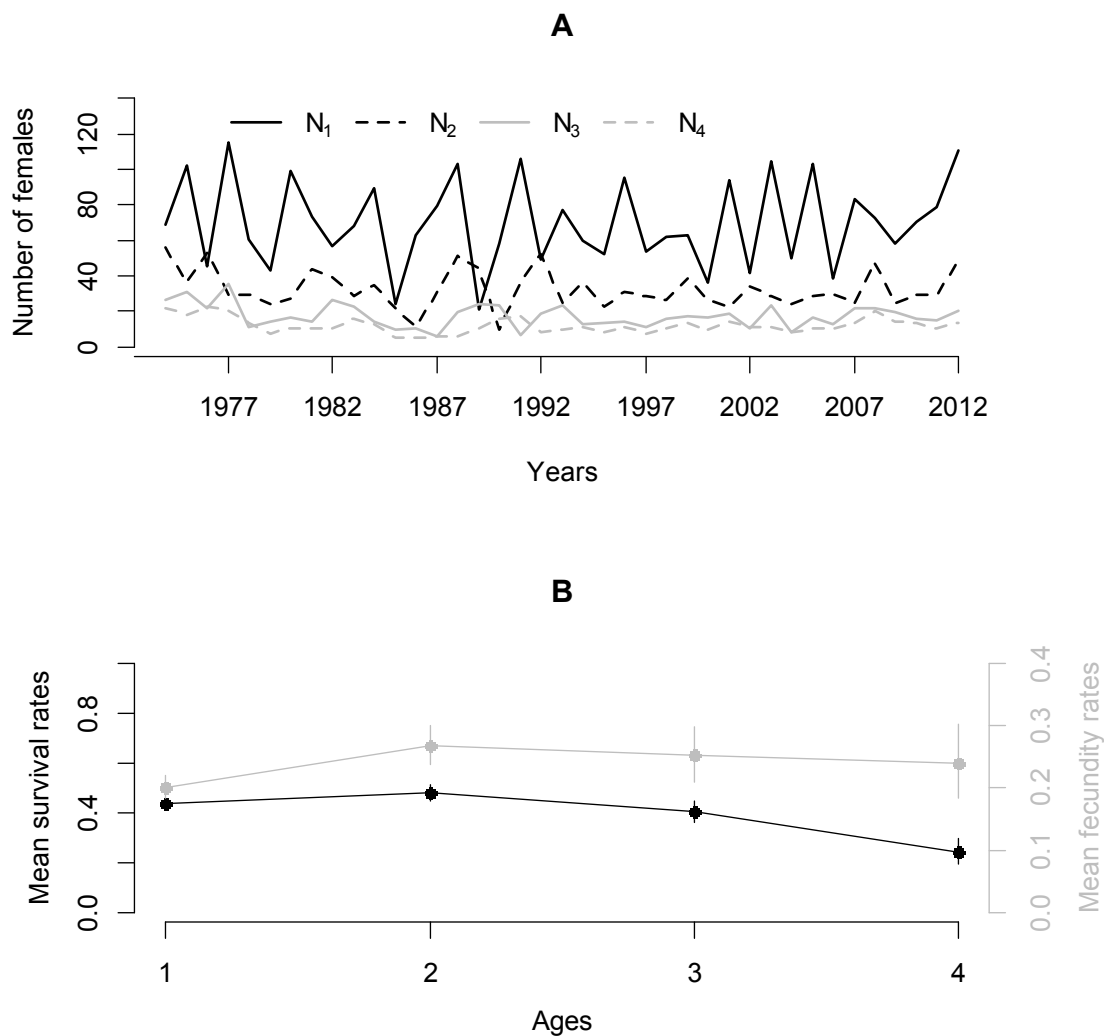
668 **Figure 2.** Posterior means of the annual recruitment rates $F_{i,t}$ (on a log-scale) of each age
669 class i plotted against posterior means of the annual age-specific numbers $N_{j,t}$. Solid lines
670 correspond to the predicted relationship between recruitment rates and numbers from Eqn. 1.

671 **Figure 3.** Posterior means of the annual survival rates $S_{i,t}$ (on a log-scale) of each age class i
672 plotted against posterior means of the annual age-specific numbers $N_{j,t}$ between 1974 and
673 2012. Solid lines correspond to the predicted relationship between survival rates and numbers
674 from Eqn. 2.

675 **Figure 4.** Posterior distribution of β_{λ, N_j} (the estimated effect of the number of breeding
676 females in age class j on the population growth rate λ). The thick lines are the age-specific
677 posterior distribution (β_{λ, N_j}) and the thin line is the effect of the total number of breeding
678 females on λ ($\beta_{\lambda, N_{tot}}$).

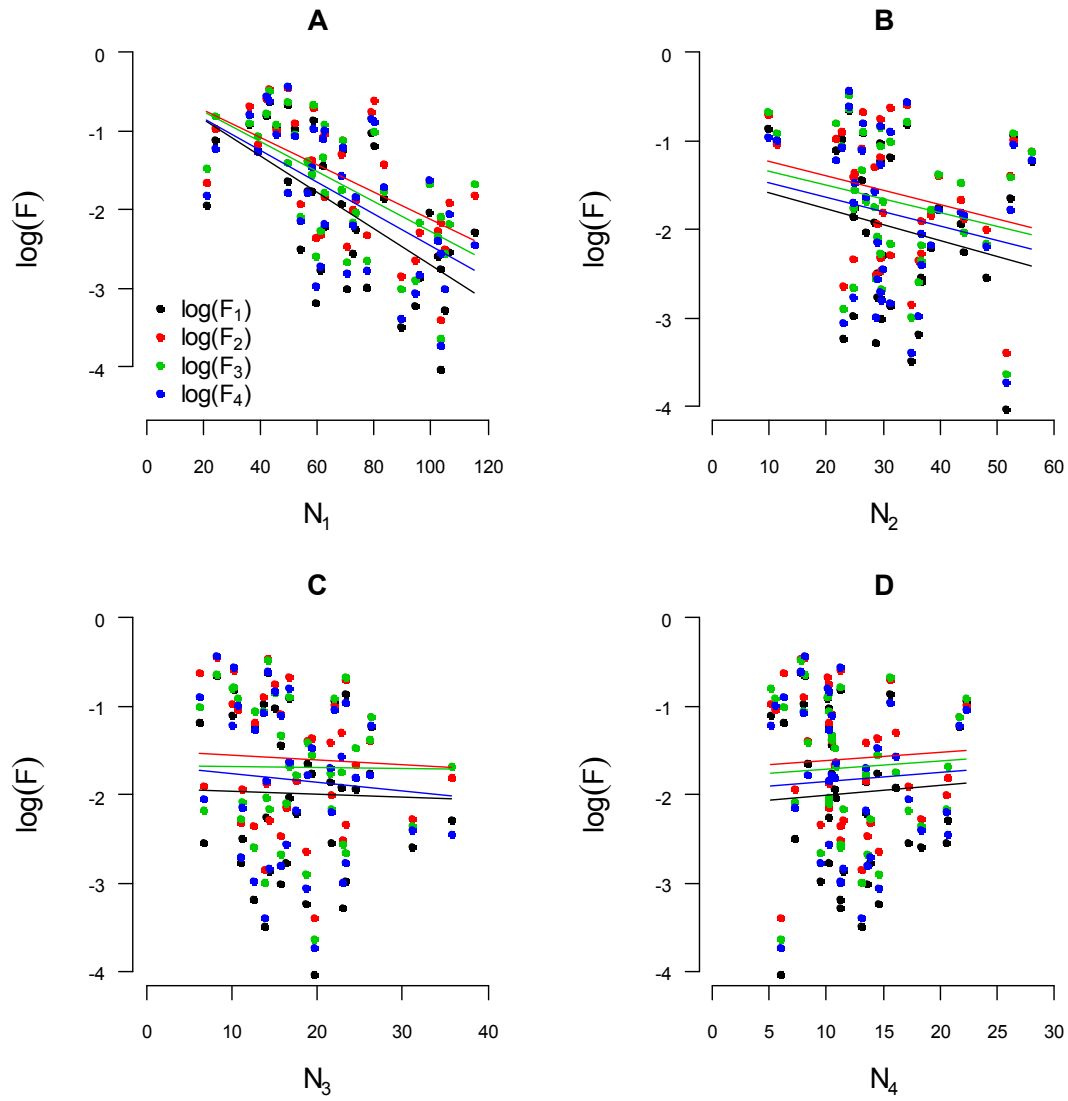
679

680 **Figure 1.**



681

682 **Figure 2.**

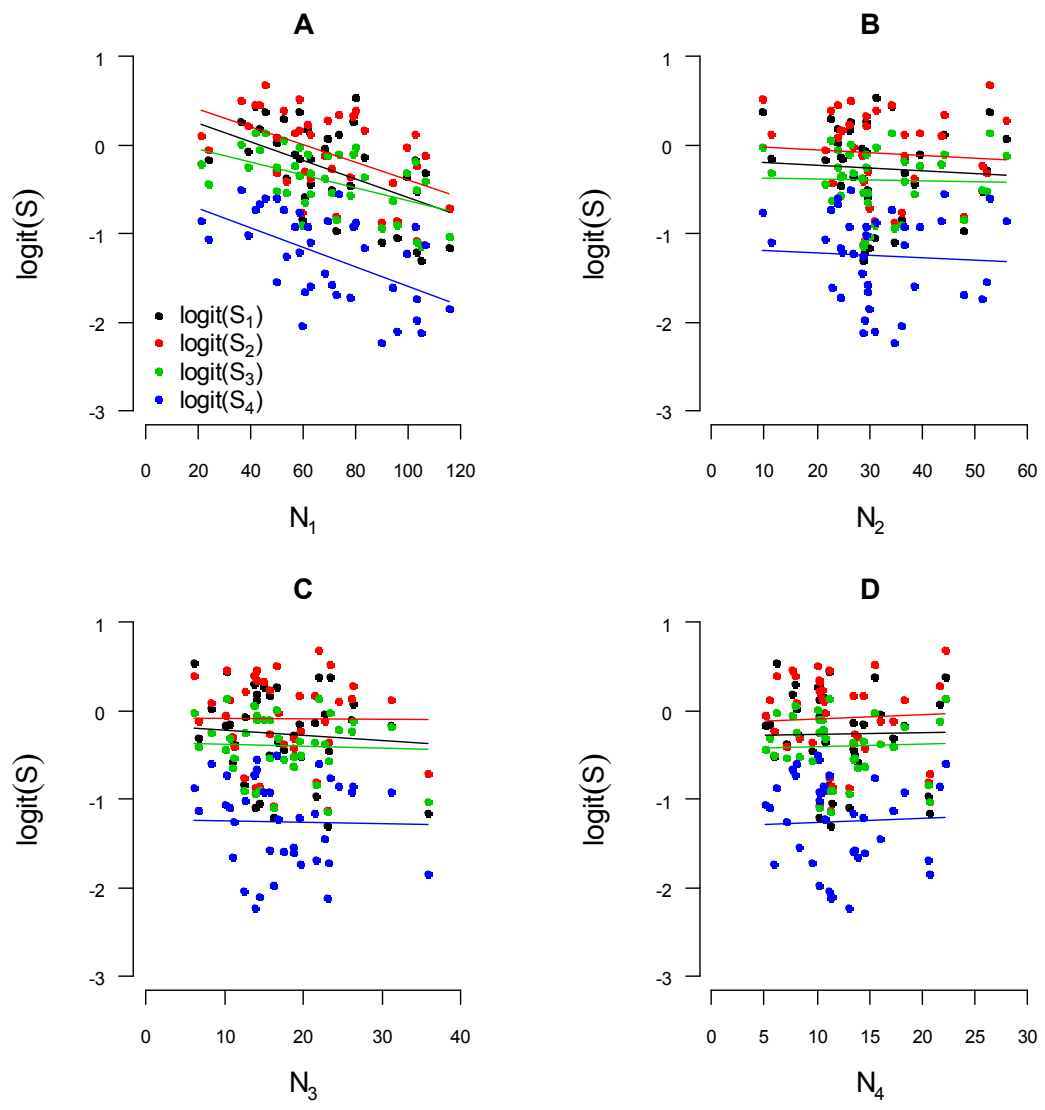


683

684

685 **Figure 3.**

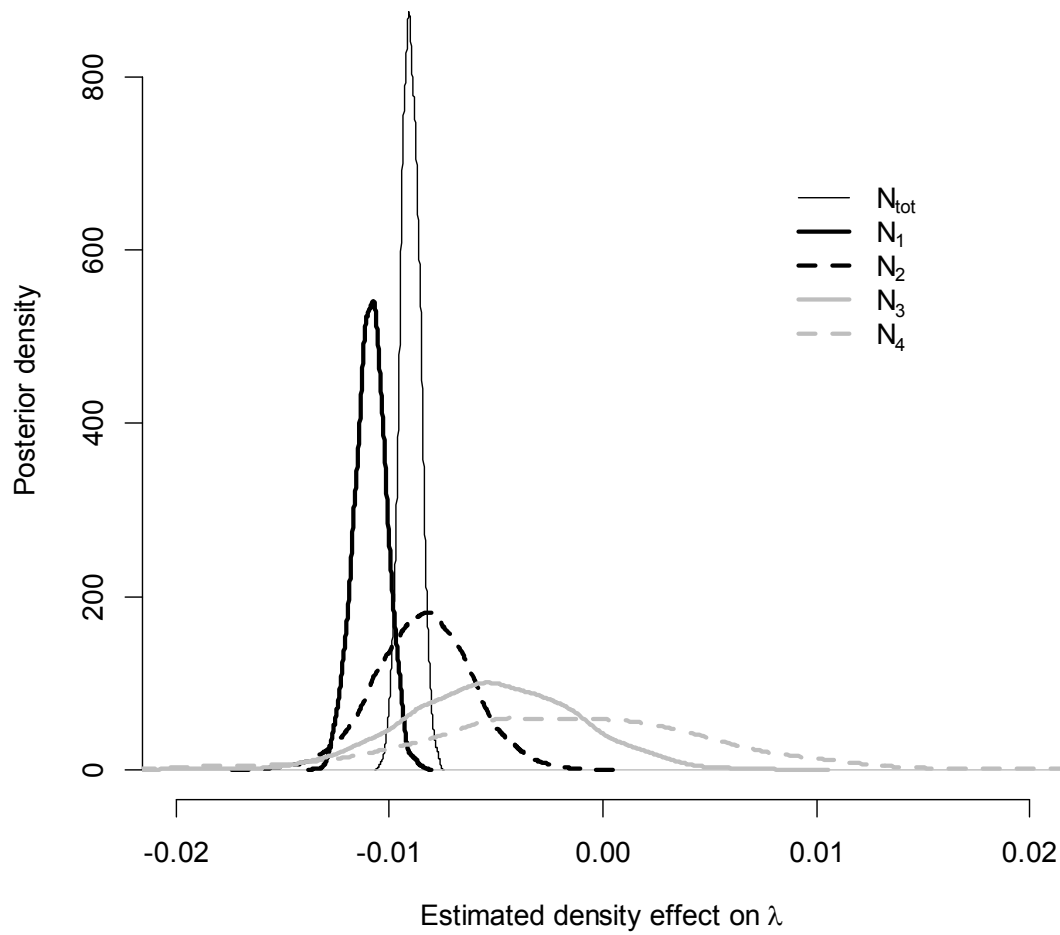
686



687

688

689

690 **Figure 4.**

691

692

693 **Appendix S1** – Prior distributions of all the parameters estimated into the integrated
 694 population model. N corresponds to the Normal distribution, U to the Uniform distribution
 695 and W to the Wishart distribution. Note that n_{4a} corresponds to the number of local breeding
 696 females coming from age class 3 and joining age class 4, and n_{4b} corresponds to the number
 697 of local breeding females that were already in age class 4.

Parameter	Prior distribution
Mean demographic rates	
$\text{logit}(S_i)^{-1}$	U(0, 1)
$\exp(F_i)$	U(0,70)
Mean recapture probability	
$\text{logit}(P)^{-1}$	U(0, 1)
Temporal variability	
Σ	W(\mathbf{I} , 9) ⁻¹ with \mathbf{I} =8x8 identity matrix
σ_P	U(0, 10)
σ^2_C	U(0, 10)
Initial population sizes (Generated numbers are rounded and truncated to positive values)	
N_1	N(200,100)
N_2	N(135,100)
N_3	N(120,100)
N_4	N(100,100)
n_1	N(130,100)
n_2	N(130,100)
n_3	N(120,100)
n_{4a}	N(30,100)
n_{4b}	N(20,100)

698

699

700

701 **Appendix S2** – R code to fit the integrated population model in JAGS.

```

702 #*****
703 # Data
704 # ## Population survey: popcount = annual number of counted breeding females
705 # ## Reproductive success:
706 #   J = Annual number of daughters locally recruited produced by each age class of mothers
707 #   B = Annual number of breeding females in each age class
708 # ## Capture-recapture data: y
709 # ## Immigrants:
710 #   Nknown = Annual number of immigrant breeding females in each age class
711 #   Nunknownobs = Annual number of immigrant breeding females of unknown age
712 #*****
713
714 sink("IPM-greattits.jags")
715   cat("
716 #*****
717 # Female-based age structured model (4 age classes)
718 # Age at first breeding = 1 year
719 # Pre-breeding census
720 # All demographic rates are time-dependent
721 # Immigration is included additively in the model as a number
722 #*****
723
724   model
725   {
726
727 #*****
728 # 1: Priors for the parameters
729 #*****
730
731 ## Relationship for demographic rates parameters
732 for (i in 1:nind){
733   for (t in f[i]:(ti-1)){
734     logit(phi[i,t]) <- eta.phi[agematrix[i,t],t] # Age and time-dependent survival probability
735     logit(p[i,t]) <- captureprob[t] # Time-dependent capture probability
736   }
737 }
738
739 # For capture parameters (with temporal variability of recapture)
740 for (t in 1:(ti-1)){
741   captureprob[t] <- mu.capt + epsiloncapt[t]
742   epsiloncapt[t] ~ dnorm(0, taucapt) # Priors for random effects of resighting rates
743 }
744 mean.capt ~ dunif(0, 1) # Priors on recapture probability
745 mu.capt <- log(mean.capt / (1-mean.capt))
746 sigmacapt ~ dunif(0, 10)
747 taucapt <- pow(sigmacapt, -2)
748 sigma2capt <- pow(sigmacapt, 2)
749 for (t in 1:(ti-1)){
750   capture.est[t] <- 1 / (1+exp(-captureprob[t]))
751 }
752
753 # For survival parameters (with temporal variability of survival independent of each age)
754 for (u in 1:4){
755   for (t in 1:(ti-1)){
756     eta.phi[u,t] <- mu.phi[u] + epsilon[t,u]
757   }
758   mean.phi[u] ~ dunif(0, 1) # Priors on mean age-specific survival

```

```

759 mu.phi[u] <- log(mean.phi[u] / (1-mean.phi[u]))
760 }
761 for (u in 1:4){
762   for (t in 1:(ti-1)){
763     phi.est[u,t] <- 1 / (1+exp(-eta.phi[u,t])) # phi.est[i,] corresponds to survival between age i and i+1
764   }
765 }
766
767 # For recruitment parameters (with temporal variability of recruitment independent of each age)
768 for (i in 1:(ti-1))
769 {
770   log(fec1[i]) <- ff1[i] # Recruitment of age class 1
771   ff1[i] <- v[1] + epsilon[i,5]
772   log(fec2[i]) <- ff2[i] # Recruitment of age class 2
773   ff2[i] <- v[2] + epsilon[i,6]
774   log(fec3[i]) <- ff3[i] # Recruitment of age class 3
775   ff3[i] <- v[3] + epsilon[i,7]
776   log(fec4[i]) <- ff4[i] # Recruitment of age class 4 (and older)
777   ff4[i] <- v[4] + epsilon[i,8]
778
779   ## Priors for random effects of demographic rates
780   eps.raw[i, 1:8] ~ dmnorm(zeros[], Tau.raw[,])
781   epsilon[i,1] <- xi.phi1 * eps.raw[i, 1]
782   epsilon[i,2] <- xi.phi2 * eps.raw[i, 2]
783   epsilon[i,3] <- xi.phi3 * eps.raw[i, 3]
784   epsilon[i,4] <- xi.phi4 * eps.raw[i, 4]
785   epsilon[i,5] <- xi.fec1 * eps.raw[i, 5]
786   epsilon[i,6] <- xi.fec2 * eps.raw[i, 6]
787   epsilon[i,7] <- xi.fec3 * eps.raw[i, 7]
788   epsilon[i,8] <- xi.fec4 * eps.raw[i, 8]
789 }
790 xi.phi1 ~ dunif(0, 2)
791 xi.phi2 ~ dunif(0, 2)
792 xi.phi3 ~ dunif(0, 2)
793 xi.phi4 ~ dunif(0, 2)
794 xi.fec1 ~ dunif(0, 2)
795 xi.fec2 ~ dunif(0, 2)
796 xi.fec3 ~ dunif(0, 2)
797 xi.fec4 ~ dunif(0, 2)
798
799 ## Priors for the mean of recruitment rates
800 for (i in 1:4)
801 {
802   v[i] ~ dunif(0,70)
803 }
804
805 ## Immigration rates
806 for (t in 1:(ti)){
807   im[1:4,t] ~ ddirch(alphaIM[]+0.001)
808 }
809
810 ## Prior for precision matrix
811 Sigma.raw[1:8,1:8] <- inverse(Tau.raw[,])
812 Tau.raw[1:8,1:8] ~ dwish(W[,], 9)
813
814 ## Prior for census error
815 sigy ~ dunif(0,10)
816 tauy <- 1/pow(sigy,2)
817
818 ## Priors for initial population sizes

```

```

819 n1 ~ dnorm(200,0.01)T(0,) # 1-year old
820 N1[1] <- round(n1)
821 n2 ~ dnorm(135,0.01)T(0,) # 2-years old
822 N2[1] <- round(n2)
823 n3 ~ dnorm(120,0.01)T(0,) # 3-years old
824 N3[1] <- round(n3)
825 n4 ~ dnorm(100,0.01)T(0,) # 4-years old
826 N4[1] <- round(n4)
827 Age1 ~ dnorm(130,0.01)T(0,) # Females of age class 1 locally produced
828 age1[1] <- round(Age1)
829 Age2 ~ dnorm(130,0.01)T(0,) # Local females of age class 2
830 age2[1] <- round(Age2)
831 Age3 ~ dnorm(120,0.01)T(0,) # Local females of age class 3
832 age3[1] <- round(Age3)
833 Age4a ~ dnorm(30,0.01)T(0,) # Local females arriving from age class 3 to age class 4
834 age4a[1] <- round(Age4a)
835 Age4p ~ dnorm(20,0.01)T(0,) # Local females of age class 4 already there
836 age4p[1] <- round(Age4p)
837
838 #####
839 # 2: Derived parameters: population growth rate "lambda" and mean population growth rate "melam"
840 ########
841
842 for(tt in 1:(ti-1))
843 {
844 lambda[tt] <- Ntot[tt+1]/Ntot[tt] # 182
845 logla[tt] <- log(lambda[tt])
846 }
847 melam <- exp((1/(ti-1))*sum(logla[1:(ti-1)]))
848
849
850 #####
851 # 3: Likelihood of the integrated population model
852 ########
853
854 #####
855 # 3.1: Likelihood for reproductive data
856 #####
857
858 # Age class 1
859 for (i in 1:(ti-1))
860 {
861 J[i,1] ~ dpois(rho1[i])
862 rho1[i] <- B[i,1] * fec1[i]
863 }
864 # Age class 2
865 for (i in 1:(ti-1))
866 {
867 J[i,2] ~ dpois(rho2[i])
868 rho2[i] <- B[i,2] * fec2[i]
869 }
870 # Age class 3
871 for (i in 1:(ti-1))
872 {
873 J[i,3] ~ dpois(rho3[i])
874 rho3[i] <- B[i,3] * fec3[i]
875 }
876 # Age class 4
877 for (i in 1:(ti-1))
878 {

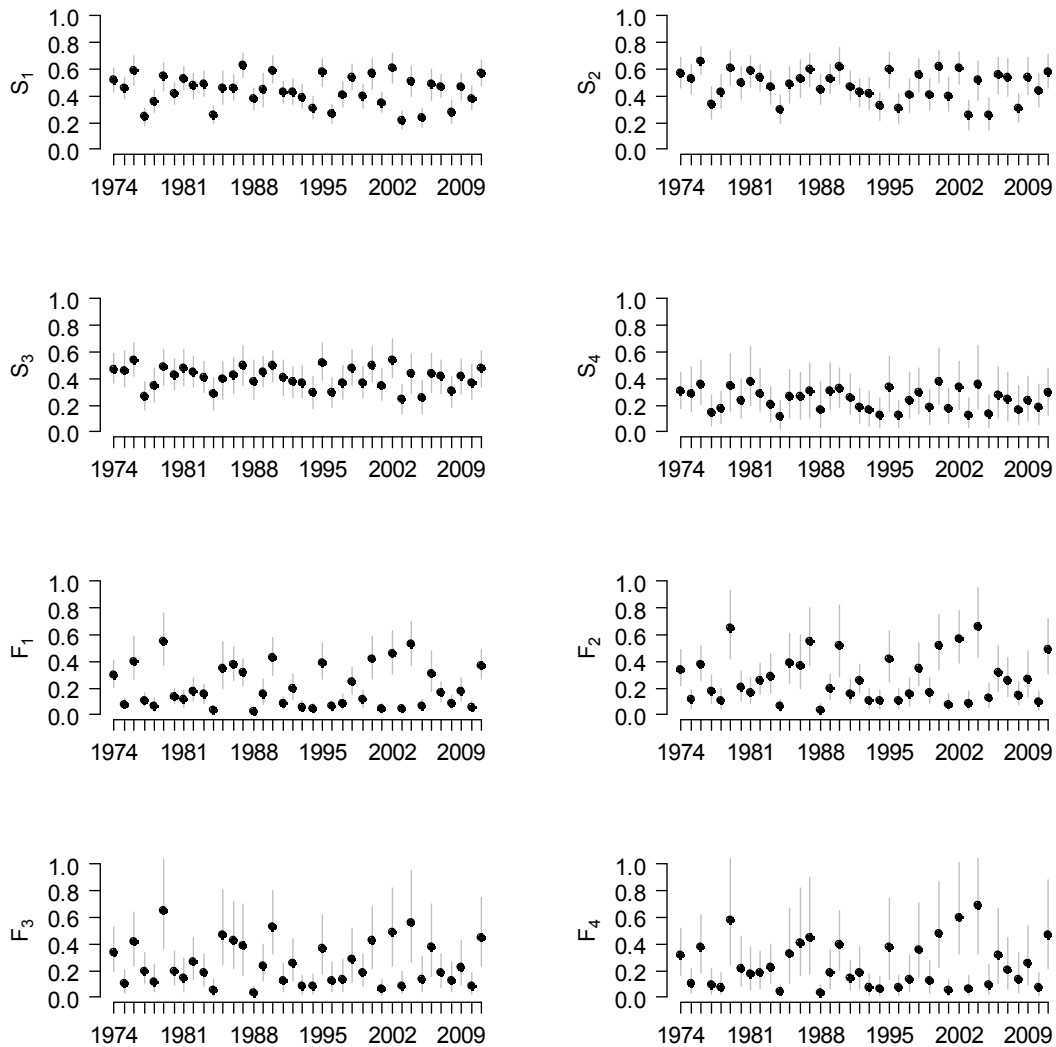
```

```

879     J[i,4] ~ dpois(rho4[i])
880     rho4[i] <- B[i,4] * fec4[i]
881   }
882
883
884   #*****
885   # 3.2: Likelihood for population survey data
886   #*****
887     #*****
888     # 3.2.1: System process
889     #*****
890     for (tt in 2:ti)
891       {
892       mean1[tt] <- fec1[tt-1]*N1[tt-1]+fec2[tt-1]*N2[tt-1]+fec3[tt-1]*N3[tt-1]+fec4[tt-1]*N4[tt-1]
893       age1[tt] ~ dpois(mean1[tt]) # 1-year old females locally produced
894       N1[tt] <- age1[tt]+ Nunknown1[tt] + Nknown[tt,1] # 1-year old local females + 1-year old
895       immigrant females
896       age2[tt] ~ dbin(phi.est[1,tt-1],N1[tt-1]) # 2-years old local females
897       N2[tt] <- age2[tt]+ Nunknown2[tt]+ Nknown[tt,2] # 2-years old local females + 2-years old
898       immigrant females
899       age3[tt] ~ dbin(phi.est[2,tt-1],N2[tt-1]) ## 3-years old local females
900       N3[tt]<- age3[tt]+ Nunknown3[tt]+ Nknown[tt,3] # 3-years old local females + 3-years old
901       immigrant females
902       age4a[tt] ~ dbin(phi.est[3,tt-1],N3[tt-1]) # 4-years old local females
903       age4p[tt] ~ dbin(phi.est[4,tt-1],N4[tt-1]) # Females older than 4 years-old who survive
904       N4[tt]<- age4a[tt]+ age4p[tt]+ Nunknown4[tt] + Nknown[tt,4] # 4-years old local females (arriving
905       from age class 3 and already in the old class) + 4-years old immigrant females
906       }
907     for (tt in 1:(ti))
908       {
909       Nunknown1[tt] ~ dbin(im[1,tt],Nunknownobs[tt]) # 1-year old immigrant females
910       Nunknown2[tt] ~ dbin(im[2,tt],Nunknownobs[tt]) # 2-years old immigrant females
911       Nunknown3[tt] ~ dbin(im[3,tt],Nunknownobs[tt]) # 3-years old immigrant females
912       Nunknown4[tt] ~ dbin(im[4,tt],Nunknownobs[tt]) # 4-years old immigrant females
913       }
914
915     #*****
916     # 3.2.2: Observation process
917     #*****
918     for (tt in 1:ti)
919       {
920       Ntot[tt] <- N1[tt] + N2[tt] + N3[tt] + N4[tt]
921       popcount[tt] ~ dnorm(Ntot[tt],tauy)T(0,)
922       }
923
924   #*****
925   # 3.3: Likelihood for capture-recapture data ( CJS models with 4 age classes)
926   #*****
927   for (i in 1:nind){
928     z[i,f[i]] <- 1
929     for (t in (f[i]+1):ti){
930       z[i,t] ~ dbern(mu1[i,t])
931       mu1[i,t] <- phi[i,t-1] * z[i,t-1]
932       y[i,t] ~ dbern(mu2[i,t])
933       mu2[i,t] <- p[i,t-1] * z[i,t]
934     }
935   }
936 } # End model
937 ",fill = TRUE)
938 sink()

```

939 **Appendix S3** - Posterior means of the annual survival rates S_i and annual recruitment rates F_i
940 (defined as the number of daughters locally recruited per breeding female) of breeding
941 females of each age class i and their associated 95% CRI (grey lines) in the great tit
942 population of Hoge Veluwe National Park, the Netherlands, between 1974 and 2011.



943