



Supplementary Materials for

Population Growth in a Wild Bird Is Buffered Against Phenological Mismatch

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Supplementary Materials for Reed et al. “Population growth in a wild bird is buffered against phenological mismatch”

Materials and Methods:

1.1 Study population and data selection

The data analysed come from a long-term (1973-2011) nest-box study of great tits (*Parus major*) at the Hoge Veluwe National Park, the Netherlands. The study area, which remained the same size across this period and is open to immigration and emigration, consisted of mixed pine-deciduous woodland. The total number of nest boxes remained constant at approximately 400 over the study period (a few were removed or replaced as the study progressed). Very few natural nests are detected each year, as the birds show a strong preference for the nest boxes. While nest box populations are slightly artificial in the sense that nest predation rates are greatly reduced and breeding densities are higher than they would be naturally (due to the increased availability of nesting sites), nest box studies can still provide useful demographic data provided the number of nest boxes does not itself regulate population size (see 31 and references therein for a full discussion). We are confident that this is indeed the case for our study population: a surplus of nest boxes is always provided (on average approximately 3 for every breeding female), so nest box availability does not regulate population numbers. The main factors believed to regulate population size in our population, and indeed other nest box study populations of great tits, are territoriality and intraspecific competition for food (31).

Nest boxes were visited at least once per week during the breeding season (April to June/July) and the number of eggs or nestlings present was counted at each visit. The annual number of first clutches was used as a measure of breeding density. Parents were caught on

the nest using a spring trap when the nestlings were 7-10 days old. Unringed birds were given a metal ring with a unique number and those already ringed were identified. Nestlings were ringed on day 7.

We focussed only on breeding females, on the assumption that female fecundity limits population growth. Rates of non-breeding are very low in our study population (32), so breeding population size is a good proxy for total population numbers. In the GLMM analysis we modelled the annual contribution of individual females (denoted $W_{i,t}$) to changes in population size, that is, the number of female offspring that a mother produces in one year that survive and recruit into the breeding population in subsequent years (including from second broods), plus one if the female herself survives (21). Breeding females caught unringed or ringed outside the study area were classified as immigrants in their year of arrival into the study population. The mean number (\pm standard deviation) of immigrants per year was 70 ± 18 , with immigrants accounting for approximately 55% of breeding females, on average, in a given year. These immigrants are included in the analysis of $W_{i,t}$ (as they breed in the study area), but note that total local fitness contributions to population growth from year t to $t+1$ is supplemented by new immigrants arriving in year $t+1$ (see section 3 below).

A small but variable number of females each year was not caught ($n=732$ across 38 years); these were not included in the analyses of fitness contributions, as their survival could not be determined, but were included in the calculation of annual breeding density. Annual recapture rates are consistently very high for this population (see 20) and thus we are confident that our survival estimates are not biased by variation in recapture rates. The analysed dataset consisted of 4177 records of 2616 females breeding in 38 years.

Dates of the peak in caterpillar biomass were estimated for 1985 to 2010 using frass fall samples collected in the study area. Mean temperatures from 8 March – 17 May provide a good predictor ($r^2 = 0.80$) of the annual caterpillar peak date, and this relationship was used to

predict caterpillar peaks from 1973 to 1984. For full details see (16, 17). In the main text of the paper, ‘late spring temperatures’ refer to temperatures (°C) averaged over the period 21 April – 17 May, which is the period after great tits have laid their eggs but before the end of the temperature sensitivity window for the caterpillars. Temperature data was obtained from De Bilt meteorological station of the Royal Netherlands Meteorological Institute (KNMI), which is situated in the centre of the Netherlands not far from the study area.

1.2 *A note on differences between this dataset and that used in Reed et al. 2012*

The dataset used for this paper was slightly different from that used in Reed et al. 2012 (20). In that paper, the goal was to characterize the effects of phenological mismatch on components of fitness at the individual and population levels (whereas here we are interested in the net effects of mismatch on population growth and the mechanisms regulating population numbers). In (20), we excluded manipulated broods from the analyses as the aim was to obtain unbiased estimates of the effects of mismatch on demographic rates, and these manipulations might have affected fledgling production rates or recruitment probabilities. We also excluded the year 1991 in that dataset, which was an anomalous year where a late frost resulted in a very late caterpillar food peak. Finally, we also included unknown females (those that could not be individually identified) in the dataset used for Reed et al. 2012 (20). The reproductive success, but not the adult survival, of these unknown females was known so they were included in that paper to make full use of all the data.

The dataset used in the current paper differed in three ways: (1) we excluded unknown females, (2) we included manipulated birds, and (3) we included the year 1991. Unknown females were excluded here because their annual survival was unknown, hence $W_{i,t}$ could only

be calculated for known females. Manipulated females and data from 1991 were included, however, because these females still contribute to annual population growth and dynamics. The dataset used in this paper (4177 records of 2616 females breeding in 38 years) was therefore larger than that used in Reed et al. 2012 (3472 records of 2599 females breeding in 37 years). All reported results were qualitatively unchanged when manipulated females were excluded, when data from 1991 were excluded, and when both were excluded.

2. *Calculating mismatch and selection gradients*

Great tits in our study population typically lay 9 eggs and incubate for 12 days, with nestling food requirements peaking ca.9 days after hatching (i.e. 30 days after laying of the first egg). Thus the mismatch between a female's breeding time and the annual caterpillar (food) peak date (FP) was defined as the difference between the laying date of her first clutch and the FP , plus 30 days. The number 30 is arbitrary here, and using a different number (e.g. 28 or 32) does not alter our results or conclusions. Annual population mismatch (PM) was defined as the arithmetic average of individual mismatch (IM) values each year. Note also that using a fixed clutch size of 9 (instead of real clutch size, which varies across individuals and years) in the calculation of IM does not introduce a significant bias into the analysis of demographic consequences (see 20 for a full justification).

Annual point estimates for the strength of directional selection on laying dates were obtained by calculating standardised selection gradients β'_i , defined as the slope of the regression of relative fitness on standardised (z-score) trait values (33). Relative fitness was obtained by dividing $W_{i,t}$ by annual means.

3. *Calculating population growth and annual mean fitness*

The population is open to immigration, so breeding population size in year $t+1$ is given by $\sum_{i=1}^{N_t} W_{i,t} + I_{t+1}$, where N_t is the population size in year t , $W_{i,t}$ is the fitness contribution of individual i in year t (i.e. the number of offspring produced by a female in year t that survive to breed in year $t+1$, plus 1 if she survived herself), and I_{t+1} is the number of new immigrants entering the population in year $t+1$. Annual changes in population size N are then given by $N_{t+1} = \Lambda_t N_t + I_{t+1}$, where Λ_t denotes the stochastic multiplication rate of the population in the absence of immigration. Population growth on the log scale is given by $\ln(\frac{N_{t+1}}{N_t})$; this is the measure plotted on the y-axis of Fig.1.

Considering the emigrants as effectively ‘locally dead’, $\Lambda_t = \frac{\sum_{i=1}^{N_t} W_i}{N_t} = \bar{W}_t$, i.e. the mean contribution of females breeding in year t to population growth in that year. Grøtan et al. (21) showed that annual variation in immigration in Dutch great tit populations is influenced by the same processes and is positively correlated with local recruitment rates. In our study, population growth was strongly linearly related ($F_{1,36} = 146.9$, $P < 0.001$, $r^2 = 0.803$) to \bar{W}_t (see Fig. S1). \bar{W}_t therefore provides a good proxy for annual population growth and year-specific variables affecting $W_{i,t}$ in the GLMM can therefore be inferred to also affect population growth. Fitting PM as a year-specific continuous fixed effect in the GLMM on $W_{i,t}$ (see section 4 below) allowed an inference to be drawn regarding the effect of interannual variation in mismatch on interannual variation in \bar{W}_t , and hence on variation in population growth. This is a more robust and powerful method for testing for effects of environmental covariates on population growth than using population growth itself as the response variable, as the full individual-level dataset can be used rather than first aggregating the data into annual values (21).

4. The GLMM

A generalized linear mixed-effects model (GLMM) was fitted with $W_{i,t}$ as the response variable (log-link function, Poisson errors) to examine whether interannual variation in fitness was associated with variation in PM , while controlling for other variables potentially affecting population growth. The following year-specific fixed effects (all continuous) were included as candidate explanatory variables in the GLMM: PM , breeding density, age structure, and beech crop. Breeding density (the annual total number of first clutches) was included as density dependence is known to be strong in our study population (20, 21). Demographic studies of great tits typically find that first-years females lay later, produce smaller clutches, and recruit fewer offspring than older age classes (see 20 and references therein); therefore the annual proportion of first-time breeders was included to control for interannual variation in age structure. Beech crop quantifies the amount of beech nuts available in winter on a 3 point scale; this index correlates positively with overwinter survival of juvenile and adults and also correlates with the crop size of other tree species in the region (see 20 and references therein). To capture the expected nonlinear effects of beech crop (20, 21), beech crop was treated as a continuous variable and linear and quadratic effects were included in the model. Treating beech crop as a factor would be an alternative way to capture its potential nonlinear effects; however, we wished to calculate effect sizes for each fixed effect and this is much more straightforward for continuous variables (33).

The response variable in the GLMM was individual-specific, and as such we could have also included individual mismatch (i.e. each female's breeding time expressed relative to the food peak) as an individual-specific covariate. Expressing individual mismatch relative to annual population mismatch, for example, would allow the within-year (i.e. individual-level) and between-year (i.e. population-level) effects of mismatch to be estimated separately in one model (20). Including individual mismatch as a covariate simply explains more of the total

variation in $W_{i,t}$ (by accounting for part of the within-year, among-individual variance), but it does not alter the effect sizes or standard errors of the year-specific covariates appreciably. Our inferences regarding the effects of PM are therefore robust to whether individual mismatch effects are modeled or not, hence for simplicity we chose not to include this covariate.

Random effects of ‘female identity’ and ‘year’ were included in each case, to account for repeat measures on individuals and years, respectively. Models were fit in R version 2.12.2 (R Development Core Team, 2011) using the function *glmer* in the package *lme4*. We started with a full model, which included two-way interactions between all fixed effects (higher order interactions were not considered). We used a backwards stepwise model simplification procedure, sequentially removing non-significant ($P > 0.05$) fixed-effects starting with higher-order terms to yield the minimum adequate model. The P values for non-significant fixed effects given in Table 1 correspond to when they were dropped from the model in the backwards elimination process.

5. *The simulation model*

The goal of the simulation model (results of which are presented in Fig. 3 of the paper) was to illustrate the interaction between the two mechanisms explaining why PM does not strongly affect population growth. To simulate the population dynamics, we let the number of female recruits per breeding female be a stochastic variable conforming to a Poisson distribution, and female survival (from one breeding season to the next) be a stochastic variable conforming to a binomial distribution. Recall that individual fitness contributions to population growth are the sum of these components: $W_{i,t} = R_{i,t} + S_{i,t}$. Reed et al. (20) presented GLMMs that assessed factors influencing the number of recruits per female (see Table 1F in that paper) and female survival (see Table 1G in that paper). These GLMMs can be used to predict $R_{i,t}$ and $S_{i,t}$ in the

simulation model as a function of annual breeding density, individual mismatch, population mismatch, and beech crop index. Reed et al. (20) used a different subsetted dataset to that used in this paper (see section 1.1 above). The GLMMs yield very similar estimates regardless of whether unknown females and manipulated broods are included or excluded, but for the purposes of the simulation model we refit the best models identified in (20) to the current dataset.

Here the focus is on females only, whereas in (20) both male and female recruits were analyzed together. We therefore refit the best GLMM on the number of recruits described in Table 1F of (20), but with number of female recruits (i.e. $R_{i,t}$) as the response variable, rather than number of total recruits. For the simulations we also ignored age effects, so the term ‘mother age’ was excluded when refitting the model. Expected $R_{i,t}$ (on the log scale) in the simulation model was calculated as follows:

$$E(R_{i,t}) = \beta_{R1}N_t + \beta_{R2}PM_t + \beta_{R3}IM_{i,t} + \beta_{R4}IM_{i,t}^2 + \beta_{R5}BCI(1)_t + \beta_{R6}BCI(2)_t + \beta_{R7}BCI(3)_t + \beta_{R8}PM_tIM_{i,t} \quad (\text{eq1}).$$

where N_t refers to annual breeding density, PM_t to annual population mismatch, $IM_{i,t}$ to individual mismatch expressed relative to PM_t (i.e. standardised IM). $BCI(1)_t$, $BCI(2)_t$ and $BCI(3)_t$ were incidence vectors that together specified the beech crop index for each year:

i.e. if { $BCI(1)_t=1$ and $BCI(2)_t=0$ and $BCI(3)_t=0$, beech crop index = 1,
 $BCI(1)_t=0$ and $BCI(2)_t=1$ and $BCI(3)_t=0$, beech crop index = 2,
 $BCI(1)_t=0$ and $BCI(2)_t=0$ and $BCI(3)_t=1$, beech crop index = 3 }.

The coefficients $\beta_{R1} \dots \beta_{R8}$ correspond to the fixed effects estimates from the GLMM on $R_{i,t}$.

Note that the model was fit without an intercept and BCI was specified as a 3-level factor. PM was projected according to four different scenarios: three climate change scenarios (described

below) and one control scenario where *PM* exhibited no directional trend, but fluctuated randomly about zero. For each scenario, the projected trend in *PM* was inputted into the simulation model and temporal stochasticity was added by drawing annual random deviates from a normal distribution centered on 0 and variance equal to the observed interannual variance in detrended *PM*. *IM* was then simulated by drawing N_t random numbers from a normal distribution of mean equal to the simulated annual *PM*, and variance equal to the observed variance in standardized *IM*. Beech crop was simulated by sampling with replacement from the observed time series (1973-2010), a period across which no directional trend was evident. Thus the simulations model a situation where climate change induces a trend in mismatch but not in beech nuts abundance. We acknowledge that climate change might also affect the abundance of beech nuts, but here our interest is in mismatch effects.

Temporal (between-year) variance in recruits per female (ε_{Rt}) was simulated by drawing a single random number each year from a normal distribution of mean 0 and variance given by the variance component estimate for the ‘year’ random effect in the GLMM on $R_{i,t}$. This same random number was added to the expected values for all individuals in a given year, with a different number being added every year. ε_{Rt} therefore captures across-year stochasticity in recruitment rates driven by (unspecified) environmental factors other than mismatch and beech crop. The estimates for the fixed effects and the random year variance component from the GLMM were on the log scale (i.e. a Poisson model). The simulated number of recruits ($R_{i,t}^*$) was therefore obtained as: $R_{i,t}^* = \exp(E(R_{i,t}) + \varepsilon_{Rt})$. This gives the simulated number of recruits as a continuous number, which was then converted to a integer Poisson variable by drawing a random number from a Poisson distribution of mean (and variance) = $R_{i,t}^*$.

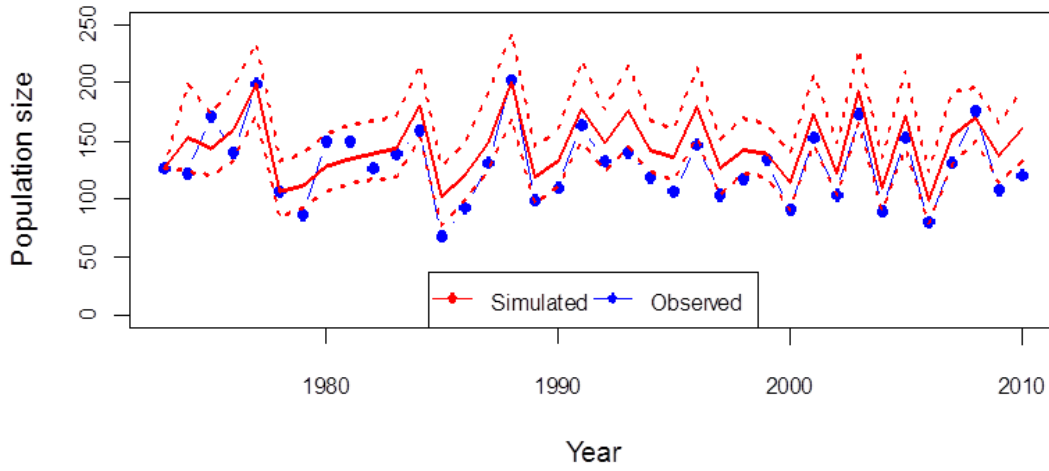
Female survival was simulated in a similar fashion. Expected individual annual survival (on the logit scale) was calculated based on the best GLMM described in Table 1G of

Reed et al. (20) (but refit to the current dataset) which included effects of breeding density and beech crop index:

$$E(S_{i,t}) = \beta_{s1}N_t + \beta_{s2}BCI(1)_t + \beta_{s3}BCI(2)_t + \beta_{s4}BCI(3)_t \quad (\text{eq. 2}).$$

where the coefficients $\beta_{s1} \dots \beta_{s4}$ correspond to the fixed effects estimates obtained from the GLMM on $S_{i,t}$, fitted without an intercept. The same values of simulated beech crop as used in eq.1 were used in eq. 2. Temporal variance in survival (ε_{st}) was simulated by drawing a single random number each year from a normal distribution of mean 0 and variance given by the variance component estimate for the ‘year’ random effect in the GLMM on $S_{i,t}$. This same random number was added to the expected values for all individuals in a given year, with a different number being added every year. The estimates for the fixed effects and the random year variance component from the GLMM on $S_{i,t}$ were on the logit scale (i.e. a binomial model). The simulated number of recruits ($S_{i,t}^*$) was therefore obtained as: $S_{i,t}^* = \text{antilogit}(E(S_{i,t}) + \varepsilon_{st})$. This gives individual survival as a continuous number between 0 and 1, which was then converted to a binary variable by drawing a random number from a binomial distribution of number of trials = 1 and per-trial probability of success = $S_{i,t}^*$.

To first check whether the simulated population sizes were realistic, we ran 1000 simulations using the observed vectors of PM , N and BCI across the period 1973-2010. The simulated population sizes provided a reasonable match with the observed population sizes across this period (graph shows median simulated population sizes and 95% confidence intervals):



Individual contributions to population growth were obtained in the simulations as:

$$W_{i,t}^* = R_{i,t} + S_{i,t}^* + \delta \quad (\text{eq 3}),$$

where δ was an offset (used only in the forward projections) introduced to ensure that a stable population (i.e. $E(N_{t+1}^*/N_t^*) = 1$) of circa 130 individuals always resulted in the absence of any climate change (whether density dependence for recruitment was on or off). As explained in section 3 above, the population is open to immigration and the number of immigrants is positively correlated with the number of new recruits each year: for every new recruit, there are 0.658 immigrants. Population size was therefore calculated iteratively in the simulation as:

$N_{t+1}^* = \sum_{i=1}^{N_t^*} W_{i,t}^* + 0.658 * \sum_{i=1}^{N_t^*} R_{i,t}^*$, i.e. the sum of individual fitness contributions plus the number of new immigrants.

In the first set of simulations, the population was projected for 100 years (from the year 2000 to the year 2100) using the above equations, under one ‘control scenario’ and 3 scenarios of climate change. In the control scenario, PM was assumed to fluctuate randomly about zero, i.e. no temporal trend in population mismatch. In climate change scenarios 1-3, PM was assumed to increase over the course of the century according to mild, moderate and extreme scenarios of climate change, respectively. These scenarios are the same as those described in Gienapp et al. (27). In that paper, the caterpillar food peak date was predicted

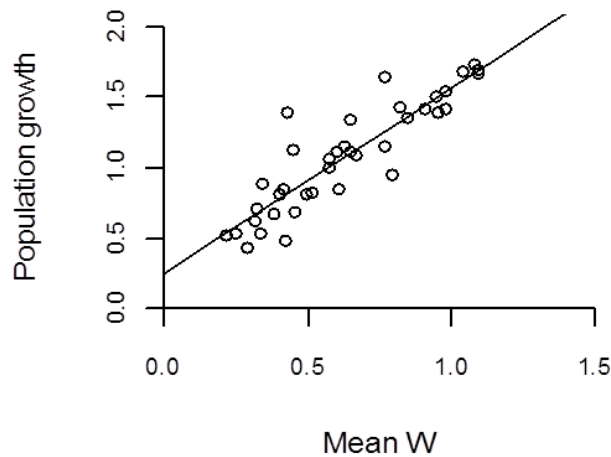
according to a mechanistic degree-day model of caterpillar development and changes in great tit laying dates (for the same study population as that analyzed here) due to phenotypic plasticity were predicted based on a proportional hazards model, which incorporated information on photoperiod and temperature. Caterpillar and great tit phenology were projected under three scenarios of climate change for the Netherlands derived from IPCC scenarios (for full details see 27). Population mismatch was then calculated as the annual estimated difference between great tit breeding time and the food peak date.

Fig. 3A in the main paper shows the resulting simulated population trajectories for each of these scenarios, with the different color lines representing the median population size calculated across 1000 simulations. The inset in that panel shows the corresponding (inputted) trajectories for *PM*, corresponding to the 3 climate change scenarios and the control scenario. The relatively slow rates of population decline in Fig. 3A that result under the 3 climate change scenarios reflect the fact that *PM* has only a weak effect on the expected number of recruits per female per year (see eq. 1 above) and no effect on expected female survival (eq. 2). The total effect of *PM* on population growth, however, is strongly modulated by density-dependence in recruitment rates. To illustrate this, the strength of density-dependence was ‘turned off’ in the second set of simulations (the results of which are shown in Fig. 3B of the main paper). This was achieved by setting the β_{R1} coefficient in eq. 1 to 0, effectively making recruitment rates density-independent. Turning off density dependence in recruitment rates leads to larger interannual fluctuations in recruitment rates (and hence in population size) in the simulations, but expected recruitment rates remain the same. Note that the density-dependence coefficient in the equation for adult survival (i.e. β_{S1} in eq. 2) was not modified in this second set of simulations, which also prevented population sizes from increasing unregulated.

As Fig. 3B shows, a stable population resulted in the control scenario when density dependence in recruitment rate was turned off, of approximately the same median size (~130 breeding females) as for the control scenario in Fig. 3A. The relative rates of population decline among the climate change scenarios are thus directly comparable between Fig. 3A ('density dependence ON') and Fig.3B ('density dependence OFF'). All simulations were initiated with 130 individuals, which is the mean of the observed population size across the study period 1973-2010 (and thus presumably reflect the ecological carrying capacity of the population).

Supplementary Information: Figures S1-S2

Figure S1

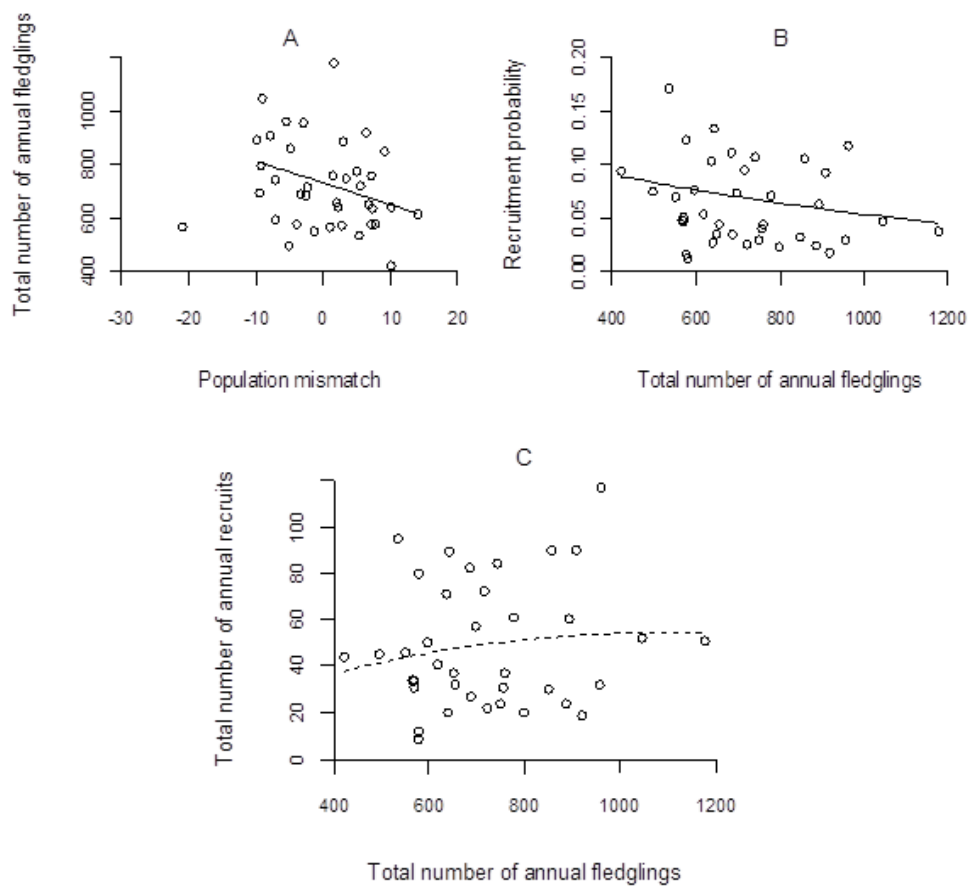


The mean contribution of individuals to local population growth is strongly positively correlated with actual population growth.

The above plot illustrates that population growth on the untransformed scale, i.e. the number of breeding females in year $t+1$ divided by the number breeding in year t , is strongly linearly

related (slope = 1.32 ± 0.11 , $t_{1,36} = 12.12$, $P < 0.001$) to the variable \bar{w}_t used in the paper, which corresponds to the mean contribution of individuals to local population growth (see section 3 of Materials and Methods). Grøtan et al. (21) showed that local recruitment and immigration rates are strongly positively correlated and are affected by similar processes (using demographic data from our study population and 4 other Dutch great tit populations). If these were not strongly correlated, the above relationship between population growth and \bar{w}_t would be much weaker and using \bar{w}_t as a proxy for population growth would not be justified.

Figure S2



A: The annual number of fledglings produced depends on population mismatch.

Panel A above shows that fewer fledglings are produced in years where population mismatch is higher (i.e. average breeding time is too late relative to the food peak) ($t_{1,35} = 2.01$, $P = 0.05$). The outlier year on the left is 1991 – an anomalous year with an extremely late food peak, and therefore excluded from the regression.

B: Average recruitment probability depends on the annual number of fledglings produced.

Panel B shows that recruitment probability is lower in years where more fledglings are produced (GLM on annual means, binomial errors: $Z_{1,35} = -6.04$, $P < 0.001$) because of increased competition for limited resources.

C: The annual number of recruits is therefore independent of the annual number of fledglings.

Finally, Panel C shows that there is no linear relationship ($t_{1,36} = 0.80$, $P = 0.43$) between the number of recruits produced each year and the number of fledglings produced. The reason is because there is strong density-dependent compensation in recruitment rates (Panel B), hence a decrease in the number of fledglings due to mismatch (Panel A) does not produce a proportional decrease in the number of recruits. The dotted line does not show the fitted regression slope (which in this case does not differ from zero), but rather the expected total number of recruits based on the predicted negative effect of density on recruitment probability shown in Panel B (i.e. expected number of recruits = observed number of fledglings \times predicted recruitment probability). The fact that the dotted line is not completely flat indicates that compensation due to density dependence is not perfect, but nonetheless substantial.

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