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1 **Detecting climate signals cascading through levels of biological organization**

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17

18 **Abstract**

19

20 Threats to species under climate change can be understood as a time at which the signal of
21 climate change in ecological processes emerges from the noise of ecosystem variability, defined
22 as ‘time of emergence’ (ToE). Here, we show that ToE for the great tit (*Parus major*) will occur
23 earlier at the level of population size than trait (laying date) and vital rates (survival, recruitment)
24 under the RCP 8.5 scenario, suggesting amplified climate change signal at the population level.
25 ToE thus varies across levels of biological organization that filter trends and variability in
26 climate differently. This has implications for the detection of climate impacts on wild species, as
27 a shift in population size may precede changes in traits and vital rates. Further work would need
28 to identify the ecological level that may experience an earlier detection of the climate signal for
29 species with contrasting life histories and climate trends and variability.
30

31 **Main Text**

32

33 The impact of anthropogenic climate change on wildlife populations is a topic of
34 profound concern. Climate change occurs in the context of broad-band natural climate
35 variability, often making it difficult to discern the explicit effects of long-term change driven by
36 forced response to greenhouse gases. In addition, ecological responses to environmental
37 variation are stochastic with multiple sources of variation, including observed and unobserved
38 variability in abiotic and biotic factors that interact with natural climate variability. Accordingly,
39 detecting responses to anthropogenically-forced changes in climate is challenging ¹. This is,
40 however, crucial for the detection and attribution of ecological responses to climate change
41 because changes in climate have direct impacts on ecosystem processes and society ².

42

43 To detect changes in climate, climatologists have extensively used the concept of time of
44 emergence in climate (ToE_{climate}) ^{3,4}. It defines the point in time when the signal of climate
45 change emerges from the noise of natural climate variability. It has been applied for instance on
46 changes in temperatures ³, rainfall ⁵ and in polar climate ^{1,4}. Here, we apply this concept, for the
47 first time, across levels of ecological organization to identify the time at which the signal of
48 climate change in ecological processes emerges from the stochastic noise associated with natural
49 climate and ecological variability (time of emergence, ToE). We assess the ToE from trait
50 (ToE_{trait}), to vital rates (e.g. survival, recruitment) (ToE_{vital}), and population size (ToE_{pop}) (Fig. 1)
51 to study how the climate signal cascades through the levels of biological organization. Climate-
52 induced changes in resources, that influence fitness-related traits, are expected to generate
53 changes in vital rates, which lead to population-level responses. We may thus expect that the
54 time of emergence is delayed across levels of biological organization, occurring earlier for traits
55 than for vital rates and population size ⁶⁻⁸. However, those responses depend on the sensitivity of
56 vital rates to climate variation and the sensitivity of population growth rate to changes in vital
57 rates, potentially driving more complex patterns across levels of biological organization ^{1,8,9}.

58

59 There are not many systems for which this hypothesis can be tested because it requires
60 long-term data at various levels of biological organization. Here, we use one of the best long-
61 term ecological time series study system on the great tit (*Parus major*) at the Hoge Veluwe
62 National Park (the Netherlands) from 1985 to 2020 (Fig. 1). The great tit is a short-lived small
63 passerine bird species abundant in European gardens and woodlands and it is not migratory.
64 Global warming influences this population in several ways. In spring, warmer temperatures lead
65 to an advanced peak date of caterpillar biomass, an important food resource for great tits for
66 feeding their offspring during the breeding season. However, the advancement in laying dates is
67 slower than the advancement in food peak date, leading to a phenological mismatch between
68 offspring requirements and food peak ¹⁰. This mismatch influences the vital rates of great tits ¹¹.
69 In summer, warmer temperatures are expected to influence the intensity and frequency of
70 beechnut production (*Fagus sylvatica*) ^{12,13}, an important food resource for great tits in winter,
71 also affecting their vital rates ¹⁴. Taking advantage of this unique system to quantify the ToE
72 across biological levels of organization, we identified the point in time when climate-driven
73 signals in trait (laying date), vital rates (survival, recruitment) and population dynamics can be
74 distinguished from noise by constructing prediction intervals of ecological projections using the
75 Community Earth System Model Large Ensemble (CESM-LE) ¹⁵.

76

77 We first quantified the ToE in caterpillar peak dynamics ($ToE_{caterpillar}$). Using the
78 established relationship between spring temperatures and caterpillar peak (period 1985 – 2020)
79 ¹⁶, we projected caterpillar peak dynamics under a high emission climate scenario with no policy
80 intervention (RCP 8.5 scenario), back in the past and into the future, from 1920 to 2100. The
81 peak date of caterpillar biomass advanced over time ¹⁶, with an expected $ToE_{caterpillar}$ in 2034, if
82 we only account for climate natural variability (Fig. 2). When many sources of ecological
83 stochasticity were included in the projections, such as uncertainty in parameter estimates and
84 process variance corresponding to unexplained temporal environmental stochasticity beyond that
85 explained by climate, $ToE_{caterpillar}$ was detected later, in 2049 (Extended Data Fig. 1).

86
87 Second, we quantified the ToE in trait dynamics, namely laying date (ToE_{laying}). Using
88 the established relationship between spring temperatures and laying dates (period 1985 – 2020)
89 ¹⁶, we projected laying dates dynamics from 1920 to 2100. Laying occurred earlier and earlier
90 over years, with an expected ToE_{laying} in 2045 and 2068 (with climate natural variability only and
91 with all sources of uncertainties, respectively) (Fig. 2, Extended Data Fig. 1). Under warmer
92 spring conditions, directional selection for earlier laying has been reported in plethora of species
93 ^{17–24}. The shift in laying date has been interpreted as a phenotypic plastic response to increasing
94 temperatures, tracking the advance in the phenology of the food peak ^{25–28}. Our results
95 demonstrate that the difference between laying dates and date of the food peak, the so-called
96 phenological mismatch (Fig. 1), might not be detectable before 2100 when including many
97 sources of ecological uncertainties in the projections (Extended Data Fig. 1). However, when
98 only climate natural variability was accounted for in the modelling, $ToE_{mismatch}$ was detectable
99 and expected to occur in 2049 (Fig. 2). Increasing ecological complexity delays the $ToE_{mismatch}$ as
100 we expected, but mainly through the interaction with environmental stochasticity.

101
102 Third, thanks to the individual long-term monitoring of great tits, we estimated annual
103 age-specific great tits vital rates (survival, recruitment) using a state-of-the-art integrated
104 population model ^{29–32} (period 1985 – 2020, Extended Data Fig. 2). Annual vital rates were
105 linked to past beechnut production, mismatch and density (period 1985 – 2020, Table S1). Then,
106 we projected age-specific vital rates by 2100 under expected future conditions of mismatch and
107 beechnut production and quantified the ToE in vital rates (ToE_{vital}). Beechnut production is
108 expected to change in the future ^{33–35}, but there is currently no predictive model available for this
109 food resource. Therefore, we simulated two extreme scenarios, one of decreasing beechnut
110 production by 2100 and another of increasing production (Extended Data Fig. 3). Under the
111 scenario of decreasing beechnut production (scenario 1), we found a decrease in vital rates over
112 time, with a ToE_{vital} between 2050 and 2060 for most of the ages when we only accounted for
113 climate natural variation (Fig. 3, Extended Data Fig. 4). When all sources of ecological
114 uncertainties were accounted for, ToE_{vital} was not detectable before 2100 (Fig. 3, Extended Data
115 Fig. 5). Similarly, under the scenario of increasing beechnut production (scenario 2), we found
116 an increase in vital rates over time, with a ToE_{vital} between 2054 and 2084 for most of them when
117 we accounted for climate natural variability only (Fig. 3, Extended Data Fig. 6). Interestingly,
118 the ToE_{vital} occurred earlier for survival than recruitment rates because of a stronger signal on
119 survival. While the ToE_{vital} did not differ much between the two scenarios for survival, it is
120 delayed up to 20 years for recruitment under the scenario of increasing, compared to decreasing,
121 beechnut production. The climate-driven signals in recruitment rates by beechnut production
122 were obscured by density dependence, which plays a stronger role under favorable conditions

123 (i.e. when there are more years with a high beech crop) and weaker under poor conditions. As
124 expected, when all sources of ecological uncertainties were accounted for, ToE_{vital} was
125 undetectable (Fig. 3, Extended Data Fig. 7).

126
127 Finally, to quantify the ToE in population size (ToE_{pop}), we projected the great tit
128 population size from 1920 to 2100 by parametrizing a stochastic age-structured population model
129 with the projected vital rates (Extended Data Fig. 4-7). Under the scenario of decreasing
130 beechnut production, population size decreased with a ToE_{pop} in 2028 when we accounted for
131 climate natural variability only, whereas population size increased under the scenario of
132 increasing beechnut production with a ToE_{pop} in 2055 (Fig. 3). When all sources of ecological
133 uncertainties were accounted for, ToE_{pop} occurred later, in 2069 under the first scenario and in
134 2074 under the second scenario (Fig. 3).

135
136 Remarkably, for any scenario of beech crop production, the ToE_{pop} occurred earlier than
137 the ToE_{vital} when all sources of uncertainties were accounted for. This is consistent with previous
138 work based on numerical simulations that has shown that under a fast rate of environmental
139 change and low predictability, a population can decline before any apparent change in mean
140 value of the trait⁸. Similarly, in an experimental design, a fast change in prey availability
141 resulted in the decline of a protozoan ciliate population preceding a shift in mean body size⁸.
142 Therefore, the ToE_{pop} can occur earlier than ToE_{vital} and the detection of ToE depends on the
143 level of biological organization considered, its sensitivity to climate (i.e. magnitude and shape of
144 the functional relationship between climate and ecological variable), but also on the amount of
145 variability both in the climate and ecological systems.

146 Climate trends and variability are differently filtered by the vital rates (survival,
147 reproduction) and the ages¹. In addition, density dependence may prolong the ToE_{pop} ¹ as
148 illustrated here with our two scenarios of changes in beech crop production. Under the scenario
149 of decreasing beech crop production (scenario 1), both survival and recruitment rates decrease,
150 the magnitude of this decrease being age-specific. Competition also decreases, allowing for more
151 immigrants. The negative influence of beech crop on vital rates, only partially compensated by
152 an increase in the number immigrants, leads to a rapid population decline, with an early ToE.
153 Under the scenario of increasing beech crop production (scenario 2), survival and recruitment
154 rates increase. However, competition also increases, leading to a weak positive effect of beech
155 crop on recruitment rates, the latter being density-regulated³⁶. Similarly, the number of
156 immigrants joining the population are positively influenced by beech crop, but strongly regulated
157 by density, resulting in fewer immigrants. The positive influence of beech crop on survival rates,
158 counterbalanced by a strong density regulation acting on the number immigrants and on
159 recruitment rates leads to a moderate increase in population size, and a later ToE_{pop} .

160 Ecological variability is also key to detect ToE. We found that ToE in mismatch and vital
161 rates are not detectable before 2100 when ecological variability is accounted for, emphasizing
162 the difficulties to detect climate change signals in ecological processes. Thankfully, some of this
163 noise from sampling and process errors can be reduced by increasing monitoring effort and
164 improving our understanding of how the biological systems respond to biotic and abiotic factors.

165
166 The detection of ToE across levels of biological organization is context-specific, and the
167 earlier detection at the population level we showed here is unlikely for semelparous species, or if

168 climate affects primarily fertility ¹. In addition, several climate variables with different ToE may
169 affect the various ecological organizational levels, hence making difficult to predict which
170 ecological level may experience an earlier detection of the climate signal. Future studies could
171 build upon our analysis to better understand and detect when climate-driven changes in
172 ecosystems will clearly emerge from the “noise” of variability across species with contrasting
173 life histories inhabiting different environments (e.g. various climate variability and trends) ¹.
174 This is particularly urgent as ecosystems have a limited ability to adapt, and large changes
175 outside past experience could be particularly devastating ^{37,38}.

176
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182
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184 Methodology: MG, SJ; Formal analysis: MG, SJ; Data acquisition: MEV; Funding acquisition:
185 MEV, BES; Writing – original draft: MG; Writing – review & editing: MG, SJ, ML, BES, MEV;
186 Visualization: MG.

187
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189
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192 Fieldwork at the National Park de Hoge Veluwe was carried out with permission of the Park.
193

194 **Figure Legends**

195 **Fig. 1. Schematic illustration of the general approach.** The first panel shows forecasted
196 caterpillar peak dates, great tit laying dates, mismatch between caterpillar peak date and laying
197 date, as well as beech crop production (two scenarios) in the studied great tit population expected
198 from 1920 to 2100. From the ecological time series, the points in time when climate-driven
199 signals in food peak, laying and mismatch can be distinguished from noise (ToE) are identified.
200 On the second panel, great tit life cycle showing age-specific vital rates (survival S_i , recruitment
201 R_i) and the number of immigrants joining the population (Nim) as functions of mismatch, beech
202 crop and density N . On the third panel, forecasted vital rates and great tit population size from
203 1920 to 2100 according to expected mismatch under global warming and beech crop (two
204 scenarios). From the time series of vital rates and population sizes, the points in time when
205 climate-driven signals in vital rates (ToE_{vital}) and population size (ToE_{pop}) can be distinguished
206 from noise are identified.

207
208 **Fig. 2. Caterpillar peak dates, great tit laying dates, and mismatch forecasted under global**
209 **warming in the studied great tit population between 1920 and 2100.** Each line corresponds to
210 one climate scenario (40 in total), and the black line corresponds to the mean. Vertical dotted
211 lines indicate the historical period (1922-1950), horizontal line indicates the lower bound of the
212 66% interval during that period. Vertical red line corresponds to the time of emergence (ToE). In
213 thick blue, annual observed values between 1985 and 2020.

214
215 **Fig. 3. Times of Emergence (ToE) from caterpillar peak dates to population size in the**
216 **Hoge Veluwe great tit population.** Columns show the ToE for the two scenarios of beech crop
217 production (scenario 1: decreasing production by 2100; scenario 2: increasing production) for the
218 different levels of biological organization (in rows). In red, ToE when only climate uncertainty is
219 accounted for, and in grey ToE when all sources of ecological uncertainties are accounted for.

220

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315

316 **Methods**

317

318 **General overview**

319

320 To detect climate signals cascading through levels of biological organization, we build a
321 reproducible three-step approach (Fig. S1). First, long-term data should be collected from trait
322 values, to vital rates and population size. In parallel, environmental variables should be available.
323 Different methods can be used to estimate annual vital rates and population size when the
324 detection probability is lower than 1, e.g. capture-recapture models or integrated population
325 models (IPM). When the detection probability equals to 1, other methods such as population
326 census or generalized linear models can be used. Second, the effects of environmental covariates
327 on annual variation in trait values, vital rates and population size is assessed. This can be done
328 using linear mixed models (see methods section). Third, these established relationships permit
329 projecting time series of trait values, vital rates and population size under various environmental
330 scenarios in the past and in the future to quantify the time of emergence (Fig. S1) by linking
331 ecological models to climate models.

332

333 Our methodological approach is divided into several objectives:

334 (1) Our first objective is to determine the point in time when climate-driven signals in
335 caterpillar peak dates timing can be distinguished from noise ($ToE_{caterpillar}$).

336 (2) Our second objective is to determine the point in time when climate-driven signals in
337 great tit laying dates can be distinguished from noise (ToE_{laying}).

338 (3) Our third objective is to determine the point in time when climate-driven signals in
339 mismatch (between laying dates and food peak) can be distinguished from noise
340 ($ToE_{mismatch}$).

341 (4) Our fourth objective is to determine the point in time when climate-driven signals in vital
342 rates can be distinguished from noise (ToE_{vital} for each age-specific vital rate).

343 (5) Our fifth objective is to determine the point in time when climate-driven signals in
344 population can be distinguished from noise (ToE_{pop}).

345

346 To achieve objectives 1-3, we use functional relationships linking caterpillar peak dates, laying
347 dates and mismatch to temperatures¹⁶. To achieve objectives 4-5, we built an IPM to estimate
348 annual age-specific vital rates. We then estimated the functional relationships between
349 environmental variables and vital rates using linear mixed models. Finally, to project the great tit
350 population dynamics from 1920 to 2100, we simulated two beech crop production scenarios.

351

352 **Study site and data collection**

353

354 The studied population is located at Hoge Veluwe National Park in the Netherlands
355 ($52^{\circ}02'N$, $5^{\circ}51'E$), a wood of 171 ha. Great tits (*Parus major*) are short-lived small passerine
356 birds, abundant in European gardens and woodlands and, in the Netherlands, not migratory. They
357 are cavity-nesters and readily accept nest boxes as nesting sites, making it possible to monitor the
358 entire breeding population. They produce one or two clutches each year³⁹. In the study area,
359 very few females bred in natural cavities and most of them bred in nest boxes⁴⁰. The population
360 is open to immigration and emigration¹¹.

361 The data used in this study were collected between 1985 and 2020. Nest boxes were
 362 visited during the breeding season and laying dates were recorded (1st egg laid). In addition,
 363 three types of demographic data were recorded. First, the total number of breeding females (C_t).
 364 As most females start to breed at one year of age, the breeding population size is a good proxy
 365 for the total number of females⁴¹. Second, fledglings were marked with a uniquely numbered
 366 leg-ring, ringed mothers identified and unringed mothers given a ring to allow for future
 367 identifications. These unringed mothers were assumed to have immigrated into the population
 368 during the year in question. The following year, they are then considered to be local females.
 369 Overall, 2,204 breeding females of known age (local and immigrant) were monitored, providing
 370 capture-recapture (CMR) data of known age females. We grouped the breeding birds of known
 371 age into four age classes: 1, corresponding to the first year of breeding (i.e., second calendar year
 372 of life); 2, corresponding to the second year of breeding; 3 corresponding to the third year of
 373 breeding; and 4, which groups breeding females in their fifth calendar year of life and older.
 374 Third, ringed fledglings were recorded as recruited to the breeding population if they were
 375 caught breeding in a subsequent year. From the monitoring of breeding females of known age,
 376 we reported for each year t the observed number of breeding females in age class i ($B_{i,t}$) and also
 377 the observed number of locally recruited females produced per age class i ($J_{i,t}$). In total, this type
 378 of demographic data based on reproductive success consisted of 3,675 breeding events.
 379

380 Environmental data collection: food peak, mismatch, beech crop index and 381 temperatures

382
 383 Between 1985 and 2020 (except 1991), annual peak dates of caterpillar biomass
 384 (hereafter food peak) were determined⁴². The annual mismatch corresponded to the difference in
 385 mean laying date for great tits minus the food peak plus 33. These 33 days accounted for
 386 incubation duration and assumed that nestlings have the highest energy demand 10 days after
 387 hatching¹⁶. In addition to caterpillars, beech mast is an important food resource for great tits,
 388 especially during winter when other resources are scarce. It is also indicative of seed production
 389 of other tree species^{14,40}. The beech crop index (BCI), measured as the net weight of all nuts per
 390 m², was recorded annually as a three-level index (1, 2 or 3).

391 Annual temperatures were recorded. Previous work showed that laying dates in this great
 392 tit population depended on spring temperatures from 11 March to 20 April (hereafter $Temp_{\text{laying}}$),
 393 whereas temperatures from 6 March to 14 May had the strongest influence on food peaks
 394 (hereafter $Temp_{\text{caterpillar}}$)¹⁶. We thus recorded mean daily temperatures during these two time
 395 windows. We standardized $Temp_{\text{laying}}$ and $Temp_{\text{caterpillar}}$ with the mean and the variance of
 396 $Temp_{\text{laying}}$ and $Temp_{\text{peak}}$ observed during this period, so $Temp_{\text{laying}}$ and $Temp_{\text{caterpillar}}$ were
 397 transformed as z-scores. Temperature data were obtained from the De Bilt station of the KNMI
 398 (Royal Dutch Meteorological Institute), less than 50 km from the Hoge Veluwe field site.
 399

400 Objective 1: Forecasting food peak and estimating $ToE_{\text{caterpillar}}$

401 In this population, food peak dates (in Julian date) are linked to temperatures
 402 ($Temp_{\text{caterpillar}}$) through this relationship¹⁶:

$$403 \quad \text{food peak} = 138.379 \text{ (se: 0.629)} - 7.162 \text{ (se: 0.629)} \times Temp_{\text{caterpillar}} + 3.719$$

404 Eqn. 1

405 From this relationship, we estimated past (1920-2019) and future (2020-2100) food peak dates
406 according to the RCP 8.5 climate scenario that considers no policy intervention. This scenario
407 brings together 40 ensemble members diagnosing the influence of internal climate variability on
408 projections¹⁵, and it is the preferred choice for assessing climate change impacts risks
409 throughout the mid-century⁴³. The mean and the standard deviation over 1985-2020 of all
410 members were used to transform temperatures ($Temp_{caterpillar}$) into z-scores. Thus, the mean and
411 the standard deviation used for standardizing each of the members was the mean of means and
412 the mean of standard deviations calculated for each member. Such a rescaling allowed observed
413 temperatures in the study site and climate scenarios (on average across all 40 of them) to be
414 aligned between 1985 and 2020 so that they had the same mean and variance. From Eqn. 1, we
415 performed 100 simulations, parameters in the equation being drawn from normal distributions.
416 This resulted in 100 simulations per member, that is 4,000 simulations from 1920 to 2100. This
417 gave us expected food peak dates when all sources of ecological uncertainties were accounted
418 for, including parameter uncertainty and process variance corresponding to unexplained temporal
419 variation in parameters beyond that explained by climate.

420 After having visually controlled for a good match between observed food peak dates and
421 predicted dates (period 1985-2020, Figure 2), we selected an historical time window during
422 which food peak dates were stable over time (1922-1950, slope of the regression between food
423 peak dates and years during this time window: 0.032 (SE: 0.025)). We computed the lower
424 bound ($LB_{caterpillar}$) of the 66% prediction interval for food peak dates during this historical
425 period, and determined the point in time when the upper bound ($UB_{caterpillar}$) of the 66%
426 prediction interval for food peak dates became lower than $LB_{caterpillar}$. This point corresponded to
427 the time of emergence for food peak ($ToE_{caterpillar}$). In addition, we forecasted food peak dates but
428 we only accounted for climate uncertainty in the projections. To do so, we turned off standard
429 errors and σ (the last term) in Eqn. 1 to obtain 40 projections of food peak dates from 1920 to
430 2100, i.e. one projection per member.

431

432 **Objective 2: Forecasting laying dates and estimating ToE_{laying} (= ToE_{trait})**

433 We replicated the same procedure for laying dates. In this population, laying dates (in
434 Julian date) are linked to temperatures ($Temp_{laying}$) through this relationship¹⁶:

435
$$laying\ date = 110.980 (se: 0.582) - 4.947 (se: 0.590) \times Temp_{laying} + 3.493 \quad Eqn. 2$$

436 We estimated the expected annual laying dates between 1920 and 2100 according to the RCP 8.5
437 climate scenario, with all sources of uncertainty, and when only climate uncertainty was
438 accounted for. We selected an historical time window during which laying dates were stable over
439 time (1922-1950, slope of the regression between laying dates and years during this time
440 window: 0.019 (SE: 0.017)), and we identified the time of emergence for laying dates (ToE_{laying}).

441

442 **Objective 3: Forecasting mismatch and estimating $ToE_{mismatch}$**

443

444 We then calculated the mismatch between laying dates and food peak from 1920 to 2100
445 as the difference in expected annual laying dates minus the expected annual food peak plus 33¹⁶.
446 This was done for the 4,000 simulations accounting for all sources of uncertainties, and for the

447 40 simulations accounting for climate uncertainty only. In both cases, we identified the time of
448 emergence for mismatch ($\text{ToE}_{\text{mismatch}}$).

449

450

451 Objectives 4-5: Forecasting vital rates and population dynamics and estimating
452 $\text{ToE}_{\text{vital}}$ and TOE_{pop}

453

454 1- Estimating annual age-specific vital rates and densities

455 For populations with a recapture rate of 1, population census can be used as a proxy of
456 population size, and survival rates can simply be estimated using generalized linear model with
457 binomial link function, based on whether or not the individual has been observed. Here, we used
458 an integrated population model (IPM) to obtain accurate and precise estimates of annual
459 population size and age-specific vital rates. Even if the recapture probability is high on the study
460 site¹¹, still not all females may be recaptured, resulting in biased estimates of vital rates and
461 number of individuals. There was also a possibility of double counts, for instance if one female
462 has produced two broods but was only identified in one of them (because she has deserted one of
463 the clutches), and a possibility that some clutches are missed (because females have bred in
464 natural cavities). To estimate age-specific demographic rates and density while accounting for
465 these issues, we integrated the recorded number of breeding females (C_t), CMR data of females
466 of known age, and data on reproductive success (i.e., $B_{i,t}$ and $J_{i,t}$) into an IPM³⁰ (Figure S2).
467 This framework allowed us to obtain the posterior median of age-specific vital rates (survival $S_{i,t}$,
468 recruitment $R_{i,t}$), the number of local (N_{local}) and immigrant (N_{im}) breeding females in each age
469 class N_i and total N (total density) for each year t with improved precision and free of observation
470 error^{29-32,44}. The joint analysis of these three datasets thus allowed us to account for observation
471 error associated with the recorded number of counted breeding females⁴⁵. It also allowed us to
472 account for the incomplete information on age structure in the monitoring data (e.g. some
473 females are of unknown age), for imperfect detection (e.g. recapture probability is not 1) and for
474 demographic stochasticity⁴⁶.

475

476 The likelihood of the IPM corresponds to the product of the likelihoods of the three
477 different datasets, namely CMR data, reproductive success data and population counts⁴⁴. For
478 CMR data of breeding females of known age, we used the Cormack-Jolly-Seber model⁴⁷ which
479 allows estimation of annual survival between age class i and $i+1$ ($S_{i,t}$) and annual recapture (p_t)
480 probabilities. For data on reproductive success, the observed number of daughters locally
481 recruited per age class i ($J_{i,t}$) is Poisson distributed with $J_{i,t} \sim \text{Poisson}(B_{i,t} \times R_{i,t})$, where R is
482 the recruitment rate of females of age class i at year t . For the population count data, we used a
483 state-space model⁴⁸ that consisted of a process model describing how the population size and
484 structure changed over time as well as an observation model²⁹. We considered a pre-breeding
485 age-structured model with the four pre-defined age classes.

486 The model was fitted within a Bayesian framework using NIMBLE (version 0.9.1)⁴⁹. We
487 ran four independent chains with different starting values for 200,000 MCMC iterations, with a
488 burn-in of 150,000 iterations, thinning every 100th observation and resulting in 2,000 posterior
489 samples. We used the Brooks and Gelman diagnostic \hat{R} to assess the convergence of the
490 simulations and used the rule $\hat{R} < 1.1$ to determine whether convergence was reached⁵⁰. For a
491 full description of the IPM, the priors used and the R code to fit the IPM, see Gamelon et al.⁵¹.

492
493

2- Linking vital rates to BCI, mismatch and density

494 The IPM was used to estimate annual age-specific vital rates and densities. Once these
495 were estimated, we linked annual age-specific vital rates and annual number of immigrants
496 joining the local population as response variables to annual density, BCI and mismatch (from
497 1985 to 2020) (see life cycle on Fig. 1). The same approach has been done in previous studies⁵²⁻
498⁵⁴ that first used an IPM to estimate vital rates and density, and then used regressions to link vital
499 rates to density and/or environmental covariates. As the annual vital rates and densities are
500 estimated in the IPM model, they are not obscured by sampling variance and observation errors
501 and thus this approach does not lead to spurious detection of density dependence^{51,55,56}. In detail,
502 survival between two successive breeding seasons t and $t+1$ could be affected by BCI at time t .
503 Therefore, we linked age-specific survival rates $S_{i,t}$ (on a logit-scale) to BCI at t . Because the
504 effect of BCI on survival may be age-specific, we included the interaction between age and BCI.
505 To account for the non-independence of the survival rates among age classes of a given year, we
506 included the year as a random effect. The linear-mixed model (LMM) took the following form:

$$507 \quad \text{logit}(S_{i,t}) = \mu + \beta_{1,i} a + \beta_2 BCI_t + \beta_{3,i} [a \times BCI_t] + \beta_{year} year + \varepsilon_{S_{i,t}} \quad \text{Eqn. 3}$$

508 where μ is the intercept, a is the age class (i.e. 1, 2, 3 and 4), β are the regression coefficients,
509 $year$ is the random effect and $\varepsilon_{S_{i,t}}$ corresponds to the residuals of the LMM. Note that the LMM
510 was weighted by the inverse of the variance of the survival rates (on a logit-scale) to account for
511 the uncertainty associated with the survival rates estimated with the IPM.

512 The recruitment rate of a given breeding season t could be affected by the number of
513 breeding females at time t in the population (density at t) and by BCI at time t . Therefore, we
514 linked the age-specific recruitment rates $R_{i,t}$ (on a log-scale) to density at t N_t and to BCI at t .
515 Because the effect of BCI and density on recruitment may be age-specific, we included the
516 interaction between age and BCI and between age and density. The LMM took the following
517 form:

$$518 \quad \log(R_{i,t}) = v + \beta_{1,i}' a + \beta_2' BCI_t + \beta_3' N_t + \beta_{4,i}' [a \times BCI_t] + \beta_{5,i}' [a \times N_t] + \beta_6' year + \\ 519 \quad \varepsilon_{R_{i,t}} \quad \text{Eqn. 4}$$

520 where v is the intercept, a is the age class, β' are the regression coefficients, and $\varepsilon_{R_{i,t}}$ corresponds
521 to the residuals of the LMM. As done for survival rates, the LMM was weighted by the inverse
522 of the variance of the recruitment rates (on a log-scale) to account for the uncertainty associated
523 with the recruitment rates estimated with the IPM.

524 The number of immigrants joining the population during the breeding season $t+1$ may be
525 influenced by BCI and mismatch as well as the number of local breeding females N_{local} at t .
526 Therefore, we linked the number of immigrant breeding females Nim_{t+1} to the number of local
527 breeding females $N_{local,t}$, BCI and mismatch at t using a generalized linear model (GLM) with
528 Poisson distribution:

$$529 \quad Nim_{t+1} = \eta + \beta_{I,1} BCI_t + \beta_{I,2} Mism_t + \beta_{I,3} N_{local,t} + \varepsilon_{I_{t+1}} \quad \text{Eqn. 5}$$

530 where η is the intercept, β_I are the regression coefficients, and $\varepsilon_{I_{t+1}}$ corresponds to the residuals
531 of the GLM.

532
533

3- Building the population model

534 For given conditions of BCI, mismatch and densities, age-specific survival and

535 recruitment rates as well as the number of immigrants joining the local population may be
 536 simulated (hereafter denoted $S_{sim\ i,t}$, $R_{sim\ i,t}$ and $Nim_{sim,t+1}$). As a result, the number of breeding
 537 females in the population $N_{sim,t}$ may be simulated.

538 In detail, the total number of breeding females in the population at time $t+1$ $N_{sim,t+1}$
 539 corresponded to the sum of breeding females in each age class i $N_{sim\ i,t+1}$ at time $t+1$ (Figure 1):

$$540 \quad N_{sim,t+1} = N_{sim\ 1,t+1} + N_{sim\ 2,t+1} + N_{sim\ 3,t+1} + N_{sim\ 4,t+1} \quad \text{Eqn. 6}$$

541 (i) As most of the immigrant breeding females were females of age class 1, we assumed that
 542 $N_{sim\ 1,t+1}$ corresponded to the sum of the number of daughters that were locally recruited into the
 543 population $n_{sim,t+1}$ (i.e. produced by the breeding females of each age class) and also of the
 544 number of immigrants $Nim_{sim,t+1}$ arriving into the population:

$$545 \quad N_{sim\ 1,t+1} = n_{sim,t+1} + Nim_{sim,t+1} \quad \text{Eqn. 7}$$

546 $n_{sim,t+1}$ was modeled using a Poisson distribution to include demographic stochasticity:

$$547 \quad n_{sim,t+1} \sim \text{Poisson}(N_{sim\ 1,t} \times R_{sim\ 1,t}) + \text{Poisson}(N_{sim\ 2,t} \times R_{sim\ 2,t}) + \text{Poisson}(N_{sim\ 3,t} \times$$

$$548 \quad R_{sim\ 3,t}) + \text{Poisson}(N_{sim\ 4,t} \times R_{sim\ 4,t}) \quad \text{Eqn. 8}$$

549 (ii) $N_{sim\ 2,t+1}$ corresponded to the number of females of age class 1 that survived from time t to
 550 time $t+1$, and was modeled using a binomial process to include demographic stochasticity:

$$551 \quad N_{sim\ 2,t+1} \sim \text{Bin}(N_{sim\ 1,t}, S_{sim\ 1,t}) \quad \text{Eqn. 9}$$

552 (iii) $N_{sim\ 3,t+1}$ and $N_{sim\ 4,t+1}$ corresponded to the number of females in the previous age class that
 553 survived from time t to time $t+1$:

$$554 \quad N_{sim\ 3,t+1} \sim \text{Bin}(N_{sim\ 2,t}, S_{sim\ 2,t}) \quad \text{Eqn. 10}$$

$$555 \quad N_{sim\ 4,t+1} \sim \text{Bin}(N_{sim\ 3,t}, S_{sim\ 3,t}) + \text{Bin}(N_{sim\ 4,t}, S_{sim\ 4,t}) \quad \text{Eqn. 11}$$

556 Therefore, for given conditions of BCI, mismatch and densities, $S_{sim\ i,t}$, $R_{sim\ i,t}$ and $Nim_{sim,t+1}$ may
 557 be computed. We accounted for sources of environmental stochasticity due to processes other
 558 than covariates included in the model with a covariance matrix Σ of “random *year* effect + $\varepsilon_{S_{i,t}}$ ”
 559 and “random *year* effect + $\varepsilon_{R_{i,t}}$ ”. The covariance matrix was estimated and new residuals were
 560 generated from a multivariate normal distribution with covariance matrix equal to Σ . Then, N_{sim}
 561 $_{1,t+1}$, $N_{sim\ 2,t+1}$, $N_{sim\ 3,t+1}$ and $N_{sim\ 4,t+1}$, functions of $S_{sim\ i,t}$, $R_{sim\ i,t}$ and $Nim_{sim,t+1}$ may be computed and
 562 finally, the density $N_{sim,t+1}$ may be simulated.

563

564 4- Forecasting vital rates and population size and estimating ToE_{vital} and ToE_{pop}

565

566 Using the age-structured population model described above, that accounted for the effects
 567 of BCI, mismatch and density on vital rates, we forecasted the great tit population under two
 568 simulated beech crop production scenarios.

569

570 a) Forecasting beech crop index under two scenarios

571

572 BCI is a categorical variable with three levels (1 (low), 2 (medium) and 3 (high
 573 production)). We simulated two extreme scenarios of beech crop production by 2100.

574 In the first scenario, we simulated a decrease in beech crop production in the future. The
 575 probability of having a year of low production (P(BCI=level 1)) increased over time, from 0.005
 576 in 1920 to 0.9 in 2100. The probability of having a year of medium production (P(BCI=level 2))
 577 was set to 0.1, the average observed between 1985 and 2020. The probability of having a year of
 578 high production (P(BCI=level 3)) corresponded to $1 - P(\text{BCI}=\text{level 1}) - P(\text{BCI}=\text{level 2})$ and thus
 579 ranged from 0.895 to 0 from 1920 to 2100 (Extended Data Fig. 3, left panel). For each year, we

580 performed 100 draws from a three-category multinomial distribution with probabilities
581 $P(\text{BCI}=\text{level } 1)$, $P(\text{BCI}=\text{level } 2)$, $P(\text{BCI}=\text{level } 3)$. This resulted in 100 simulated time-series of
582 BCI between 1920 and 2100. These projections of BCI expressed as levels (1, 2 and 3) were
583 used afterwards to project the great tit population size.

584 In the second scenario, we simulated an increase in beech crop production in the future.
585 The probability of having a year of high production ($P(\text{BCI}=\text{level } 3)$) increased over time, from
586 0.005 in 1920 to 0.9 in 2100. The probability of having a year of medium production
587 ($P(\text{BCI}=\text{level } 2)$) was set to 0.1. The probability of having a year of low production ($P(\text{BCI}=\text{level } 1)$)
588 corresponded to $1 - P(\text{BCI}=\text{level } 2) - P(\text{BCI}=\text{level } 3)$ and thus ranged from 0.895 to 0 from
589 1920 to 2100 (Extended Data Fig. 3, right panel). For each year, we performed 100 draws from a
590 three-category multinomial distribution with probabilities $P(\text{BCI}=\text{level } 1)$, $P(\text{BCI}=\text{level } 2)$,
591 $P(\text{BCI}=\text{level } 3)$. This resulted in 100 simulated time-series of BCI between 1920 and 2100.

592

593 b) Forecasting vital rates and great tit population size

594

595 Using trajectories of mismatch expected from 1920 to 2100 under the RCP 8.5 scenario
596 that accounted for all sources of uncertainties (see objective 3) and simulated trajectories of BCI
597 simulated according to the first scenario (decreasing beech crop production) as well as the age-
598 specific densities in 1987 estimated with the IPM, we simulated 100 stochastic trajectories in
599 vital rates and population sizes per ensemble member from 1920 to 2100, resulting in a total of
600 4,000 stochastic trajectories. We computed the 95% and 66% prediction intervals of the
601 predicted age-specific vital rates, number of immigrants and total population size. We then
602 selected an historical time window during which population size was stable over time (1922 –
603 1950, slope of the regression between population size and years during this time window: 0.092
604 (SE: 0.217)) and estimated the time of emergence for population size (ToE_{pop}) and vital rates
605 ($\text{ToE}_{\text{vital}}$). In addition, we forecasted the great tit population but accounted for climate uncertainty
606 only in the projections. To do so, we used trajectories of mismatch expected from 1920 to 2100
607 that accounted for climate uncertainty only, and turned off stochasticity in Eqn. 8-11 as well as
608 the covariance matrix, to obtain 40 projections of age-specific vital rates and population sizes
609 from 1920 to 2100, i.e. one projection per member.

610 We replicated the exact same procedure with trajectories of BCI simulated according to
611 the second scenario (increasing beech crop production) to obtain forecasted time-series of vital
612 rates and population size.

613

614 All of these analyses were performed with R software⁵⁷.

615

616 **Data availability:** Data used in the analysis are available at

617 https://github.com/marleng/ToE_greattit⁵⁸.

618 Data on past observed beech crop index, past observed mismatch between laying dates and food
619 peaks, expected spring temperature according to the RCP 8.5 scenario, past observed annual age-
620 specific population size and vital rates and their variance are provided.

621

622 **Code availability:** R code used for the analysis is available at

623 https://github.com/marleng/ToE_greattit⁵⁸.

624

626 **Methods-only references:**

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