Age-dependent phenological plasticity in a wild bird

Suzanne Bonamour, Luis-miguel Chevin, Denis Réale, Céline Teplitsky, A. Charmantier

► To cite this version:

Suzanne Bonamour, Luis-miguel Chevin, Denis Réale, Céline Teplitsky, A. Charmantier. Age-dependent phenological plasticity in a wild bird. *Journal of Animal Ecology*, 2020, 89 (11), pp.2733-2741. 10.1111/1365-2656.13337 . hal-02998152

HAL Id: hal-02998152

<https://hal.science/hal-02998152>

Submitted on 23 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Age-dependent phenological plasticity in a wild bird

Suzanne Bonamour¹, Luis-Miguel Chevin¹, Denis Réale², Céline Teplitsky^{1*} and Anne Charmantier^{1*}

*Co-last authors

Author's affiliation:

¹ CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France.

² Université du Québec à Montréal, Département des sciences biologiques, Case postale 8888, succursale Centre-ville, Montréal (Québec), H3C 3P8, Canada.

Author for correspondence:

Suzanne Bonamour

E-mail: suzannebonamour@protonmail.com

Abstract

1. Life-history traits are often plastic in response to environmental factors such as temperature or precipitation, and they also vary with age in many species. Trait variation during the lifetime could thus be partly driven by age-dependent plasticity in these traits.

2. We study whether plasticity of a phenological trait – the egg-laying date – with respect to spring temperature, varies with age, and explore whether this variation relates to changes in breeding success throughout the life cycle.

3. We use data from a four-decade long-term monitoring of a wild population of blue tits in Corsica to estimate age-dependent plasticity of reproductive phenology and annual reproductive success.

4. We show that both laying date plasticity and annual reproductive success vary with age: young and old females are less plastic, and fledge fewer offspring, than middle-age females. Furthermore, in contrast to young and prime-age females, in old females fledging success does not depend on laying date.

5. Phenological plasticity is a major mechanism for coping with rapid environmental variation. Our results suggest that understanding its role in adaptation to climate change and population persistence requires integrating the age structure of the population.

Key words: Phenotypic plasticity, Laying date, Phenology, Aging, Passerines, Wild birds

40 Introduction

41 Phenotypic plasticity – the capacity of a given genotype to express different phenotypes according to
42 environmental conditions (Pigliucci, 2001) – is a widespread phenomenon in nature (DeWitt &
43 Scheiner, 2004). Theoretical and empirical studies highlight the importance of phenotypic plasticity for
44 population persistence (e.g. Ashander et al., 2016; Chevin et al., 2010; Reed et al., 2011). When
45 plasticity is adaptive, it may allow the population mean phenotype to track an environment-dependent
46 phenotypic optimum, thus minimizing the impact of environmental change on mean fitness and
47 population growth. This is especially true for phenological traits, which determine the timing of key
48 life history events such as reproduction, dormancy/diapause, or dispersal, synchronizing these events
49 with the optimal timing set by a seasonal – and often also noisy – environment (e.g. Visser, 2008).
50 Phenological traits have been shown to represent a major phenotypic response to rapid climate change
51 (Davis et al., 2005; Parmesan & Yohe, 2003; Radchuk et al., 2019; Visser & Both, 2005; Walther et al.,
52 2002). It is also increasingly clear that plastic changes contribute a large proportion of observed
53 phenotypic change in the wild (e.g. Gienapp et al., 2007; Merilä & Hendry, 2014; Walther et al., 2002),
54 especially for phenological traits (Anne Charmantier & Gienapp, 2014; Vedder et al., 2013).

55 Life-history traits (e.g. fecundity), in addition to often being phenotypically plastic, also vary
56 with age in many iteroparous species. Empirical studies in vertebrates commonly show patterns of
57 age-dependent reproductive performance, with increasing annual reproductive success in the
58 beginning of life, followed by maximal reproductive performance in middle age, and finally, a
59 decreasing success due to reproductive senescence (e.g. Balbontín et al., 2007; Clutton-Brock, 1988;
60 Dingemanse et al., 2020; Warner et al., 2016). Since plastic phenology is a strong driver of reproductive
61 performance in many species, notably in birds inhabiting temperate forests (e.g. Marrot et al., 2018;
62 Perrins & McCleery, 1989), it is likely that variation with age of phenological reaction norms underlies
63 age-dependent patterns in reproductive success to some extent. If reaction norms vary with age, then

understanding the role of plasticity in adaptation to rapid environmental change and population persistence requires integrating the age structure of the population (see e.g. van de Pol et al., 2012).

Theoretical studies on the evolution of age-dependent plasticity are still rare. They have focused so far on traits that are established once during development (developmental plasticity, according to West-Eberhard, 2003) in binary environments, and predict a decrease of plasticity with age (e.g. Fawcett & Frankenhuis, 2015; Fischer et al., 2014; Stamps & Krishnan, 2017). Formal theoretical predictions are still missing for traits that change repeatedly in life (labile traits), and with continuous expression under continuous environmental variation. But the general mechanisms responsible for an effect of senescence on plasticity, such as the decrease of selection strength with age (Charlesworth, 1993; Hamilton, 1966; Monaghan et al., 2008; Williams, 1957), should lead to a similar decrease in plasticity as individuals get older.

Within-individual variation of plasticity over the lifetime of individuals has been highlighted in some experimental studies, mainly in behavioural traits (e.g. Atwell & Wagner, 2014; Ericsson et al., 2016), with highest plasticity in juveniles or young adults followed by decreasing plasticity with age, thus corroborating theoretical predictions. However, evidence is scarce for age-specific plasticity in wild populations. Araya-Ajoy & Dingemanse (2016) compared the seasonal plasticity of aggressiveness in great tits (*Parus major*) between two age classes, and found that first-year-old breeders showed higher seasonal plasticity than older birds, also aligned with theoretical predictions. A study on phenological trait plasticity in superb fairywrens (*Malurus cyaneus*) demonstrated that the variation of moult timing with rainfall changed with age (van de Pol et al., 2012). Contrary to theoretical predictions, in this study older birds were more plastic than younger ones. Overall, the scarce empirical evidence means we still poorly understand the origin of age-dependent plasticity of labile phenotypic traits over a lifetime. The study of age-specific variation in plasticity in wild populations is an arduous task because of the combined challenges of studying phenotypic plasticity and senescence (Nussey et al., 2013; Nussey, Wilson, et al., 2007), both of which demand a long-term study with individual

marking and repeated measures on the same individuals. In addition, plasticity estimation requires identifying the main environmental cue(s) explaining within-individual phenotypic variation (Gienapp, 2018). These challenges explain why age-specific variation of plasticity has been widely neglected so far in empirical studies.

We studied age-specific plasticity of a phenological trait, the egg-laying date, in a wild blue tit population. We used linear mixed models to explore the relationship between age-related plasticity and annual reproductive success across female lifetime. In this species, as in most temperate passerines, laying date varies plastically among years in response to spring temperature (e.g. Porlier et al., 2012). This variation allows birds to synchronize their reproductive period with the timing of maximal abundance of caterpillars, which constitute the main nutritive resource for nestlings (Blondel et al., 1991). Annual reproductive performances also vary with age in blue tits: young birds have low annual reproductive success (partially) due to inexperience (Gienapp & Brommer, 2014), while old individuals suffer from reproductive senescence (Auld & Charmantier, 2011). As a result, reproductive success increases and then decreases with age, with most traits peaking around 3 years of age. Since laying date is a plastic trait in response to temperature, age-related variation of reproductive timing and annual reproductive success could be associated with age-specific laying date plasticity with temperature. We expected a nonlinear variation of laying date plasticity with age. Plasticity should first increase in the early years of life, because of maturation and learning processes as suggested by an empirical study of Grieco et al. (2002). It should then decrease in old ages, because senescence is generally expected to lead to an overall decrease in performance. We expected similar quadratic age-specific variation in reproductive success.

Materials & Methods

Species and data collection

We used a long-term study (initiated by Jacques Blondel in 1975) of a wild Mediterranean population of Blue tit (*Cyanistes caeruleus ogliastreae*), a small insectivorous and cavity-nesting passerine. Breeding

114 dates were collected every spring on the study site. The population is on the island of Corsica, in an
115 evergreen forest (E-Pirio population, 42°34'N, 08°44'E) dominated by holm oaks (*Quercus ilex*) (see
116 reviews on the long-term study in Blondel et al., 2006; Charmantier et al., 2016). Blue tits bred in 205
117 nest boxes (natural cavities are rare in this forest, Charmantier, pers. com.), which were monitored
118 weekly from March to June to record laying date, clutch size and reproductive success. Breeding birds
119 and nestlings were individually marked with a unique numbered metal ring.

120 We restricted our analyses to first broods of the season only (second broods represent less
121 than c. 1% of the clutches). Age was estimated based on birth year for individuals born in nest boxes,
122 or on plumage patterns for immigrants (see Supporting Information 1 Figure S1 for the number of
123 females in each age class). Based on plumage patterns, captured immigrant females can be classified
124 either as one year old (juvenile plumage), or two years or older (mature plumage pattern). In the
125 present dataset, the exact age was known for c. 60% of females (corresponding to locally born and
126 immigrant females first captured at one year old), while we used minimum age for the remaining 40%
127 (corresponding to immigrant females first captured at two years or older). Dispersal in blue tits mainly
128 happens before the first breeding event (i.e. natal dispersal, Greenwood & Harvey, 1982; Matthysen
129 et al., 2010), and the mortality rate in the focal population was high (about half of the individuals in
130 each age class die every year, Dubuc-Messier et al., 2016). Hence the recruitment in the focal nest-box
131 area of birds older than two years was likely to be uncommon (see Supporting Information 1 Figure
132 S1). This suggests that allocating a minimum age of two years to immigrant females displaying adult
133 plumage should lead to a low error rate in age estimation, as we confirmed by a sensitivity analysis
134 (see Supporting Information 2).

135 Overall, the dataset contained 1696 laying date observations from 1976 to 2017, for 854
136 identified females (Supporting Information 1 Figure S1 and Table S1, Bonamour et al., 2020). The
137 temperature cue was the average daily temperature between 31st March and 7th May, which is the

period most correlated with inter-annual laying date variation at the population scale according to sliding-window analyses (Bonamour et al., 2019).

Statistical analyses

We estimated age-dependent laying date plasticity in response to temperature using the following linear mixed model (e.g. Nussey, Kruuk, et al., 2007),

$$LD_{ij} = \mu + \alpha_1 T_j + \alpha_2 A_{ij} + \alpha_3 A_{ij}^2 + \alpha_4 (T_j A_{ij}) + \alpha_5 (T_j A_{ij}^2) + \alpha_6 ALR_i + ind_i + year_j + \varepsilon_{ij} \text{ (model 1)}$$

where the laying date LD ($1 = 1^{\text{st}}$ January) of female i in year j is explained by several fixed effects: cue temperature T_j of year j (temperature was mean-centered across years), age A_{ij} and age-squared A_{ij}^2 of female i in year j (with age a continuous variable ranking from 1 to 9 years old). The terms $T_j A_{ij}$ and $T_j A_{ij}^2$ are interactions estimating respectively the linear and quadratic age dependence of plasticity in laying date with temperature. We controlled for female longevity by adding an effect of age at last reproduction of female i , ALR_i , modelling a selective disappearance effect on laying date variation (e.g. Bouwhuis et al., 2009). To account for the non-independence of data collected on the same female and the same year, we included female identity (ind_i) and year ($year_j$) as random effects. The final term in model 1 is the residual error term ε_{ij} . Avian laying date is expressed by females, but can also be seen as a trait shared by the two sexes as some male characteristics may influence the timing of reproduction (e.g. Brommer & Rattiste, 2008). However, in this population, a previous analysis detected no effect of male identity on breeding time (Auld & Charmantier, 2011) and we thus restricted analyses to female birds. We also confirmed that there was no difference between the population- and individual-level plasticity (i.e. variation in laying date with temperature was not driven

by between-female differences in reaction norm intercept across years), using the within-subject centering method (Supporting Information 3; van de Pol & Wright, 2009).

We estimated the effects of age and laying date on annual reproductive success ARS (approximated as the number of fledglings per breeding attempt) using the following generalized linear mixed model,

$$ARS_{ij} = \gamma + \beta_1 A_{ij} + \beta_2 A_{ij}^2 + \beta_3 LD_{ij} + \beta_4 (A_{ij} LD_{ij}) + ind_i + year_j + r_{ij} \quad (\text{model 2})$$

where annual reproductive success ARS_{ij} of female i in year j is explained by the female age A_{ij} and age-square A_{ij}^2 , the laying date LD_{ij} and the interaction between laying date and age ($A_{ij} LD_{ij}$). We included two random effects, female identity (ind_i) and year ($year_j$), and r_{ij} are residuals. Annual reproductive success was not normally distributed (see Supporting Information 1 Figure S2), we thus ran the model as a generalized linear mixed model with a Poisson distribution. Females with clutch manipulation and all other experiments that could affect reproductive success were removed from the data set for model 2, reducing the dataset to 1092 laying date observations for 667 identified females.

All statistical analyses were carried out using the software R (version 3.3.2, R Core Team, 2016), and performed in a Bayesian framework using a Markov Chain Monte Carlo estimation algorithm (R package MCMCglmm, Hadfield, 2010). For all random effects (including the residual variance), we used a weakly informative prior, corresponding to an inverse-Wishart $W^{-1}(\psi, \nu)$ distribution with ψ equal to the phenotypic variance of laying date (or ARS variance, depending on the model 1 or 2) divided by the number of estimated variance components. ν is the degree of belief in the prior and we tested the robustness of results to the prior specification using $\nu = 1, 0.2$ or 0.02 . The default Gaussian non-informative prior in MCMCglmm with mean zero and variance 10^8 was used for the fixed effects. Models were run for 1,010,000 iterations, including a burn-in period of 10,000 iterations. We ran three

chains which were sampled every 1000 iteration to avoid autocorrelation. The maximum autocorrelation between estimates was < 0.05 for fixed and random effects. Convergence of chains was tested using Gelman and Rubin's convergence diagnostic (Brooks & Gelman, 1998; Gelman & Rubin, 1992) and models converged well, with average Gelman's diagnostic $\hat{R} = 1.00$ for fixed and random effects, comparing chains from different priors.

Results

Laying date varied within a female's lifetime, in response to both temperature and age (Table 1). Laying date was earlier with warmer springs, with a median value of c. 3 days earlier every 1°C warmer (Table 1, Figure 1a&b). It also varied non-linearly with age, decreasing until age 4 and then increasing (Table 1, Figure 1a&c). Our results suggested that shorter-lived females tend to breed later, but note that the 95% credible interval in the posterior distribution of the *ARS* marginally included zero (Table 1, but see Supporting Information 2 Table S3).

We also found age-dependent plasticity in reproductive phenology. The response of laying date to temperature changed with age, as evidenced by the interaction between temperature and the linear age effect (Table 1). This resulted in reaction norm slopes getting steeper as female age increased, until c. 5 years old (Figure 1b&c). In addition, our results suggested that plasticity declines for older females (after 6 years old, Figure 1c); however small sample sizes for these late age classes resulted in large credible intervals (Table 1, Supporting Information 1 Figure S1). The largest difference in reaction norm slopes was between 1 year-old (i.e. yearling) and 5 year-old females: the estimated median slope of laying date reaction norm with respect to temperature was $-3.68 \text{ days}/^{\circ}\text{C}$ (± 0.002 , p -value $< 2.10 \times 10^{-16}$) for yearlings, and $-4.94 \text{ days}/^{\circ}\text{C}$ (± 0.001 , p -value $< 2.10 \times 10^{-16}$) for 5 year-old females (Figure 1b), leading to a median difference of c. $1.5 \text{ days}/^{\circ}\text{C}$ between both age classes.

Annual reproductive success also varied with female age (Table 2). Model 2 revealed a quadratic relationship between annual reproductive success and age, such that young and especially old females displayed lower annual reproductive success than middle-age females (Table 2, Figure 2a).

Annual reproductive success also decreased with laying date (Table 2, Figure 2b). There was no statistical evidence for an interaction between age and laying date (Table 2; preliminary analyses showed no evidence for an interaction between laying date and age-squared). Importantly, the relationship between laying date and reproductive success was negative for all ages except for females older than 5 years old (Figure 2b). Hence, despite low statistical power in old age classes (Supporting Information 1 Figure S1), these results suggest that reproductive success in old females was low independently of their laying date.

Discussion

To our knowledge, our study is the first to report age-dependent phenotypic plasticity of laying date with temperature. Laying date plasticity with spring temperature is a common pattern observed in many avian natural populations (e.g. Dunn, 2004; Visser et al., 2009). In temperate regions, this plasticity causes among-year variation in phenology, which allows synchronization between predators (birds) and their preys (in particular caterpillars, see e.g. Dunn, 2004; Van Noordwijk et al., 1995). Laying date variation with female age is likewise a well-known pattern in free-living as well as in controlled iteroparous animal populations (e.g. Auld & Charmantier, 2011; Nussey et al., 2008), although the senescent delay in avian breeding phenology was only revealed in the last two decades. Similarly to previous investigations (Auld & Charmantier, 2011), model 1 shows that young and old females lay later than middle-age birds (Table 1, Figure 1).

More importantly, model 1 also reveals changes in plasticity with age. The age dependence of laying date reaction norms is complex, as both the slope and intercept vary with female age (Table 1, Figure 1). This leads to a pattern whereby young and old females lay later on average (i.e. higher median reaction norm intercept), and the age-dependent reaction norm slope accentuates the phenological delay between young or old and middle-age females (Figure 1). For instance, in warm springs with temperature 1.5 °C higher than average, the resulting median laying date is ≈ 5 days earlier in 5-year-old than 1-year-old females (Figure 1b). This difference among age classes represents about

13% of the total phenotypic range in laying date in the entire dataset (c. 39 days), while the among-individual (averaged across years and environments) and among-year effects explain respectively about 28% (c. 11 days) and 36% (c. 14 days) of this range.

Under current environmental conditions, age-dependent laying date plasticity should not have extensive impacts on population dynamics and persistence in our short-lived passerine population, because females of 5 years and older represent only 8% of the total population (Supporting Information 1 Figure S1 and population annual adult survival probability of c. 0.5, Dubuc-Messier et al., 2016). However, warmer springs in the future should lead to higher among-individual variation of laying date, as the influence of age-dependent plasticity on laying date variation becomes more marked (assuming no evolutionary change of laying date reaction norm).

Our results seem consistent with theoretical models of age-dependent plasticity (e.g. Fawcett & Frankenhuis, 2015; Fischer et al., 2014; Stamps & Krishnan, 2017) despite substantial differences between our blue tit biological model and some assumptions of the theoretical models. As predicted by theoretical studies, plasticity decreased at old ages in our study population. However, the pattern was complex, as we observed quadratic variation of both laying date plasticity (Table 1, Figure 1) and annual reproductive success (Table 2, Figure 2). From a more mechanistic perspective, Fawcett & Frankenhuis (2015) highlight that age-dependent plasticity will evolve if there is variation across the lifetime of either i) cue reliability, ii) the relationship between fitness and the plastic response, or iii) constraints on the expression of phenotypic plasticity. First, we have no a priori reason to expect changes in cue reliability with female blue tit age: spring temperature should predict the caterpillar peak date independently of female age. However, the physiological ability to detect environmental cues such as temperature (Caro et al., 2013; Visser et al., 2009) or photoperiod (Dawson, 2008) may change with age. This could explain age-dependent plasticity, since the optimal reaction norm slope increases as a function of cue reliability (Gavrilets & Scheiner, 1993), but little is known about changes in perception abilities with age in birds. Second, the fitness benefits associated with laying date

plasticity may vary during female lifetime. For example, their foraging capacity may increase with age, leading to a reduced importance – for annual reproductive success – of the synchronisation between the peak of nutritive resources and bird reproductive timing in older females. In our population, such age-dependent fitness benefits of plasticity could not explain the increasing plasticity before 5 years old. However, the fitness advantage of earlier breeding seems to decrease in old ages (Figure 2b), which could lead to lower fitness benefits to being plastic and induce selection for reduced (assumed costly) plastic capacity in old female birds. Third, a learning process of plasticity early in life may explain variation in laying date plasticity. Grieco et al. (2002) showed that blue tits laid in the same period as their previous breeding season if they were supplied with additional food, but they laid earlier if they were short of nutritive resources. Such a pattern may explain increasing plasticity in young females, especially following warmer springs, when the caterpillar peak is earlier than the average. Finally, plasticity is expected to require resources, especially to acquire information to track environmental changes (Dewitt, 1998), which may lead to constraints on plastic capacity. Hence, yearlings may not have accumulated enough resources during their first winter to adequately modulate their laying date according to temperature, again especially in warmer years when breeding phenology is optimally early. In the same vein, old females suffering from reproductive senescence may not be able to display steeper plasticity because of lack of resources. Further investigations on the physiological conditions of young and old females are needed to better understand proximal causes of age-dependent plasticity.

To evaluate the fitness costs of a late laying date, which partially depends on a lack of plastic response to temperature, we analysed the relationships between laying date, age and a fitness component. We used an estimate of annual reproductive success – the number of fledglings – as fitness component. Results from model 2 and Figure 2 show that breeding too late decreases annual reproductive success for young and middle-age females but not for the oldest birds. In other words, plasticity of laying date, has no consequences on reproductive success of old females. This suggests that selection for plasticity could decrease with age in this population. Exploring whether the selection

on laying date reaction norms changes with age, including the possibility that selection on laying date across environments (i.e. selection depending on temperature) causes indirect selection on its plasticity (e.g. Ramakers et al., 2018; van Tienderen & Koelewijn, 1994) is an exciting perspective. However, such a study would require a data set much larger than ours based on 42 years of monitoring. A full understanding of these complex relationships between laying date, age and fitness would also require to investigate selection beyond fledging (e.g. through recruitment success) but also including lifetime reproductive success and/or survival, to integrate the potential fecundity-survival trade-offs.

Conclusion and perspectives

To conclude, this study reveals age-dependent plasticity of laying date in response to spring temperature in a wild blue tit population. Young and old females were less plastic than middle-aged females. Our results suggest that, unlike prime-age females, young females may have not reached their full reproductive capacities, while the older ones may no longer be subject to natural selection on laying date. Such age-dependent effects result in a quadratic variation of laying date plasticity. Considering the importance of plastic responses for population persistence in a rapidly changing world (Chevin et al., 2013; Reed et al., 2010), within-individual variability of plasticity has to be taken into account in studies of plasticity in the wild. Models of age-structured populations could help to comprehend how age-related plasticity impacts adaptation and population persistence. As chronic stress is known to speed up senescence (Hayward et al., 2009; Monaghan et al., 2008; Ricklefs, 2008), current global change could increase variation of plasticity with age, and its impact could be even stronger for phenological traits for which plasticity is an important component of response to climate change (Davis et al., 2005; Parmesan & Yohe, 2003; Radchuk et al., 2019; Visser & Both, 2005; Walther et al., 2002). We suggest that age-specific phenological plasticity should be studied in other systems, particularly in long-lived species, to get a fuller understanding of the importance of within-individual variation in plasticity for population persistence in nature.

310 References

- 311 Araya-Ajoy, Y. G., & Dingemanse, N. J. (2016). Repeatability, heritability, and age-dependence in the
312 aggressiveness reaction norms of a wild passerine bird. *Journal of Animal Ecology*, 227–238.
313 <https://doi.org/10.1111/1365-2656.12621>
- 314 Ashander, J., Chevin, L.-M., & Baskett, M. L. (2016). Predicting evolutionary rescue via evolving
315 plasticity in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences*,
316 283(1839), 20161690. <https://doi.org/10.1098/rspb.2016.1690>
- 317 Atwell, A., & Wagner, W. E. (2014). Female mate choice plasticity is affected by the interaction
318 between male density and female age in a field cricket. *Animal Behaviour*, 98, 177–183.
319 <https://doi.org/10.1016/j.anbehav.2014.10.007>
- 320 Auld, J. R., & Charmantier, A. (2011). Life history of breeding partners alters age-related changes of
321 reproductive traits in a natural population of blue tits. *Oikos*, 120(8), 1129–1138.
322 <https://doi.org/10.1111/j.1600-0706.2010.19161.x>
- 323 Balbontín, J., Hermosell, I. G., Marzal, A., Reviriego, M., De Lope, F., & Møller, A. P. (2007). Age-
324 related change in breeding performance in early life is associated with an increase in
325 competence in the migratory barn swallow *Hirundo rustica*. *Journal of Animal Ecology*, 76(5),
326 915–925. <https://doi.org/10.1111/j.1365-2656.2007.01269.x>
- 327 Blondel, J., Dervieux, A., Maistre, M., & Perret, P. (1991). Feeding ecology and life history variation of
328 the blue tit in Mediterranean deciduous and sclerophyllous habitats. *Oecologia*, 88(1), 9–14.
329 <http://link.springer.com/article/10.1007/BF00328397>
- 330 Blondel, J., Thomas, D. W., Charmantier, A., Perret, P., Bourgault, P., & Lambrechts, M. M. (2006). A
331 thirty-year study of phenotypic and genetic variation of blue tits in mediterranean habitat
332 mosaics. *BioScience*, 56(8), 661. [https://doi.org/10.1641/0006-](https://doi.org/10.1641/0006-3568(2006)56[661:ATSOPA]2.0.CO;2)
333 [3568\(2006\)56\[661:ATSOPA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[661:ATSOPA]2.0.CO;2)

334 Bonamour, S., Chevin, L., Charmantier, A., & Teplitsky, C. (2019). Phenotypic plasticity in response to
 335 climate change : the importance of cue variation. *Philosophical Transactions of the Royal*
 336 *Society B*, 374: 20180178. <https://doi.org/http://dx.doi.org/10.1098/rstb.2018.0178>

337 Bonamour, S., Réale, D., Chevin, L., Teplitsky, C., & Charmantier, A. (2020). Data from: Age-
 338 dependent phenological plasticity in a wild bird. *Journal of Animal Ecology*.
 339 <https://doi.org/10.5061/dryad.msbcc2fw8>

340 Bouwhuis, S., Sheldon, B. C., Verhulst, S., & Charmantier, A. (2009). Great tits growing old: selective
 341 disappearance and the partitioning of senescence to stages within the breeding cycle.
 342 *Proceedings of the Royal Society B: Biological Sciences*, 276(1668), 2769–2777.
 343 <https://doi.org/10.1098/rspb.2009.0457>

344 Brommer, J. E., & Rattiste, K. (2008). “Hidden” reproductive conflict between mates in a wild bird
 345 population. *Evolution*, 62(9), 2326–2333. <https://doi.org/10.1111/j.1558-5646.2008.00451.x>

346 Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative
 347 simulations. *Journal of Computational and Graphical Statistics*, 7(4), 434–455.

348 Caro, S. P., Schaper, S. V., Hut, R. A., Ball, G. F., & Visser, M. E. (2013). The case of the missing
 349 mechanism: how does temperature influence seasonal timing in endotherms? *PLoS Biology*,
 350 11(4). <https://doi.org/10.1371/journal.pbio.1001517>

351 Charlesworth, B. (1993). Evolutionary mechanisms of senescence. *Genetica*, 91(1–3), 11–19.

352 Charmantier, Anne, Doutrelant, C., Dubuc-Messier, G., Fargevieille, A., & Szulkin, M. (2016).
 353 Mediterranean blue tits as a case study of local adaptation. *Evolutionary Applications*, 9(1),
 354 135–152. <https://doi.org/10.1111/eva.12282>

355 Charmantier, Anne, & Gienapp, P. (2014). Climate change and timing of avian breeding and
 356 migration: evolutionary versus plastic changes. *Evolutionary Applications*, 7(1), 15–28.
 357 <https://doi.org/doi:10.1111/eva.12126>

358 Chevin, L.-M., Gallet, R., Gomulkiewicz, R., Holt, R. D., & Fellous, S. (2013). Phenotypic plasticity in
 359 evolutionary rescue experiments. *Philosophical Transactions of the Royal Society of London.*
 360 *Series B, Biological Sciences*, 368(1610), 20120089. <https://doi.org/10.1098/rstb.2012.0089>

361 Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing
 362 environment: towards a predictive theory. *PLoS Biology*, 8(4), e1000357.
 363 <https://doi.org/10.1371/journal.pbio.1000357>

364 Clutton-Brock, T. H. (1988). *Reproductive success: studies of individual variation in contrasting*
 365 *breeding systems*. (University).

366 Davis, M. B., Shaw, R. G., & Etterson, J. R. (2005). Evolutionary responses to changing climate.
 367 *Ecology*, 86(7), 1704–1714. <https://doi.org/https://doi.org/10.1890/03-0788>

368 Dawson, A. (2008). Control of the annual cycle in birds: Endocrine constraints and plasticity in
 369 response to ecological variability. *Philosophical Transactions of the Royal Society B: Biological*
 370 *Sciences*, 363(1497), 1621–1633. <https://doi.org/10.1098/rstb.2007.0004>

371 Dewitt, T. J. (1998). Costs and limits of phenotypic plasticity : Tests with morphology and life history
 372 in a freshwater snail. *Journal of Evolutionary Biology*, 11, 465–480.
 373 <https://doi.org/https://doi.org/10.1046/j.1420-9101.1998.11040465.x>

374 DeWitt, T. J., & Scheiner, S. M. (2004). *Phenotypic plasticity: Functional and conceptual approaches*
 375 (T. J. DeWitt & S. M. Scheiner (eds.)). Oxford University Press.

376 Dingemanse, N. J., Moiron, M., Araya-Ajoy, Y. G., Mouchet, A., & Abbey-Lee, R. N. (2020). Individual
 377 variation in age-dependent reproduction: Fast explorers live fast but senesce young? *Journal of*
 378 *Animal Ecology*, 89(2), 601–613. <https://doi.org/10.1111/1365-2656.13122>

379 Dubuc-Messier, G., Réale, D., Perret, P., & Charmantier, A. (2016). Environmental heterogeneity and
 380 population differences in blue tits personality traits. *Behavioral Ecology*, 00(00), 1–12.
 381 <https://doi.org/10.1093/beheco/arw148>

382 Dunn, P. (2004). Breeding dates and reproductive performance. *Advances in Ecological Research*,
383 35(04), 69–87. [https://doi.org/10.1016/S0065-2504\(04\)35004-X](https://doi.org/10.1016/S0065-2504(04)35004-X)

384 Ericsson, M., Henriksen, R., Bélteky, J., & Sundman, A. (2016). Long-term and transgenerational
385 effects of stress experienced during different life phases in chickens (*Gallus gallus*). *PLoS ONE*,
386 11(4), 9–12. <https://doi.org/10.1371/journal.pone.0153879>

387 Fawcett, T. W., & Frankenhuis, W. E. (2015). Adaptive explanations for sensitive windows in
388 development. *Frontiers in Zoology*, 12(Suppl 1), 1–14.

389 Fischer, B., van Doorn, G. S., Dieckmann, U., & Taborsky, B. (2014). The evolution of age-dependent
390 plasticity. *The American Naturalist*, 183(1), 108–125. <https://doi.org/10.1086/674008>

391 Gavrillets, S., & Scheiner, S. M. (1993). The genetics of phenotypic of reaction norm shape V .
392 Evolution of reaction norm shape. *Journal of Evolutionary Biology*, 6, 31–48.

393 Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences.
394 *Statistical Science*, 7(4), 457–511.

395 Gienapp, P. (2018). The choice of the environmental covariate affects the power to detect variation
396 in reaction norm slopes. *BioRxiv*, 1–19. <https://doi.org/10.1101/311217>

397 Gienapp, P., & Brommer, J. E. (2014). Evolutionary dynamics in response to climate change. In A
398 Charmantier, D. Garant, & L. Kruuk (Eds.), *Quantitative genetics in the wild* (pp. 254–272).
399 Oxford University Press.

400 Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2007). Climate change and evolution:
401 Disentangling environmental and genetic responses. *Molecular Ecology*, 17(1), 167–178.
402 <https://doi.org/10.1111/j.1365-294X.2007.03413.x>

403 Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of*
404 *Ecology and Systematics*. Volume 13, 1–21.

405 Grieco, F., van Noordwijk, A. J., & Visser, M. E. (2002). Evidence for the effect of learning on timing of
 406 reproduction in blue tits. *Science*, 296(April), 136–138.
 407 <https://doi.org/10.1126/science.1068287>

408 Hadfield, J. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
 409 MCMCglmm R Package. *Journal of Statistical Software*, 33(2), 1–22.

410 Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical*
 411 *Biology*, 12(1), 12–45. [https://doi.org/10.1016/0022-5193\(66\)90184-6](https://doi.org/10.1016/0022-5193(66)90184-6)

412 Hayward, A. D., Wilson, A. J., Pilkington, J. G., Pemberton, J. M., & Kruuk, L. E. B. (2009). Ageing in a
 413 variable habitat: environmental stress affects senescence in parasite resistance in St Kilda Soay
 414 sheep. *Proceedings of the Royal Society B: Biological Sciences*, 276(1672), 3477–3485.
 415 <https://doi.org/10.1098/rspb.2009.0906>

416 Marrot, P., Charmantier, A., Blondel, J., & Garant, D. (2018). Current Spring Warming as a Driver of
 417 Selection on Reproductive Timing in a Wild Passerine. *Journal of Animal Ecology*, May 2016, 1–
 418 11. <https://doi.org/10.1111/ijlh.12426>

419 Matthysen, E., van Overveld, T., van de Castele, T., & Adriaensen, F. (2010). Family movements
 420 before independence influence natal dispersal in a territorial songbird. *Oecologia*, 162(3), 591–
 421 597. <https://doi.org/10.1007/s00442-009-1483-x>

422 Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem
 423 and the evidence. *Evolutionary Applications*, 7(1), 1–14. <https://doi.org/10.1111/eva.12137>

424 Monaghan, P., Charmantier, A., Nussey, D. H., & Ricklefs, R. E. (2008). The evolutionary ecology of
 425 senescence. *Functional Ecology*, 22(3), 371–378. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2435.2008.01418.x)
 426 [2435.2008.01418.x](https://doi.org/10.1111/j.1365-2435.2008.01418.x)

427 Nussey, D. H., Coulson, T., Festa-Bianchet, M., & Gaillard, J. M. (2008). Measuring senescence in wild
 428 animal populations: Towards a longitudinal approach. *Functional Ecology*, 22(3), 393–406.

429 <https://doi.org/10.1111/j.1365-2435.2008.01408.x>

430 Nussey, D. H., Froy, H., Lemaitre, J. F., Gaillard, J. M., & Austad, S. N. (2013). Senescence in natural
431 populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing*
432 *Research Reviews*, 12(1), 214–225. <https://doi.org/10.1016/j.arr.2012.07.004>

433 Nussey, D. H., Kruuk, L. E. B., Morris, A., & Clutton-Brock, T. H. (2007). Environmental conditions in
434 early life influence ageing rates in a wild population of red deer. *Current Biology*, 17(23), 1000–
435 1001. <https://doi.org/10.1016/j.cub.2007.10.005>

436 Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual
437 phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, 20(3), 831–844.
438 <https://doi.org/10.1111/j.1420-9101.2007.01300.x>

439 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across
440 natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>

441 Perrins, C. M., & McCleery, R. H. (1989). Laying date and clutch size in the great tit. *Wilson Bulletin*,
442 101(2), 236–253. <http://elibrary.unm.edu/sora/Wilson/v101n02/p0236-p0253.pdf>

443 Pigliucci, M. (2001). *Phenotypic plasticity: beyond nature and nurture* (John Hopkins University Press
444 (ed.)).

445 Porlier, M., Charmantier, A., Bourgault, P., Perret, P., Blondel, J., & Garant, D. (2012). Variation in
446 phenotypic plasticity and selection patterns in blue tit breeding time: Between- and within-
447 population comparisons. *Journal of Animal Ecology*, 81(5), 1041–1051.
448 <https://doi.org/10.1111/j.1365-2656.2012.01996.x>

449 Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P.,
450 Adriaensen, F., Ahola, M. P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K. S., Borrás, A.,
451 Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A. A., ... Kramer-Schadt, S. (2019).
452 Adaptive responses of animals to climate change are most likely insufficient. *Nature*

453 *Communications*, 10(1), 3109. <https://doi.org/10.1038/s41467-019-10924-4>

454 Ramakers, J. J. C., Gienapp, P., & Visser, M. E. (2018). Phenological mismatch drives selection on
455 elevation, but not on slope, of breeding time plasticity in a wild songbird. *Evolution*, 175–187.
456 <https://doi.org/10.1111/evo.13660>

457 Reed, T. E., Schindler, D. E., & Waples, R. S. (2011). Integrating effects of phenotypic plasticity and
458 evolution on population persistence in a changing climate. *Conservation Biology*, 25(1), 56–63.
459 <https://doi.org/10.1111/j.1523-1739.2010.01552.x>

460 Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J., & Kinnison, M. T. (2010). Phenotypic plasticity
461 and population viability: the importance of environmental predictability. *Proceedings of the*
462 *Royal Society B: Biological Sciences*, 277(1699), 3391–3400.
463 <https://doi.org/10.1098/rspb.2010.0771>

464 Ricklefs, R. E. (2008). The evolution of senescence from a comparative perspective. *Functional*
465 *Ecology*, 22(3), 379–392. <https://doi.org/10.1111/j.1365-2435.2008.01420.x>

466 Stamps, J. A., & Krishnan, V. V. (2017). Age-dependent changes in behavioural plasticity: insights from
467 Bayesian models of development. *Animal Behaviour*, 126, 53–67.
468 <https://doi.org/10.1016/j.anbehav.2017.01.013>

469 van de Pol, M., Osmond, H. L., & Cockburn, A. (2012). Fluctuations in population composition
470 dampen the impact of phenotypic plasticity on trait dynamics in superb fairy-wrens. *Journal of*
471 *Animal Ecology*, 81(2), 411–422. <https://doi.org/10.1111/j.1365-2656.2011.01919.x>

472 van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-
473 subject effects using mixed models. *Animal Behaviour*, 77(3), 753–758.
474 <https://doi.org/10.1016/j.anbehav.2008.11.006>

475 Van Noordwijk, A. J., McCleery, R. H., & Perrins, C. M. (1995). Selection for the timing of great tit
476 breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology*, 64(4),

477 451–458.

478 van Tienderen, P. H., & Koelewijn, H. P. (1994). Selection on reaction norms, genetic correlations and
479 constraints. *Genet. Res., Camb.*, 64, 115–125.

480 Vedder, O., Bouwhuis, S., & Sheldon, B. C. (2013). Quantitative assessment of the importance of
481 phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biology*,
482 11(7), 1–10. <https://doi.org/10.1371/journal.pbio.1001605>

483 Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate
484 change. *Proceedings of the Royal Society B: Biological Sciences*, 275(1635), 649.
485 <https://doi.org/10.1098/rspb.2007.0997>

486 Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: the need for a
487 yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2561–2569.
488 <https://doi.org/10.1098/rspb.2005.3356>

489 Visser, M. E., Holleman, L. J. M., & Caro, S. P. (2009). Temperature has a causal effect on avian timing
490 of reproduction. *Proceedings of the Royal Society B: Biological Sciences*, 276(1665), 2323–2331.
491 <https://doi.org/10.1098/rspb.2009.0213>

492 Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M.,
493 Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change.
494 *Nature*, 416(6879), 389–395. <https://doi.org/10.1038/416389a>

495 Warner, D. A., Miller, D. A. W., Bronikowski, A. M., & Janzen, F. J. (2016). Decades of field data reveal
496 that turtles senesce in the wild. *PNAS*, 113(23). <https://doi.org/10.1073/pnas.1600035113>

497 West-Eberhard, M. J. (2003). *Developmental plasticity and evolution* (Oxford Uni).

498 Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*,
499 11(4), 398–411.

500 Ethics

501 All experimental protocols described here were approved by the ethics committee for animal
502 experimentation of Languedoc Roussillon (305-CEEA-LR-12066 approved in 2012 and 2018) as well as
503 by Regional Institutions (bylaw issued by the Prefecture on 08/12/2015 n° 2015-491). Captures and
504 bird ringing were performed under a personal ringing permit delivered by the CRBPO (Centre de
505 Recherches par le Bagueage des Populations d'Oiseaux) to Anne Charmantier (ringing permit number
506 1907).

507 Data accessibility

508 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.msbcc2fw8>

509 Author's contributions

510 C.T., A.C., L.-M.C. and S.B. designed the research. A.C., C.T. and S.B. (and many other contributors)
511 collected field data. S.B. conducted statistical analyses. S.B., C.T., L.-M.C., A.C., D.R. wrote the paper.

512 Competing interests

513 We declare we have no competing interests.

514 Acknowledgments

515 We thank Andy Russel and Patrice David for useful discussions. We also thank Maxime Dubart for
516 useful advice for the statistical analyses. We thank all the people who helped maintain the study site
517 and conduct the blue tit monitoring in the past 45 years, in particular Jacques Blondel, Phillippe Perret,
518 Marcel Lambrechts, Claire Doutrelant, Christophe de Franceschi (who also managed the database),
519 Annick Lucas and Pablo Giovannini. We thank the APEEM, the ONF and Achille Sanroma for field
520 logistics, and the Fango valley MAB reserve.

521 Funding

522 This project was funded by a long-term support by the OSU-OREME, and by the European Research
523 Council (Starting grant ERC-2013-StG-337365-SHE to AC).

524 Tables and Figures

525 Table 1: Model 1 for laying date.

526 Laying date variation according to temperature and age. Results are from the mixed model 1
527 implemented with MCMCglmm on 1696 laying date observations from 854 females. Posterior modes
528 of estimates are indicated together with 95% credible intervals. Fixed effect estimates with 95%
529 credible intervals that do not include zero are represented in bold. ALR = age at last reproduction.

Term	Posterior mode	Lower 95%CI	Upper 95%CI
Fixed effects			
Intercept (μ)	134.14	132.39	135.36
Temperature (α_1)	-2.92	-4.79	-1.62
Age (α_2)	-3.43	-3.87	-2.81
Age² (α_3)	0.40	0.33	0.50
Temperature : Age (α_4)	-0.73	-1.31	-0.07
Temperature : Age ² (α_5)	0.06	-0.03	0.15
ALR (α_6)	-0.22	-0.43	0.02
Random effects			
Year	13.80	8.77	22.49
Ind	10.90	9.05	13.40
Residuals (ε_{ij})	14.37	13.14	15.88

Table 2: Model 2 for annual reproductive success.

Annual reproductive success variation according to laying date (LD) and age. Results are from the mixed model 2 implemented with MCMCglmm on 1092 laying date observations from 667 females. Posterior modes of estimates are represented together with 95% credible intervals. Fixed effect estimates with 95% credible intervals that do not include zero are represented in bold.

Term	Posterior mode	Lower 95%CI	Upper 95%CI
Fixed effects			
Intercept (γ)	3.84	2.76	5.25
Age (β_1)	-0.37	-0.64	0.15
Age² (β_2)	-0.01	-0.03	-0.002
LD (β_3)	-0.02	-0.03	-0.01
Age * LD (β_4)	0.002	-0.0003	0.006
Random effects			
Year	0.08	0.05	0.14
Ind	0.03	0.03	0.04
Residuals (r_{ij})	0.03	0.02	0.04

Figure 1: Age-dependent reaction norm of laying date with respect to temperature.

Age-dependent reaction norm of laying date with respect to mean-centered temperature. a) Bivariate reaction norm representing predicted laying date (vertical axis and colour gradient) against temperature and age. Also represented are the univariate reaction norms with respect to the environment showing plasticity at age 1 (dotted line) and 5 (long dashed line). b) Reaction norms of predicted laying date with respect to temperature at age 1 (dotted line) and 5 (long dashed line, same as Figure 1a) are shown together with the average reaction norm across all females regardless of age (solid line). For a and b, predicted values of laying date were obtained from the posterior mode of predictions across all iterations from model 1. Predictions were estimated for all combinations of temperature (from -2.5 to +1.5 degree around the average cue temperature) and age (from 1 to 9 years old). c) Median reaction norm intercept (in grey) and slope (in black) of laying date with respect to temperature are plotted against female age (over its observed range). The slope was estimated as $\alpha_1 + \alpha_4 A_{ij} + \alpha_5 A_{ij}^2$ (model 1 and Table 1).

Figure 2: Influence of age and phenology on annual reproductive success.

Average annual reproductive success ($\pm$ standard error) plotted according to a) age categories, or to b) laying date for different female age categories. In b), the slopes of average annual reproductive success with respect to laying date are significantly negative for the three first age classes (slope= -0.05 [SE= 0.02, p-value= 0.01], -0.08 [SE= 0.01, p-value= 4.88e-08], and -0.06 [SE= 0.01, p-value= 1.99e-05], for 1-year-old, 2-3 year-old, and 4-5 year-old females, respectively), but not for the oldest females of 6 and more years old (slope= 0.01 [SE= 0.03, p-value= 0.67]). Annual reproductive success is estimated as the number of fledglings per breeding attempt in the year. Note that some points have no standard error bars because of a single observation in the laying date – age class combination.