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Age-dependent phenological plasticity in

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a wild bird

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18

19 **Abstract**

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

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

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

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

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

35

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

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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 Dingemans 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

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

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

75 Within-individual variation of plasticity over the lifetime of individuals has been highlighted in
76 some experimental studies, mainly in behavioural traits (e.g. Atwell & Wagner, 2014; Ericsson et al.,
77 2016), with highest plasticity in juveniles or young adults followed by decreasing plasticity with age,
78 thus corroborating theoretical predictions. However, evidence is scarce for age-specific plasticity in
79 wild populations. Araya-Ajoy & Dingemanse (2016) compared the seasonal plasticity of aggressiveness
80 in great tits (*Parus major*) between two age classes, and found that first-year-old breeders showed
81 higher seasonal plasticity than older birds, also aligned with theoretical predictions. A study on
82 phenological trait plasticity in superb fairywrens (*Malurus cyaneus*) demonstrated that the variation
83 of moult timing with rainfall changed with age (van de Pol et al., 2012). Contrary to theoretical
84 predictions, in this study older birds were more plastic than younger ones. Overall, the scarce empirical
85 evidence means we still poorly understand the origin of age-dependent plasticity of labile phenotypic
86 traits over a lifetime. The study of age-specific variation in plasticity in wild populations is an arduous
87 task because of the combined challenges of studying phenotypic plasticity and senescence (Nussey et
88 al., 2013; Nussey, Wilson, et al., 2007), both of which demand a long-term study with individual

89 marking and repeated measures on the same individuals. In addition, plasticity estimation requires
90 identifying the main environmental cue(s) explaining within-individual phenotypic variation (Gienapp,
91 2018). These challenges explain why age-specific variation of plasticity has been widely neglected so
92 far in empirical studies.

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

110 [Materials & Methods](#)

111 [Species and data collection](#)

112 We used a long-term study (initiated by Jacques Blondel in 1975) of a wild Mediterranean population
113 of Blue tit (*Cyanistes caeruleus ogliastrae*), 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

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

140 Statistical analyses

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

143

$$144 \quad LD_{ij} = \mu + \alpha_1 T_j + \alpha_2 A_{ij} + \alpha_3 A_{ij}^2 + \alpha_4 (T_j A_{ij}) + \alpha_5 (T_j A_{ij}^2) + \alpha_6 ALR_i + ind_i + year_j + \varepsilon_{ij} \text{ (model}$$

145 1)

146

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

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

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

166

$$167 \quad ARS_{ij} = \gamma + \beta_1 A_{ij} + \beta_2 A_{ij}^2 + \beta_3 LD_{ij} + \beta_4 (A_{ij} LD_{ij}) + ind_i + year_j + r_{ij} \quad (\text{model 2})$$

168

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

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

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

190 Results

191 Laying date varied within a female's lifetime, in response to both temperature and age (Table 1). Laying
192 date was earlier with warmer springs, with a median value of c. 3 days earlier every 1°C warmer (Table
193 1, Figure 1a&b). It also varied non-linearly with age, decreasing until age 4 and then increasing (Table
194 1, Figure 1a&c). Our results suggested that shorter-lived females tend to breed later, but note that the
195 95% credible interval in the posterior distribution of the *ARS* marginally included zero (Table 1, but
196 see Supporting Information 2 Table S3).

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

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

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

217 Discussion

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

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

235 13% of the total phenotypic range in laying date in the entire dataset (c. 39 days), while the among-
236 individual (averaged across years and environments) and among-year effects explain respectively
237 about 28% (c. 11 days) and 36% (c. 14 days) of this range.

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

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

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

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

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

293 Conclusion and perspectives

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

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500 Ethics

501 All experimental protocols described here were approved by the ethics committee for animal
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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.

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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

530

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).

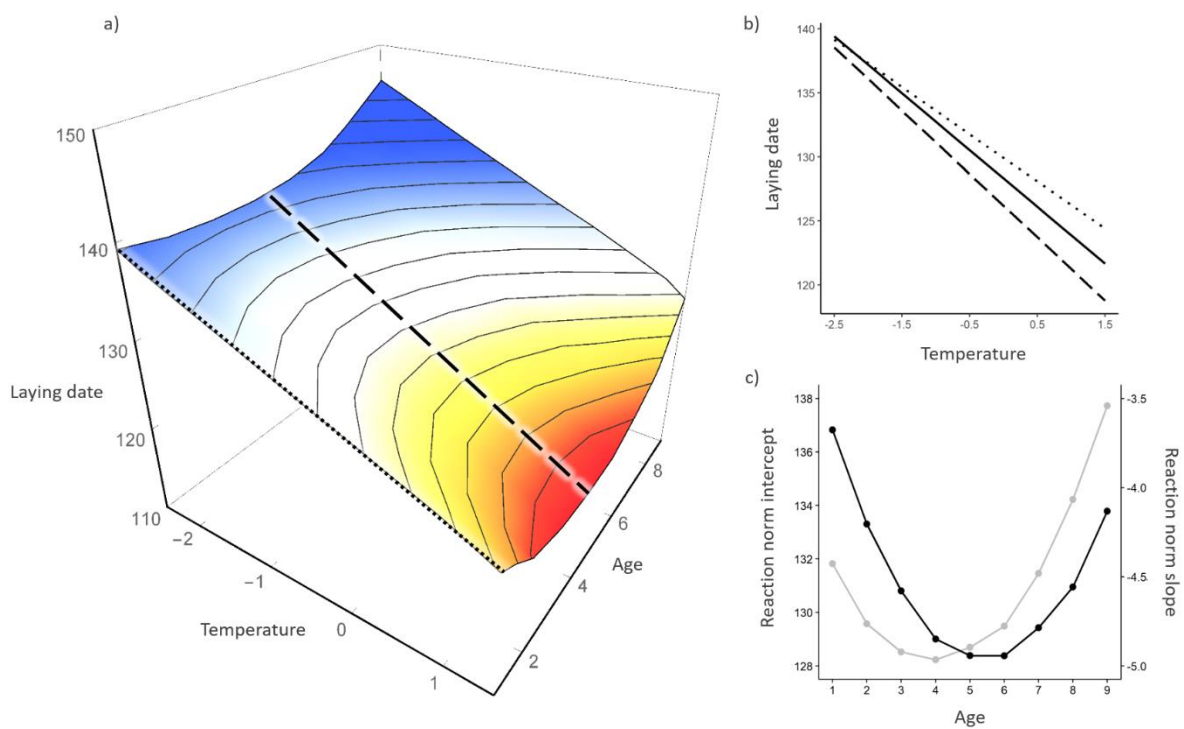


Figure 2: Influence of age and phenology on annual reproductive success.

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.

