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**Current Spring Warming as a Driver of Selection on
Reproductive Timing in a Wild Passerine**

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1 **Full title**

2 Current Spring Warming as a Driver of Selection on Reproductive Timing in a Wild Passerine

3

4 **Running head**

5 Warming Induces Strong Selection on Lay Date

6

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14 **Keywords:**

15 Natural selection, *Cyanistes caeruleus*, Spring warming, Laying date, Blue tit, Model
16 averaging

17

18

19 **Abstract**

20 1. Evolutionary adaptation as a response to climate change is expected for fitness-related traits
21 affected by climate and exhibiting genetic variance. Although the relationship between
22 warmer spring temperature and earlier timing of reproduction is well documented,
23 quantifications and predictions of the impact of global warming on natural selection acting on
24 phenology in wild populations remain rare. If global warming affects fitness in a similar way
25 across individuals within a population, or if fitness consequences are independent of
26 phenotypic variation in key-adaptive traits, then no evolutionary response is expected for
27 these traits.

28 2. Here we quantified the selection pressures acting on laying date during a 24-year
29 monitoring of blue tits in southern Mediterranean France, a hot spot of climate warming. We
30 explored the temporal fluctuation in annual selection gradients and we determined its
31 temperature-related drivers.

32 3. We first investigated the month-specific warming since 1970 in our study site and tested its
33 influence on selection pressures using a model averaging approach. Then, we quantified the
34 selection strength associated with temperature anomalies experienced by the blue tit
35 population.

36 4. We found that natural selection acting on laying date significantly fluctuated both in
37 magnitude and in sign across years. After identifying a significant warming in spring and
38 summer, we showed that warmer daily maximum temperatures in April were significantly
39 associated with stronger selection pressures for reproductive timing. Our results indicated an
40 increase in the strength of selection by 46% for every +1°C anomaly.

41 5. Our results confirm the general assumption that recent climate change translates into strong
42 selection favouring earlier breeders in passerine birds. Our findings also suggest that
43 differences in fitness among individuals varying in their breeding phenology increase with
44 climate warming. Such climate driven influence on the strength of directional selection acting
45 on laying date could favour an adaptive response in this trait, since it is heritable.

46

47

48 **Introduction**

49 Global climate change results in an increase in temperature mean and variability and
50 generates new environmental conditions for wild populations (Coumou & Rahmstorf 2012).
51 Rising temperatures are known to alter the timing of vegetation development (Fu *et al.* 2012),
52 leading to shifts in phenology and range shifts of many taxa (Chen *et al.* 2011) such as plants
53 (Svenning & Sandel 2013), birds (Crick 2004), insects (Parmesan & Yohe 2003) and
54 mammals (Moritz *et al.* 2008). These responses to climate warming can be due to non-genetic
55 changes (*i.e.* phenotypic plasticity) or to evolutionary adaptations (Gienapp *et al.* 2008).
56 Whereas evidence of phenotypic plasticity in this context is often reported in the literature
57 (Merilä & Hendry 2014), studies showing an evolutionary response to climate change are still
58 rare (Gienapp *et al.* 2008; Merilä 2012). This “missing evidence” (Merilä 2012) is worrying
59 because phenotypic plasticity alone is unlikely to sustain population responses to climate
60 change over a long term warming period (Hoffmann & Sgro 2011).

61 Evolutionary adaptation under climate change is expected if climate-induced selective
62 pressures are found for key adaptive traits with significant genetic variance (Hoffmann &
63 Sgro 2011). While most life history traits affected by the recent climate warming were shown
64 to possess some level of genetic variance in the wild (Postma 2014), strong selective pressures
65 resulting from climate change have always been assumed, but rarely quantified empirically
66 (MacColl 2011). Global warming is often expected to generate strong selection pressures
67 because numerous phenotypic mismatches between adaptive optima and population
68 phenotypic mean have been documented following a warming trend (Gienapp *et al.* 2008). In
69 particular, theoretical modelling has shown that climate change should increase selection on
70 consumer phenology, even if the environmental changes affecting consumer and resource

71 phenologies are of similar magnitude (Gienapp, Reed & Visser 2014). However, one of the
72 basic assumptions for natural selection to occur is that fitness varies among individuals and
73 that this variance in fitness is related to their phenotypes. Hence, for climate warming to
74 induce a selective pressure on wild populations, it should cause differences in individual
75 fitness depending on specific phenotypes. In other words, if a phenotypic mismatch affects all
76 individuals similarly, climate warming will not result in a new selective pressure, and no
77 evolutionary response is expected. So far, although many shifts in phenology have been
78 shown in response to warming across all living taxa (Parmesan & Yohe 2003), few studies
79 have attempted to assess changes in selection under climate change (Domínguez & Dirzo
80 1995; McAdam & Boutin 2003; Reale *et al.* 2003; Maad & Alexandersson 2004; Nussey *et*
81 *al.* 2005; Husby *et al.* 2010; Karell *et al.* 2011; Anderson *et al.* 2012; Campbell & Powers
82 2015; Chevin, Visser & Tufto 2015; Kingsolver & Buckley 2015; Visser *et al.* 2015). These
83 studies showed no clear pattern of new selective regime resulting from global warming, with
84 both increases (Domínguez & Dirzo 1995; Maad & Alexandersson 2004; Nussey *et al.* 2005;
85 Anderson *et al.* 2012) and decreases (McAdam & Boutin 2003; Karell *et al.* 2011; Campbell
86 & Powers 2015) in the strength of natural selection. Moreover, most studies compared
87 selection pressures between only two years (e.g. Domínguez & Dirzo 1995; Maad &
88 Alexandersson 2004) and/or failed to identify a significant climate warming over the study
89 period (e.g. Maad & Alexandersson 2004; Anderson *et al.* 2012; Visser *et al.* 2015). Despite
90 these limitations, previous studies showed an increase in the strength of selection along with
91 temperatures in different birds species such as the Pied Flycatcher, *Ficedula hypoleuca*
92 (Visser *et al.* 2015), the Great Tit, *Parus major* (Visser *et al.* 1998; Charmantier *et al.* 2008;
93 Husby, Visser & Kruuk 2011; Gienapp *et al.* 2013; Reed, Jenouvrier & Visser 2013; Vedder,
94 Bouwhuis & Sheldon 2013; Chevin, Visser & Tufto 2015) and the Blue Tit, *Cyanistes*
95 *caeruleus* (Phillimore *et al.* 2016). Overall, these previous studies explored a potential

96 influence of temperature, partially neglecting the investigation of climate warming (*i.e.* an
97 exploration of warming patterns over the study period). In order to predict the evolutionary
98 response of populations to climate warming, it is crucial to go beyond an assessment of the
99 impact of temperature on natural selection, and to quantify and predict variation in the
100 strength of selection beyond the current warming period.

101 Here we investigated temperature-related changes in selection pressures acting on the timing
102 of reproduction in a wild population of blue tits (*Cyanistes caeruleus*). The Blue tit is an
103 insectivorous passerine living in temperate forests of Europe and in parts of the Middle East,
104 breeding from March to June in southern France (Blondel *et al.* 2006). The amount of food
105 availability for offspring (mostly leaf-eating caterpillars) is dependent on the timing of
106 budding of oaks (*Quercus sp.*), which is highly responsive to ambient temperature (Van
107 Noordwijk, McCleery & Perrins 1995). Thus, like most passerines in temperate forests, blue
108 tits must adjust their laying date to track the amount of food available (Visser *et al.* 1998;
109 Thomas *et al.* 2001). Fitness differences among birds breeding at different dates are strong
110 with earlier breeders achieving higher reproductive success (Blondel *et al.* 2006; Porlier *et al.*
111 2012). Previous studies on a closely related species, the Great tit (*Parus major*) have shown
112 that the selection differential on breeding dates is correlated with the mean temperature during
113 the period when birds are incubating (Van Noordwijk, McCleery & Perrins 1995; Chevin,
114 Visser & Tufto 2015). Warmer springs generated an increased mismatch between great tit
115 breeding phenology and seasonal food peak, leading to intensifying directional selection on
116 laying dates (Visser, Holleman & Gienapp 2006; Reed, Jenouvrier & Visser 2013). Warmer
117 spring temperatures are thus expected to drive patterns of selection for earlier laying date in
118 the blue tit. However, contrary to the previous work exploring the temperature-induced
119 selection on laying date in great tits in North-Western Europe, we explored the impact of
120 warming on blue tits in the Mediterranean area, which is a warming “hot spot” (*i.e.* a

121 responsive region to climate change, Giorgi 2006). Indeed, a pronounced decrease in
122 precipitation and increase in warming, especially in summer, is forecasted in this region for
123 the next decades (Giorgi & Lionello 2008). The relative importance of climate warming on
124 ecological processes may also depend on temperature seasonality. For example, budburst
125 seems to be more sensitive to spring warming than to winter warming (Fu *et al.* 2012).
126 Moreover, the influence of climate warming might depend on the type of temperature because
127 patterns of warming are different among mean, minimum and maximum temperatures
128 (Rebetez & Reinhard 2008). In order to investigate in detail these climatic drivers, we
129 explored the increase in monthly minimum, mean and maximum temperatures across the
130 calendar year, and assessed their roles as potential determinants of selection acting on blue tit
131 laying date. In addition to these climatic drivers, we also took into account the selective
132 impact of two non-climatic variables: annual predation rate on nestlings and population
133 density. Predation on nestlings by small carnivores (in particular the weasel *Mustela nivalis*)
134 has strong but variable impacts on blue tit reproductive success in our study population.
135 Population density has previously been shown to increase the strength of selection acting on
136 laying date (e.g. in pied flycatchers, *Ficedula hypoleuca*, Ahola *et al.* 2011). These variables
137 were taken into account because they fluctuated across years, potentially shaping the climatic
138 signal on selection acting on laying date. Finally, after assessing the relative impact of
139 climatic and non-climatic drivers of selection on laying date, we quantified the relationship
140 between temperature drivers and selection strength.

141

142

143 **Materials and Methods**

144

145 ***Study area and field work***

146 Our analyses were based on data from a long-term study of blue tits in the forest of La
147 Rouvière, near the city of Montpellier (43°40'N, 03°40'E), southern France. This forest is
148 dominated by downy oaks (*Quercus humilis*) but also contains 10% of holm oaks (*Quercus*
149 *ilex*) and it is equipped with 227 nest boxes over 175 ha. Since 1991, nest boxes are routinely
150 monitored from the onset of nest construction until all nestlings have fledged (see
151 Charmantier *et al.* 2016 for further details). For each brood, laying date (date of the first egg
152 laid, March 1st = 1), clutch size (number of eggs laid) and number of fledglings (number of
153 chicks leaving the nest) are recorded. Parents are captured in nest boxes when chicks are *c.*9
154 days or older, and are uniquely marked with metal rings (provided by C.R.B.P.O). Nestlings
155 are ringed when 9-15 days old. Only first clutches that were not manipulated were included in
156 the analyses (second clutches represent less than 1% of total number of clutches). Bird
157 capture, ringing and measurement were performed under individual ringing permits delivered
158 by the Centre de Recherche sur la Biologie des Populations d'Oiseaux, C.R.B.P.O, Paris
159 (France). The monitoring protocol was approved by the Animal Care and Use Committee
160 Languedoc-Roussillon (CEEA-LR-12066).

161 ***Environmental variables***

162 Data on daily minimum (Tn), maximum (Tx) and mean (estimated as (Tn+Tx)/2)
163 temperatures were obtained from a weather station (43°24'N, 03°57'E) located approximately
164 24km from the breeding site, provided by Meteo France
165 (<https://donneespubliques.meteofrance.fr/>). Anomalies in temperatures were estimated as the

166 difference between monthly temperatures and temperatures averaged for each month across
167 all years during the 1970-2000 period. Annual predation rate was estimated as the ratio of the
168 number of broods predated by the number of nest boxes occupied by blue tits within each
169 year. Because annual predation rate ranged from 0 to 0.4, and because 80% of annual
170 predation rates were below 0.1, its skewed distribution prevented model convergence. Hence,
171 we considered this variable as a categorical variable taking two different modalities: low and
172 high corresponding to a predation rate below or above 0.1 respectively. Only 4 years
173 corresponded to a high predation rate (2001, 2006, 2009 and 2010, *i.e.* 16% of the time span
174 of the study). Note that variation in predation rate does not result solely from the natural
175 dynamics of predators, but also from hunting practices and various anti-predator protocols
176 that have changed over the monitoring years in order to limit the impact of predators on the
177 study population. Population density was estimated as the inverse of the mean distance (in
178 km) between each nest box occupied by blue tits and its closest neighbour (including nest
179 boxes occupied by great tits). Instead of using the proportion of occupied nest-boxes, we used
180 this metric to estimate local density around the nest boxes since the number and the density of
181 nest boxes within the population changed across years.

182 *Statistical analyses*

183 All statistical analyses were carried out using the software R (version 3.1.1) (R Core Team
184 2014).

185 *Climatic analyses*

186 Mean, minimum and maximum monthly temperatures were estimated as the daily temperature
187 averaged during each month. Smoothed monthly temperatures were obtained from a 2-years
188 moving average window (supplementary material, Fig. S1). Temperature changes for each

189 month were estimated as the slope of anomalies in monthly temperatures regressed over time
190 (years) across the period 1970-2015.

191 *Selection analyses*

192 Analyses were conducted on female individual data that were not subject to any experimental
193 manipulation, with a dataset of 1024 breeding observations on 721 female blue tits breeding
194 between 1991 and 2014. Selection acting on laying date was defined as the slope of the
195 regression of relative fitness (*i.e.* number of fledglings) on laying date (Lande & Arnold
196 1983). Clutch size was also included as covariate in the fixed part of the model to estimate the
197 selection acting on laying date independently from selection acting on the highly correlated
198 clutch size (Perrins & McCleery 1989). Thus, selection was estimated from the effect of
199 laying date on the proportion of a clutch that fledged (*i.e.* brood fledging success). Nonlinear
200 selection acting on laying date was not analysed further because quadratic and correlational
201 selection were not significant (results not shown). Relative fitness corresponded to the
202 individual fitness divided by the annual mean fitness of the population, and followed a
203 Gaussian distribution (Fig. S2). All selection analyses were conducted on laying dates
204 standardized annually (zero mean and unit variance within each year) in order to control for
205 an environmental covariance between fitness and the trait across years. As this dataset
206 includes repeated values within each year and for some individuals, year and individual
207 identities were included in the random part of the selection models to control for
208 pseudoreplication. The significance of selection gradients was estimated using F tests using
209 *lmerTest* (Kuznetsova, Brockhoff & Christensen 2015) package in R. Temporal variation in
210 selection gradients across years was assessed by including an interaction term between laying
211 date and years (considered as a discrete variable) in the random part of the selection model.
212 This method allows to account for errors in the estimation of annual selection gradients when
213 exploring their fluctuation (Morrissey & Hadfield 2012). Mixed models were fitted using the

214 *lmer* function from the *lme4* package (Bates *et al.* 2015) in R and the significance of random
215 terms was tested by Likelihood Ratio Tests (LRT).

216 *Model averaging approach*

217 The model averaging analysis was conducted following methods provided by Grueber *et al.*
218 (2011) and by Symonds and Moussalli (2011). Based on information theory, the aim of model
219 averaging is to evaluate relative supports for a given hypothesis over others instead of null
220 hypothesis testing (Burnham, Anderson & Huyvaert 2011). In a first step, we determined
221 which variable to include in the models. Focusing on the four months covering the blue tit
222 breeding season (March, April, May and June), we explored the influence of 14 potential
223 drivers (daily minimum, mean and maximum monthly temperatures (for each of the four
224 months), predation rate and population density) on annual selection by including, in the
225 selection models, interaction terms between laying date and the drivers. In a second step, we
226 generated a "model set" by adjusting all possible submodels from the set of predictors of
227 interest. All submodels included laying date, clutch size, and a combination of drivers
228 (interaction terms between environmental variables and laying date). Since 14 environmental
229 variables were investigated, 16384 models could potentially be fitted (2^{14}). Because
230 collinearity among predictors can be a problem in model selection (Freckleton, Cooper & Jetz
231 2011), we constrained the number of possible submodels by avoiding models including
232 temperatures from the same month (*e.g.* maximum March temperature did not appear in a
233 model including mean or minimum temperatures in March), leading to 1024 models
234 generated. In a third step, we employed the model averaging procedure on our set of models
235 (based on their AIC) in order to obtain robust environmental driver estimates (associated with
236 their standard errors) accounting for model selection uncertainty. This approach is particularly
237 suitable when the Akaike weight of the best model is not considerably higher than the next
238 best model (*i.e.* it has an Akaike weight of >0.9) (Symonds & Moussalli 2011), which was the

239 case in our analysis since the Akaike weight of the best model was 0.66. Because employing a
240 model averaging procedure on the full set of models can be spurious (due to models with very
241 low Akaike weight), we selected the 95% confidence set of models (Symonds & Moussalli
242 2011). This procedure led to a set of 17 best models identified (Table S1). Moreover, relative
243 importance of each of the 14 environmental variables was estimated by summing the Akaike
244 weights from each model in which the specific variable appeared. This relative importance
245 can be interpreted as the probability that the variable is a component of the best model
246 (Symonds & Moussalli 2011). A variable was considered as driving selection if its relative
247 importance was above 80%. Note that this relative importance should not be interpreted as a *p*
248 value.

249

250 **Results**

251 *Patterns of temperature increase*

252 The first aim of our analysis was to assess the recent warming in the forest of La Rouvière
253 near Montpellier. Over the last 45 years (1970-2015), the trend in mean annual temperatures
254 in this habitat was +0.44°C / decade ($P < 0.001$) (Fig. S1). The warming trend was slightly
255 stronger for minimum annual temperature (+0.51°C / decade, $P < 0.001$) than for maximum
256 annual temperature (+0.33°C / decade, $P < 0.001$). While warming was negligible (between -
257 0.20°C and +0.20°C per decade) during winter months (Dec.-Feb.), the increase in
258 temperatures in spring (March-May) and summer (June-August) ranged between +0.30°C and
259 +0.80°C per decade (Fig. 1). Warming during autumn (Sept.-Nov.) was also high with trends
260 ranging between +0.20°C and +0.90°C per decade. Minimum monthly temperatures increased
261 all year long except in winter and maximum monthly temperatures increased more strongly in
262 spring-early summer with more than 0.5°C per decade in March, April, May and June (Fig.

263 1). Our results thus show a strong seasonality in the warming trend experienced by birds at
264 our study site, along with differences between warming in minimum and maximum monthly
265 temperatures.

266

267 *Selection on laying date and its temporal variation*

268 The fixed effects of the model revealed that the selection gradient on laying date was
269 significantly negative over the 24 years of monitoring ($\beta = -0.049 \pm 0.009$, $F = 26.15$, $P <$
270 0.001). Clutch size was under a strong and significant positive selection ($\beta = 0.119 \pm 0.009$, F
271 $= 149.34$, $P < 0.001$).

272 Our analyses of annual variation in selection gradients for laying date revealed highly
273 significant fluctuations ($\chi^2 = 21.86$, $P < 0.001$) in sign and magnitude, across the 24-years of
274 monitoring (Fig. 2). For example, while early breeders were strongly favoured in 2008
275 (estimates obtained from a model of selection fitted in 2008: $\beta = -0.155 \pm 0.036$, $F = 33.84$, P
276 < 0.001), selection favouring late breeders was found in 2009 (albeit not significant, $\beta = 0.130$
277 ± 0.068 , $F = 2.54$, $P = 0.133$) (Fig. 2). Overall, the annual standard deviation in the slope of
278 the selection gradients was relatively strong ($\sigma_{\text{year}}(\beta_{\text{LD}}) = 0.063$).

279

280 *Climate warming and selection*

281 Among the 14 possible drivers tested, the model averaging analysis showed that only daily
282 maximum April temperature and predation rate influenced selection on laying date, with a
283 probability to be a component of the best model (relative importance; e.g. from the fixed
284 effect part of the model) of respectively 89% and 88% (Table 1). Warm maximum April
285 temperatures and low predation rates increased the strength of selection on laying date (since

286 selection acting on laying date is negative overall – earlier breeders are favoured). Note that
287 these two drivers also significantly altered the strength of selection when tested using a null
288 hypothesis statistical framework ($F = 12.12$, $P < 0.001$ and $F = 16.57$, $P < 0.001$ for the
289 interaction terms between laying date with predation rate and maximum April temperatures
290 respectively).

291 All other potential drivers had probabilities $\leq 6\%$ of influencing breeding selection patterns.
292 Given the values of the overall linear selection gradient for laying date (-0.050 ± 0.009) and
293 the interaction term between laying date and maximum April temperature (-0.024 ± 0.013),
294 these results suggest an increase in the strength of selection by 46% (95% confidence
295 intervals (CI): 30%-63%) for a $+1^\circ\text{C}$ anomaly (Fig. 3, Table 1). This means that the difference
296 in relative fledging success between breeders laying 38 days apart (5 standard deviation in
297 laying date, *i.e.* encompassing 97% of the laying dates) are 0.32 and 0.72 for 0°C and $+3^\circ\text{C}$
298 anomalies respectively (Fig. S3). To illustrate further the selective effect of anomalies in
299 maximum April temperatures, we conducted selection models on three sub-datasets,
300 depending on temperature: 12 years, 3 years and 5 years in which anomalies in April
301 temperature were lower than 1°C , ranged from 1°C to 2°C , and were higher than 2°C
302 respectively. Results from these three models of selection confirmed that higher temperature
303 anomalies translated into stronger selection acting on laying date ($\beta_{\text{LD}} = -0.0267 \pm 0.0139$, β_{LD}
304 $= -0.0789 \pm 0.0335$ and $\beta_{\text{LD}} = -0.1307 \pm 0.0201$ for $T^\circ\text{C} < 1^\circ\text{C}$, $1^\circ\text{C} < T^\circ\text{C} < 2^\circ\text{C}$ and $T^\circ\text{C} >$
305 2°C respectively; see Fig. 4). While selection acting on laying date was marginally non-
306 significant for years experiencing a temperature anomaly lower than 1°C ($F = 3.72$, $P =$
307 0.054), the selection gradient was significant for years experiencing a temperature anomaly
308 higher than 1°C ($F = 5.54$, $P = 0.021$ and $F = 42.30$, $P < 0.001$, for $1^\circ\text{C} < T^\circ\text{C} < 2^\circ\text{C}$ and $T^\circ\text{C}$
309 $> 2^\circ\text{C}$ respectively). Finally, the selection gradients acting on clutch size were not stronger
310 with greater temperature anomalies ($\beta_{\text{CS}} = 0.1321 \pm 0.0139$, $\beta_{\text{CS}} = 0.1310 \pm 0.0336$ and $\beta_{\text{CS}} =$

311 0.0703 ± 0.0196 for $T^{\circ}\text{C} < 1^{\circ}\text{C}$, $1^{\circ}\text{C} < T^{\circ}\text{C} < 2^{\circ}\text{C}$ and $T^{\circ}\text{C} > 2^{\circ}\text{C}$ respectively; all P -value
312 were < 0.001).

313

314 **Discussion**

315 Our analyses confirmed that selection favors earlier breeding in Mediterranean blue tits
316 overall, but also that natural selection showed important fluctuations both in sign and
317 magnitude over the past 25 years. Importantly, we showed that daily maximum April
318 temperature was the main climatic variable correlated with the strength of selection on laying
319 date.

320 In temperate forests, spring temperatures are tightly linked to the annual laying date
321 adjustment of insectivorous passerines (Visser, Holleman & Caro 2009) that are faced with
322 the challenge of matching maximum caterpillar availability to nestling food demand (e.g. Van
323 Noordwijk, McCleery & Perrins 1995; Visser, Holleman & Gienapp 2006). As a result, avian
324 ecologists have emphasized that warmer spring temperatures should contribute to
325 strengthening selection for earlier laying date (Crick 2004; Gienapp, Reed & Visser 2014).

326 This assumption is potentially misleading because natural selection is caused by a variance in
327 fitness and phenotypic performances of individuals, which have rarely been shown to be
328 driven by climate warming (but see Reed, Jenouvrier & Visser 2013; Chevin, Visser & Tufto
329 2015). In other words, a mismatch between trophic levels induced by warming temperatures
330 does not always represent a selection pressure, in particular if all individuals are affected
331 similarly by the warming. Hence, our results represent a rare demonstration of an increase in
332 natural selection strength following a strong spring warming. This warming experienced by
333 blue tits was linked to an increase in the variation in their expected fledging success,
334 depending on their timing of reproduction. This result is concordant qualitatively with those

335 found in two great tit populations monitored for more than 40 years in the Netherlands (e.g.
336 Visser *et al.* 1998; Husby, Visser & Kruuk 2011; Reed, Jenouvrier & Visser 2013; Chevin,
337 Visser & Tufto 2015) and the United Kingdom (e.g. Charmantier *et al.* 2008). It is informing
338 to compare the strength of the relationship between the directional selection on laying date
339 and spring temperature among studies. This relationship, termed the thermal sensitivity of
340 selection (B , Chevin, Lande & Mace 2010), has been estimated at $= -5.30$ days/ $^{\circ}\text{C}$ for great
341 tits in Wytham Woods (UK, Vedder, Bouwhuis & Sheldon 2013) and at -5.01 days/ $^{\circ}\text{C}$ for the
342 same species in Hoge Veluwe (Netherlands, Chevin, Visser & Tufto 2015). Considering our
343 estimate of the interaction term between maximum April temperatures and laying date ($=$
344 0.024 ± 0.013 , Table 1), we expect a thermal sensitivity $B = -9.6$ days/ $^{\circ}\text{C}$ in the present
345 Mediterranean blue tit population. This discrepancy between our and previous estimates may
346 have several origins, such as the time period considered for the temperature measure and/or
347 the warming intensity (Phillimore *et al.* 2016). Indeed, previous work investigated the thermal
348 sensitivity during a period that was preliminary identified to be the best predictor of the laying
349 date using a sliding-window analysis (Bailey & van de Pol 2016a). Moreover, the only
350 estimation of B for blue tits in the literature (Phillimore *et al.* 2016) revealed a disparity by a
351 factor of three between latitude (B_{lat}) and longitude (B_{long}) thermal sensitivity ($B_{\text{lat}} = -3.84$
352 days/ $^{\circ}\text{C}$ and $B_{\text{long}} = -9.34$ days/ $^{\circ}\text{C}$, see Table S2 in Phillimore *et al.* 2016). Note also that
353 Phillimore *et al.* (2016) found no disparity between B_{lat} and B_{long} estimates for great tits,
354 which could suggest a species-dependent thermal sensitivity. Since the period, as well as the
355 type of measure (minimum, maximum or average temperature), varies systematically among
356 studies, it greatly limits the quantitative comparison in selection sensitivity.

357 Even within a single species, life history responses to temperature variation is known to differ
358 among populations (Husby *et al.* 2010). Since the Mediterranean area is considered a hotspot
359 of climate disruption (Giorgi 2006), similar studies on the force of natural selection across the

360 blue tit distribution range would provide crucial comparative insights. Up to now, the
361 selective influence of climatic warming has rarely been showed in the wild, with some
362 previous studies showing an increase in the strength of natural selection in plants with
363 climatic warming (e.g. Domínguez & Dirzo 1995; Maad & Alexandersson 2004; Anderson *et*
364 *al.* 2012), while others showed a decrease, mainly in animals (McAdam & Boutin 2003;
365 Karell *et al.* 2011; Campbell & Powers 2015). Moreover, estimating the drivers of selection
366 remains challenging because of several interactions and covariances between potential drivers
367 and traits shaping the causal paths to selection. Our current approach based on multi-model
368 inference (Grueber *et al.* 2011) proved to be powerful to disentangle the different months and
369 modes of temperature that are related to the strength of selection.

370 Rather than analyzing a general relationship between selective forces and temperature, we
371 explored temporal changes in a variety of temperature modes and seasonality, which could
372 affect spring phenology in several ways. By showing a warming close to zero in winter, our
373 study confirms results obtained in previous studies in Switzerland (Rebetez & Reinhard
374 2008), UK (Prior & Perry 2014) and southern France (Chaouche *et al.* 2010). Trends in
375 temperatures during the blue tit breeding season (around 0.6°C per decade from March to
376 June) were similar to trends found previously for the same region during the same period
377 (+0.7°C per decade) (Chaouche *et al.* 2010). Such temperature warming in spring and summer
378 provides scope for potentially important mismatches across tropic levels (Harrington,
379 Woiwod & Sparks 1999).

380 Although this is not a causal relationship, April maximum temperatures were the main
381 variable impacting the strength of selection on laying date. The causal path behind this
382 relationship is certainly linked to the date of emergence of the main food resource of blue tit
383 nestlings (*i.e.* the caterpillars). Indeed, because the caterpillars hatching is tracking April
384 temperatures (through the bud burst oaks), blue tits are desynchronised with their main food

385 resource, and selection for early laying is occurring in a warming context. Such mistiming has
386 been shown in great tits in the UK (Charmantier *et al.* 2008) and the Netherlands (Chevin,
387 Visser & Tufto 2015), where birds could not track the advancement in caterpillar emergence
388 date. Moreover, spring warming could also decrease the caterpillar biomass by disrupting the
389 synchrony between tree and caterpillar phenology, as shown in European oaks (*Quercus*
390 *robur*, Visser & Holleman 2001) and in Sitka spruces (*Picea sitchensis*, Dewar & Watt 1992).
391 In this context, it would be relevant to explore the effect of warming seasonality on the
392 caterpillar emergence date and its relationship with selection for early breeding in blue tits.
393 Unfortunately, only 10 years of data on caterpillar biomass were available in this study site,
394 preventing us from conducting such a long-term analysis.

395 Maximum April temperatures anomalies increased significantly since 1970 in the forest of La
396 Rouvière (slope = 0.056 ± 0.012 , $P < 0.001$), yet we did not detect any significant pattern in
397 selection gradients across years since 1991 (Fig. 2). This discrepancy is due to the fact that
398 spring temperatures, while getting warmer, did not significantly increase during the 1991-
399 2015 period (slope = 0.051 ± 0.035 , $P = 0.16$), arguably due to a smaller sample size for this
400 period ($n = 24$ versus 45 years). If the warming mechanism involved until now remains stable
401 over time, average maximum April temperature anomalies, compared to the 1970-2000
402 period, are predicted to reach $+3^{\circ}\text{C}$ in 2050 (predictions extracted from an autoregressive
403 integrated moving average model conducted on the 1970-2015 period, see Fig S4). Such
404 spring warming might reinforce the strength of selection acting on laying date by 139% (a
405 multiplication by almost 2.5), meaning that differences in fledging success between blue tits
406 will keep increasing depending on their laying dates. However, these results must be
407 considered with caution because the population should theoretically respond by advancing its
408 breeding timing (a heritable trait in this population, $h^2 = 0.11$ Delahaie *et al.* 2017). Moreover,
409 mean laying date is expected to advance only if the causal factor (the caterpillar peak)

410 modulating selection pressure remains associated with spring warming (Charmantier &
411 Gienapp, 2014). Indeed, a desynchronization between the caterpillar peak and the anomalies
412 in spring temperature could modify the evolutionary trajectory of the population, making
413 future predictions challenging.

414 Several processes other than warming could influence the strength of selection on the timing
415 of reproduction of blue tits and shape its evolutionary trajectory. For instance, the selection
416 gradient acting on laying date was lower under higher annual predation rate in our study site
417 (see Table 1). Although the difference in mean absolute fitness was non-significant between
418 high and low predation years ($F = 2.87$, $P = 0.09$), the variance in relative fitness was
419 significantly ($F = 1.70$, $P < 0.001$) lower in high predation ($=0.064$) than in low predation
420 years ($=0.109$), which could potentially explain the reduction in the magnitude of selection in
421 high predation years. This result, however, is only based on four years of high predation rates
422 and thus needs to be confirmed and refined by a longer term study of predation and selection
423 in order to refine the biological interpretation of this relationship. Additionally, while
424 climate warming is mainly characterized by an increase in mean temperature, an increase in
425 climate variability among years is also observed and predicted in the future (Coumou &
426 Rahmstorf 2012), especially in the Mediterranean area (Giorgi & Lionello 2008). Hence, an
427 increase in the variability of selection regimes among years could occur in the future, and
428 could shape the adaptive response to warming. For instance, Kingsolver and Buckley (2003)
429 found that the predicted evolutionary response to mean climate warming is small in an alpine
430 butterfly (*Colias meadii*) studied since 1980, mainly because of the variability in selection.
431 While climatic variability is increasing along with warming, the impact of this variability on
432 evolutionary response will be difficult to predict, especially in term of extreme climatic events
433 (Bailey & van de Pol 2016b). For instance, a previous study in the same population showed
434 that when 10% of broods experienced an extremely hot day, selection for earlier breeding

435 increased by 39% (Marrot, Garant & Charmantier 2017). In addition, besides global warming,
436 climate change is also characterized by changes in precipitation regimes. Indeed, heavy
437 rainfalls are expected to be more frequent (Giorgi & Lionello 2008), which could impact the
438 amount of caterpillar available for tits during the breeding season. We did not explore the
439 influence of monthly precipitations on selection because no change in precipitation regime
440 was detected in our study site since 1975 (unpubl. data). Another possible limitation of our
441 study is the fact that selection was investigated using fledging success as a fitness proxy.
442 Although laying date mainly affects the number of fledglings (Perrins 1970), climate warming
443 could also influence the selection acting on nestling survival until recruitment and/or adult
444 survival (Grosbois *et al.* 2006). However, nestling recruitment is linked to winter survival and
445 although the investigation of the effect of winter climate on number of recruits and selection
446 would be interesting, this would require to take into account 36 additional climatic variables
447 in our models (three climatic variables per month), leading to challenging interpretation of
448 results. Moreover, although number of recruits is more closely related to the true fitness than
449 fledging success is, the number of fledglings is more tightly linked with adult reproductive
450 performance than number of recruits (which depends more on the offspring phenotypes).

451 To conclude, this study reveals that climate warming induces an increase in selection pressure
452 during reproduction for a blue tit population in the Mediterranean region. This finding implies
453 that recent climate change results in strong selection favouring specific phenotypes (e.g.
454 earlier laying dates). This means that over and above the common phenological plasticity
455 observed (Charmantier & Gienapp 2014), natural selection could allow populations to cope
456 with global warming, if the lag between the increase in selection strength and the evolutionary
457 response remains short (Hendry & Gonzalez 2008). While increasing natural selection under
458 climate change could be a route for populations to adapt to climate change, it could also be an

459 indicator of increased extinction risk since it suggests that part of the population has reduced
460 fitness (Bell 2013).

461

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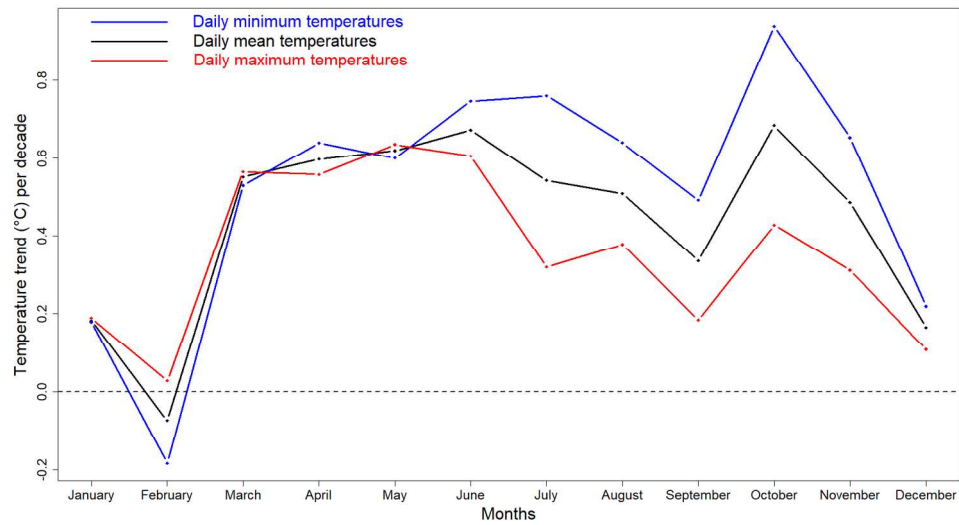
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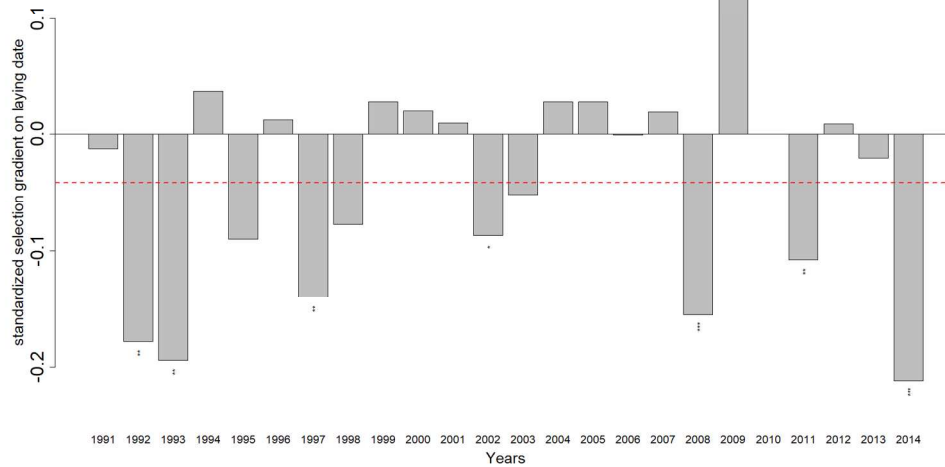
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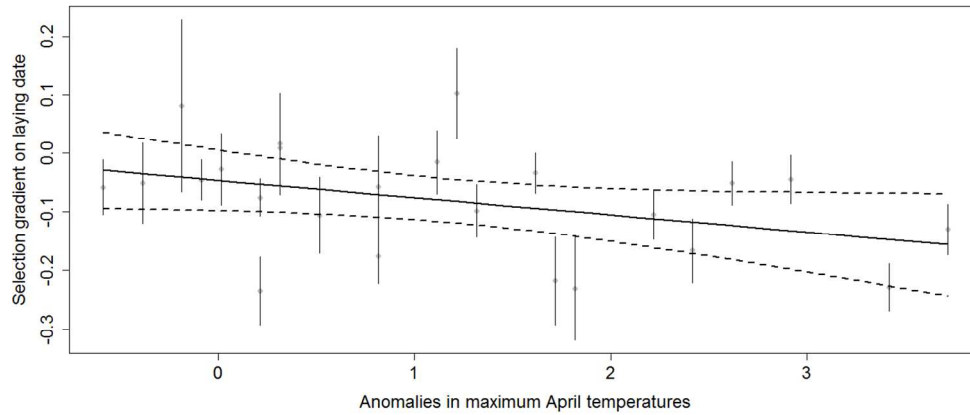
Temperature change (in °C per decade) for daily minimum (in blue), mean (in black) and maximum (in red) monthly temperatures over the 1970-2014 period near the forest of La Rouvière, southern France.

677x381mm (72 x 72 DPI)



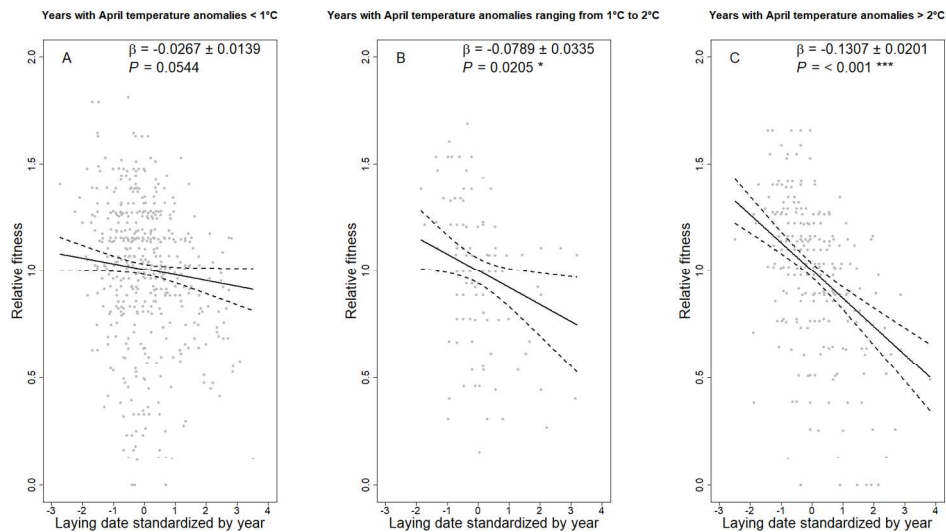
Temporal fluctuation of standardized selection gradient on laying date across years. The red dashed line indicates the mean selection gradient over 24-years. *, ** and *** represent P-values < 0.05, < 0.01 and < 0.001 respectively.

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Annual selection gradients acting on laying date related to annual anomalies in maximum April temperatures. Error bars represent the standard deviation of each estimate. The black line represents the estimate of the interaction term between maximum April temperature anomalies and laying date extracted from our best model during the model averaging procedure. Dashed lines represent 95% confidence intervals.

480x229mm (72 x 72 DPI)



Directional selection gradients for laying date (solid lines) estimated on three datasets containing only years experiencing three different warming context: (A) 12 years experiencing anomalies in maximum April temperatures lower than 1°C ($n = 530$ broods); including 4 years (1994, 1998, 2000 and 2013) associated with negative temperatures anomalies, (B) 3 years experiencing anomalies in maximum April temperatures ranging from 1°C to 2°C ($n = 104$ broods) and (C) 5 years experiencing anomalies in maximum April temperatures higher than 2°C ($n = 288$ broods). Temperatures anomalies correspond to the temperatures compared to the average temperatures over the 1970-2000 period. Years associated with a high predation rate (2001, 2006, 2009 and 2010) were removed from these datasets to avoid confounding their effect with the climatic signal (see Table 1). Dashed lines represent 95% CIs. The mean annual standard deviation of laying date was 7.6 days in our population.

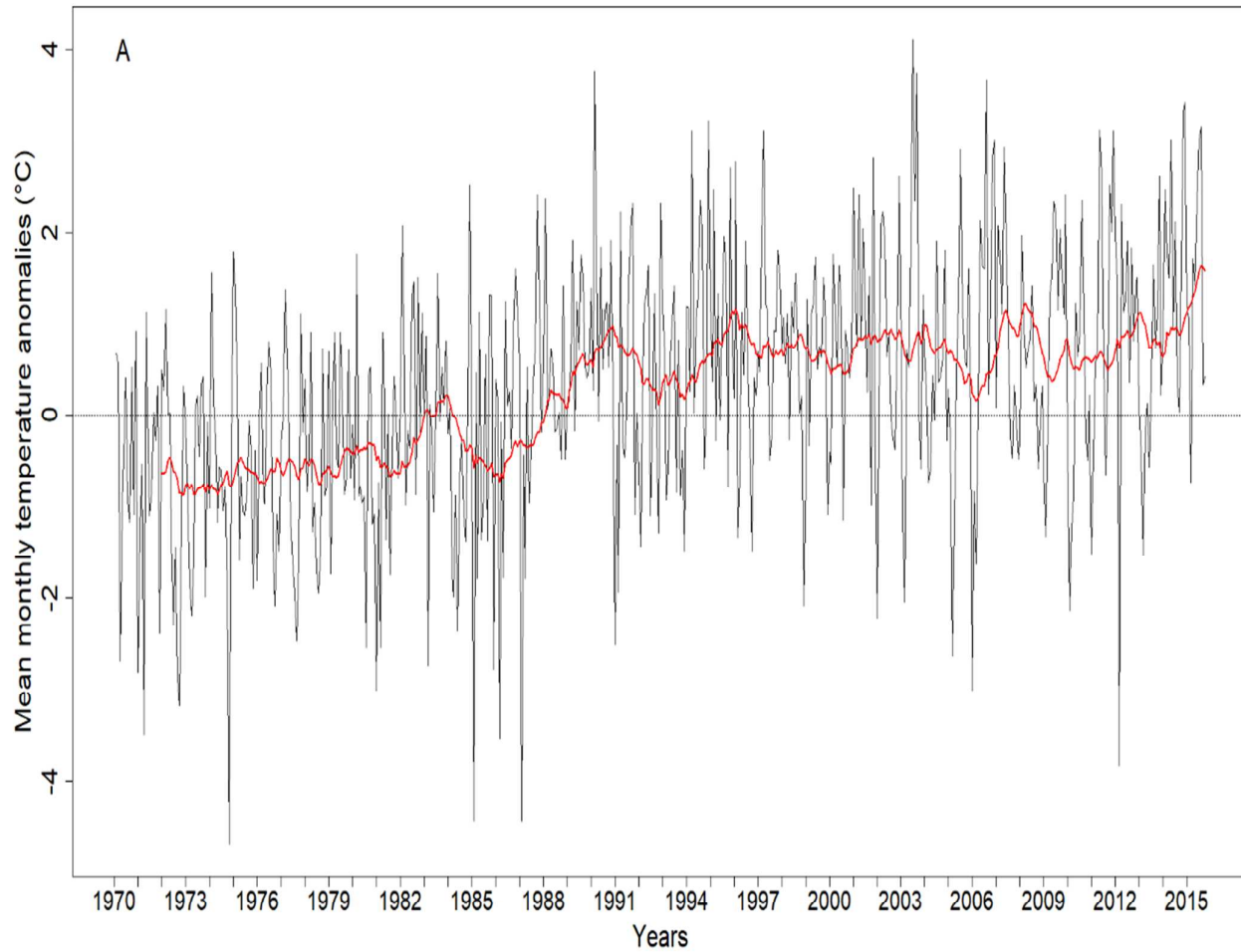
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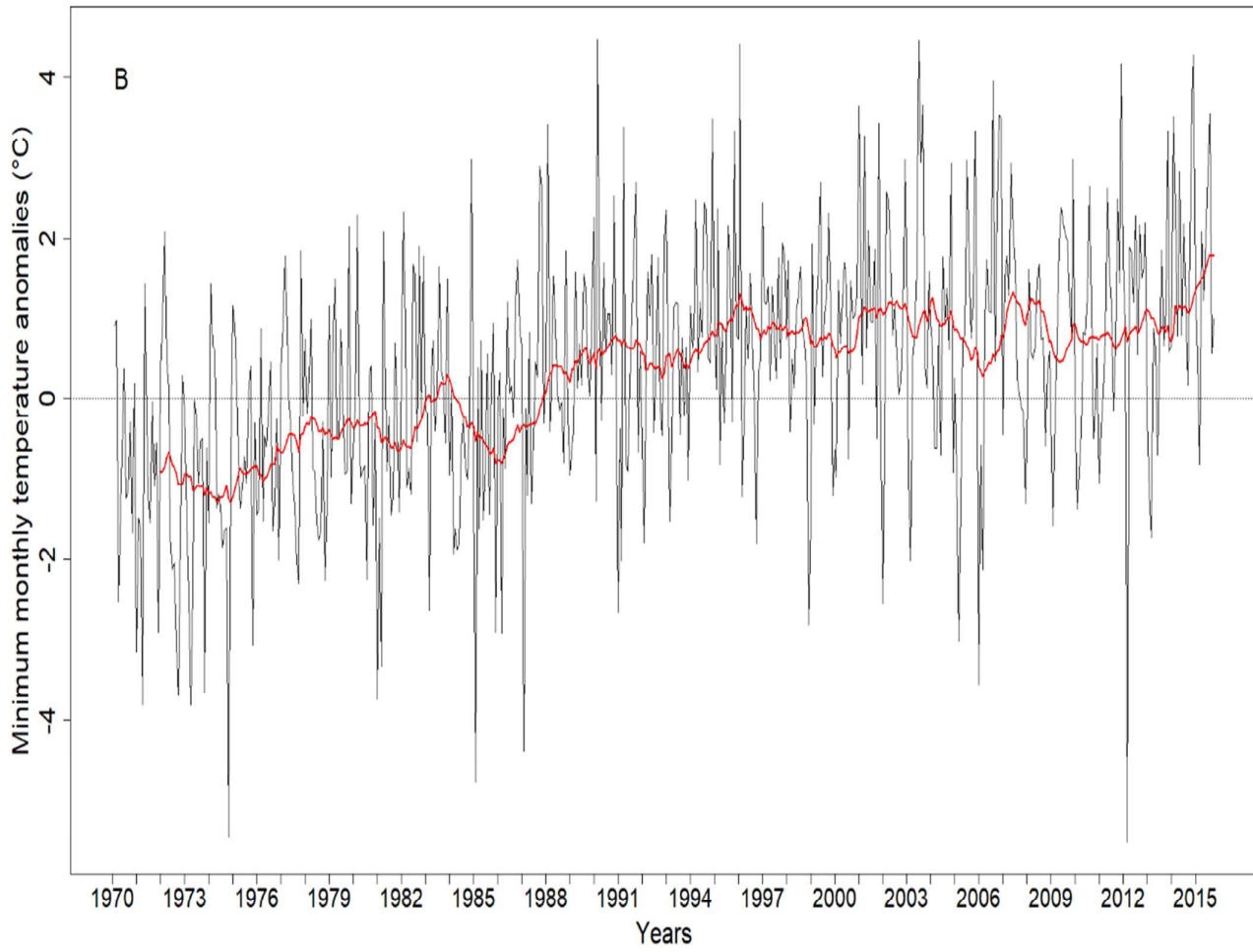
Table 1: Summary results of the model averaging approach to assess climatic variables driving selection on laying date.

Variable in interaction with laying date	Averaged estimates	Relative importance
T°C min – March	0.0000 (\pm 0.0006)	1 %
T°C mean - March	0.0000 (\pm 0.0004)	< 1 %
T°C max - March	0.0000 (\pm 0.0004)	< 1 %
T°C min – April	0.0000 (\pm 0.0000)	< 1 %
T°C mean - April	-0.0016 (\pm 0.0068)	6 %
T°C max – April	-0.0244 (\pm 0.0108)	89 %
T°C min – May	0.0000 (\pm 0.0008)	1 %
T°C mean – May	0.0002 (\pm 0.0022)	2 %
T°C max – May	0.0013 (\pm 0.0058)	6 %
T°C min – June	0.0000 (\pm 0.0011)	1 %
T°C mean – June	0.0001 (\pm 0.0013)	1 %
T°C max - June	0.0000 (\pm 0.0010)	1 %
Population density	0.0001 (\pm 0.0015)	1 %
Predation rate (Low)	-0.0725 (\pm 0.0351)	88 %

T°C min, T°C mean and T°C max represent the daily minimum, mean and maximum monthly temperatures respectively. Relative importance represents the probability that the variable was included in the best model. In bold, the only variable with a relative importance above 70%. Population density represents the annual mean distance between an occupied nest box and its closest neighbour. Predation rate was estimated as a categorical variable taking two different modalities: low and high corresponding to a predation rate below or above 0.1 respectively.

Figure S1: Daily (A) mean, (B) minimum and (C) maximum monthly temperature anomalies over the 1970-2015 period compared to the 1970-2000 period. The red line displays a smooth trend based on a 2-year moving window.





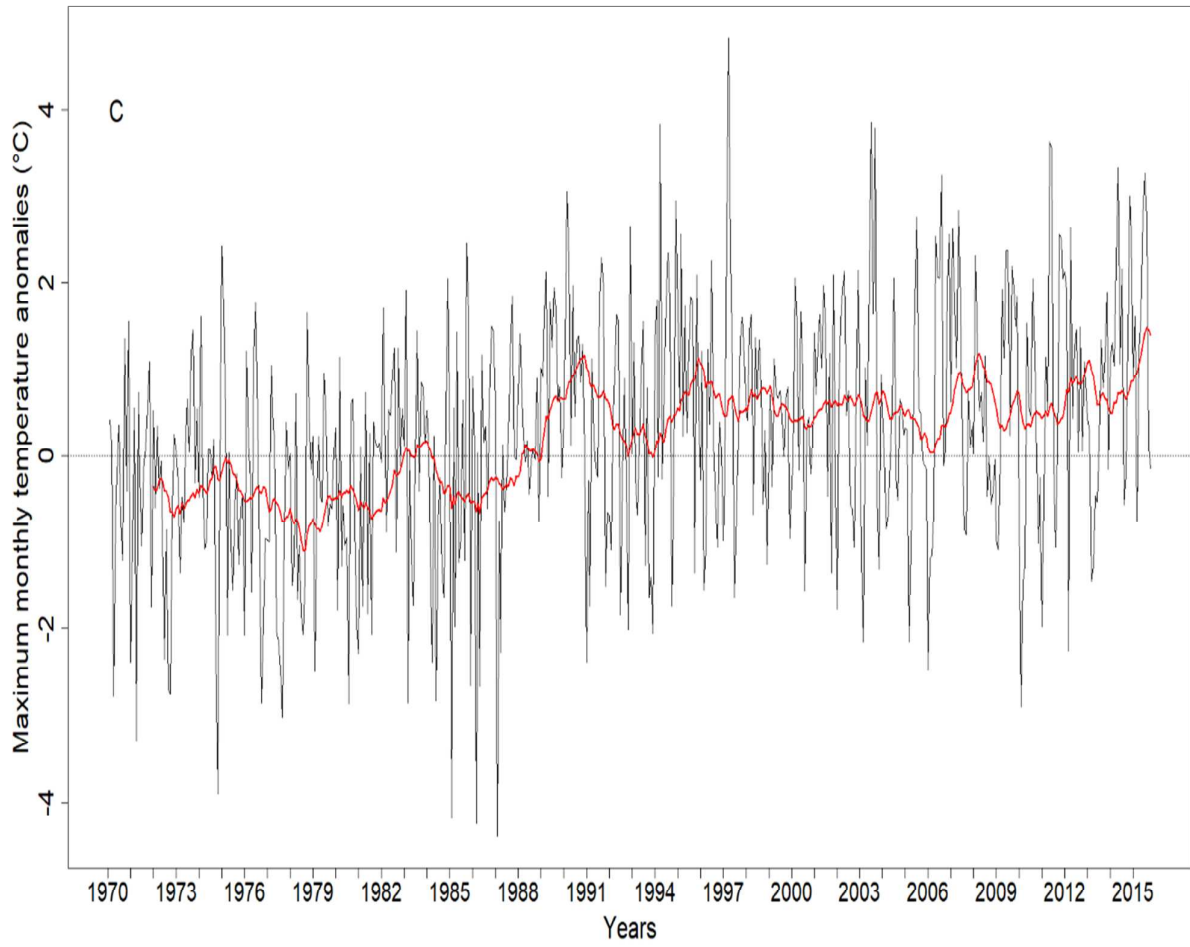


Figure S2: Distribution of relative fitness (*i.e.* number of fledglings) of female blue tits in La Rouvière, southern France.

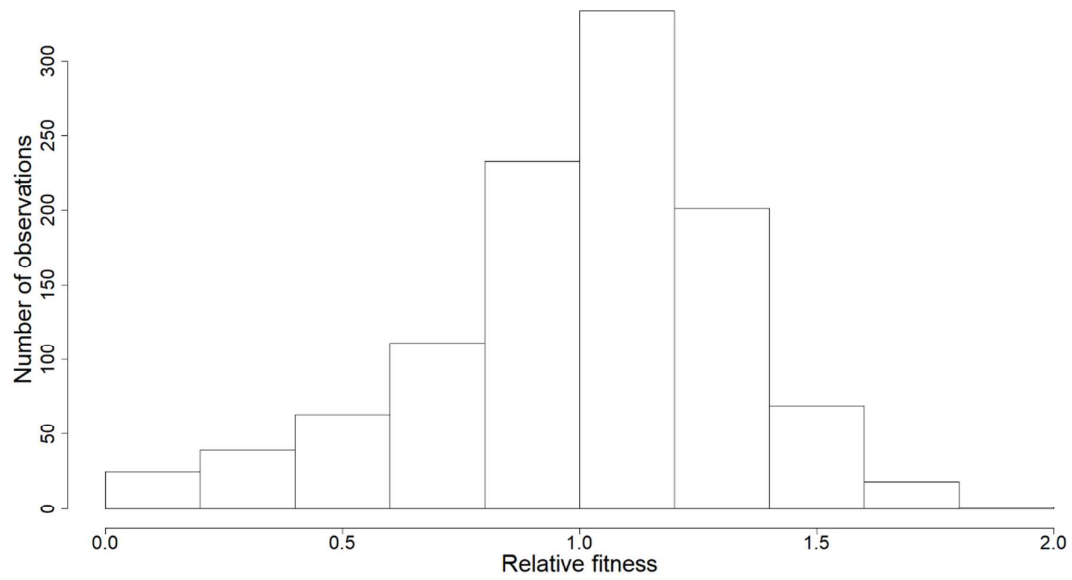


Figure S3: Standardized selection gradients on laying date for anomalies in daily maximum April temperatures ranging between 0 and 3°C. Selection gradients were extracted from the best model of the model averaging approach (including an interaction between laying date and predation rate and maximum April temperature). The mean annual standard deviation of laying date was 7.6 days in our population.

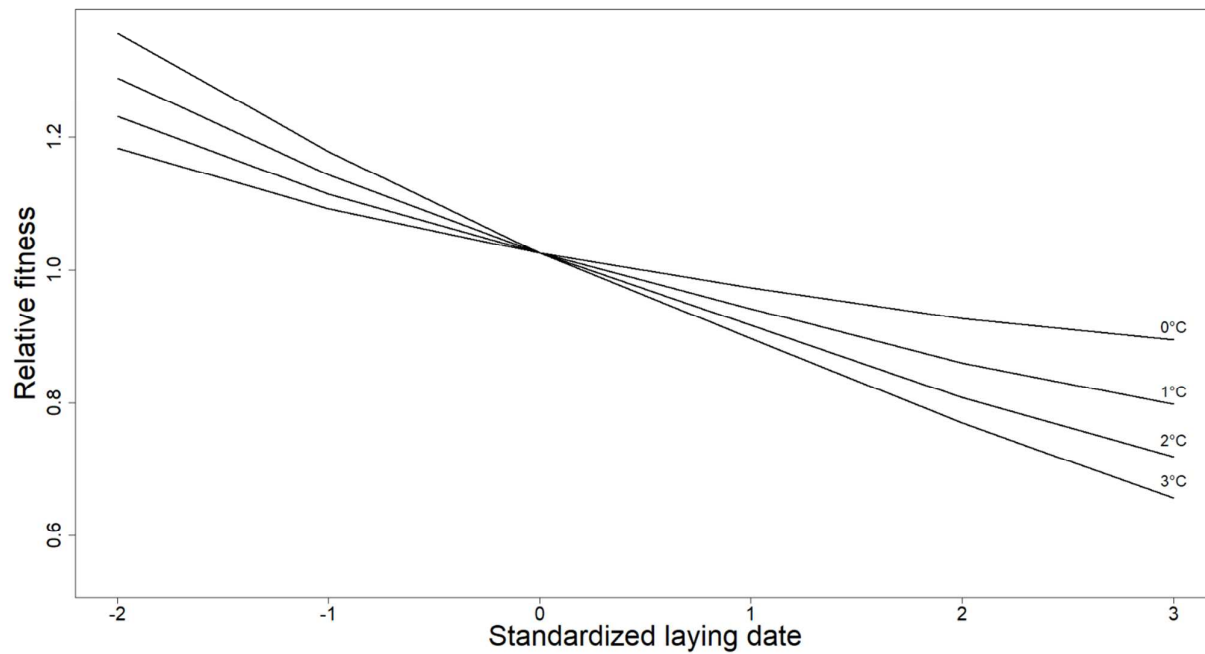
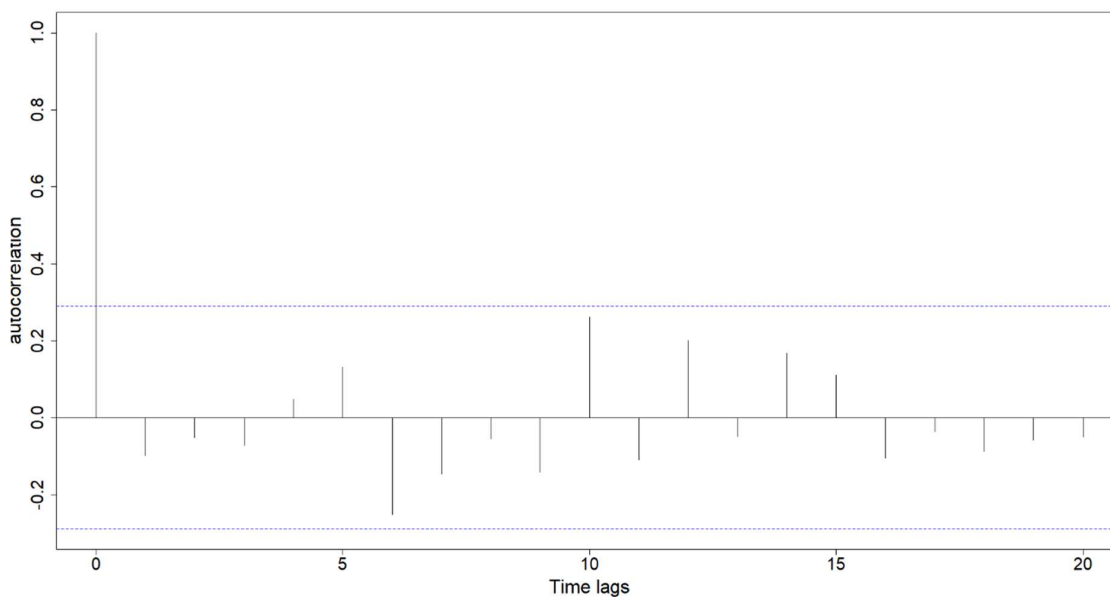
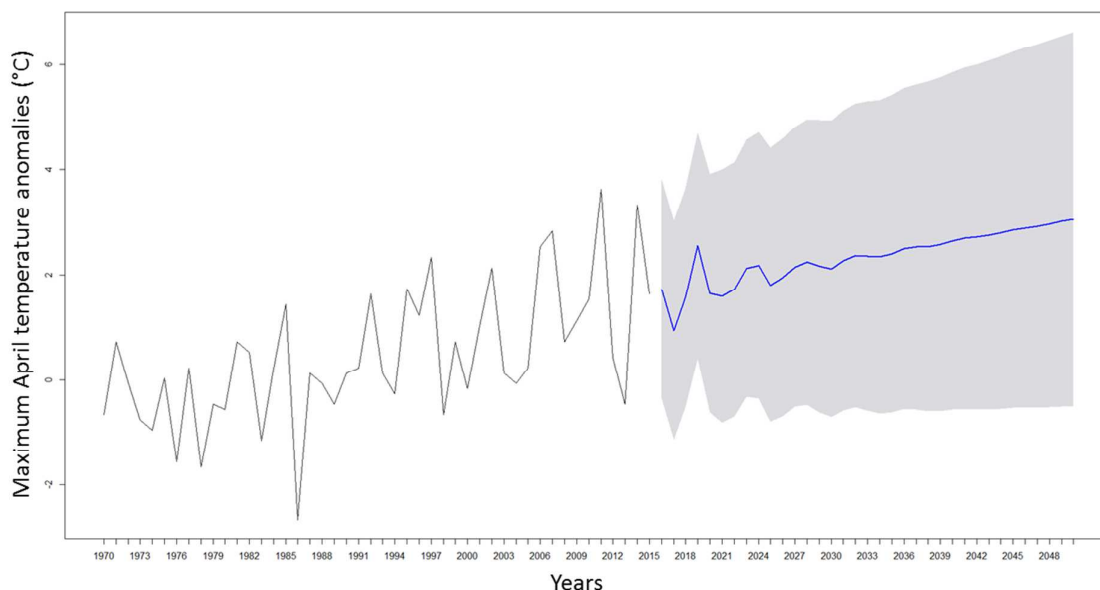


Figure S4: (A) ARIMA procedure. The graph show temporal autocorrelation in April maximum temperature. Dotted blue lines represent significance thresholds. Temperatures were autocorrelated at time lags of 3, 4 and 5 years. (B) Anomalies in daily maximum April temperatures over the 1970-2050 period compared to the 1970-2000 period. Predictions (blue line) for the 2015-2050 period were extracted from an autoregressive integrated moving average model including a temporal autocorrelation order = 4. The grey area shows the 95% confidence intervals.

A:



B:

ARIMA procedure:

First, we tested for temporal autocorrelation in temperatures using the *acf* function in R. Because significant temporal autocorrelation was detected in the temperature series (based on the visualization of the correlogram), an autoregressive model structure was needed. Commonly used in temporal series analysis, autoregressive models are a special case of statistical models, allowing to take into account temporal autocorrelation at several lags, and integrating a moving average (Brockwell & Davis, 2002). Because several ARIMA are possible for a time series, we used the *auto.arima* function from the package *forecast* (Hyndman & Khandakar, 2008) in R, in order to select the best ARIMA describing temperatures changes. The best ARIMA included a degree of differencing of 1 (which allows to take into account the positive trend) and a negative autoregressive order of 4, meaning that temperatures identified as a driver of selection were negatively autocorrelated for up to four years.

Brockwell PJ, Davis RA (2002) *Introduction to Time Series and Forecasting*, New York, NY, Springer New York.

Hyndman RJ, Khandakar Y (2008) Automatic Time Series Forecasting: The forecast Package for R. 2008, **27**, 22.

Table S1: 95% confidence set of models. These models were extracted from the 95% confidence set of best models (see text). Because laying date, clutch size, as well as individual and years random intercept were constrained to be included in all models, they are not displayed. ΔAIC and w_i represent the difference between each model and the best model and the Akaike weights respectively.

Model	T°C min - March	T°C mean - March	T°C max - March	T°C min - April	T°C mean - April	T°C max - April	T°C min - May	T°C mean - May	T°C max - May	T°C min - June	T°C mean - June	T°C max - June	Population density	Predation rate	AIC	ΔAIC	w_i
M1	-	-	-	-	-	-0.02744	-	-	-	-	-	-	-	-0.08386	379.4	0.00	0.677
M2	-	-	-	-	-	-0.02371	-	-	-	-	-	-	-	-	383.8	4.40	0.075
M3	-	-	-	-	-	-0.03300	-	-	0.02088	-	-	-	-	-0.08005	384.4	5.08	0.053
M4	-	-	-	-	-0.02860	-	-	-	-	-	-	-	-	-0.07561	384.8	5.49	0.044
M5	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.06828	385.6	6.27	0.029
M6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	386.1	6.71	0.024
M7	-	-	-	-	-	-0.03043	-	0.01415	-	-	-	-	-	-0.08051	387.0	7.61	0.015
M8	-	-	-	-	-0.02596	-	-	-	-	-	-	-	-	-	387.1	7.75	0.014
M9	-	-	-	-	-	-0.02801	-	-	-	-	-	-	0.01087	-0.08529	387.6	8.22	0.011
M10	-	-	-	-	-	-0.02555	-	-	-	-	0.00976	-	-	-0.08328	387.7	8.38	0.010
M11	-	-	-	-	-	-0.03013	-	-	0.02340	-	-	-	-	-	387.7	8.39	0.010
M12	-	-	-	-	-	-0.02515	-	-	-	-	-	0.00827	-	-0.08106	388.1	8.71	0.009
M13	-	-	-	-	-	-0.02651	-	-	-	0.00856	-	-	-	-0.08630	388.1	8.72	0.009
M14	-	-	-	-	-	-0.02735	-0.00055	-	-	-	-	-	-	-0.08403	388.7	9.34	0.006
M15	0.00300	-	-	-	-	-0.02777	-	-	-	-	-	-	-	-0.08351	389.1	9.79	0.005
M16	-	0.00012	-	-	-	-0.02746	-	-	-	-	-	-	-	-0.08394	389.4	10.04	0.004
M17	-	-	-	-0.00184	-	-0.02688	-	-	-	-	-	-	-	-0.08135	389.8	10.40	0.004