

Climate warming explains half of the magnitude of temporal changes in life-history traits

Nina McLean (✉ nina.m.mclean@gmail.com)

The Australian National University <https://orcid.org/0000-0001-7468-9515>

Loeske E. B. Kruuk

The Australian National University

Henk van der Jeugd

Dutch Centre for Avian Migration and Demography

Dave Leech

British Trust for Ornithology

Chris van Turnhout

Sovon, Dutch Center for Field Ornithology

Martijn van de Pol

Netherlands Institute of Ecology (NIOO-KNAW) <https://orcid.org/0000-0003-4102-4079>

Article

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1 Article: Nature Climate Change

2 **Climate warming explains half of the magnitude of temporal**
3 **changes in life-history traits**

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5 Nina McLean^{1*}, Loeske E. B. Kruuk¹, Henk P. van der Jeugd^{2,3}, David Leech⁴, Chris A. M. van
6 Turnhout^{5,6}, Martijn van de Pol^{1,2}

7 ¹Division of Ecology & Evolution, Research School of Biology, The Australian National University,
8 Daley Road, Canberra, Australia

9 ²Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The
10 Netherlands

11 ³Vogeltrekstation - Dutch Centre for Avian Migration and Demography, Netherlands Institute of
12 Ecology (NIOO-KNAW), Wageningen, The Netherlands

13 ⁴British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

14 ⁵Sovon Dutch Centre for Field Ornithology, Nijmegen, the Netherlands

15 ⁶Dept of Animal Ecology, Inst. for Water and Wetland Research, Radboud University, Nijmegen, the
16 Netherlands.

17 *Corresponding author

18 Email: nina.m.mclean@gmail.com

Abstract

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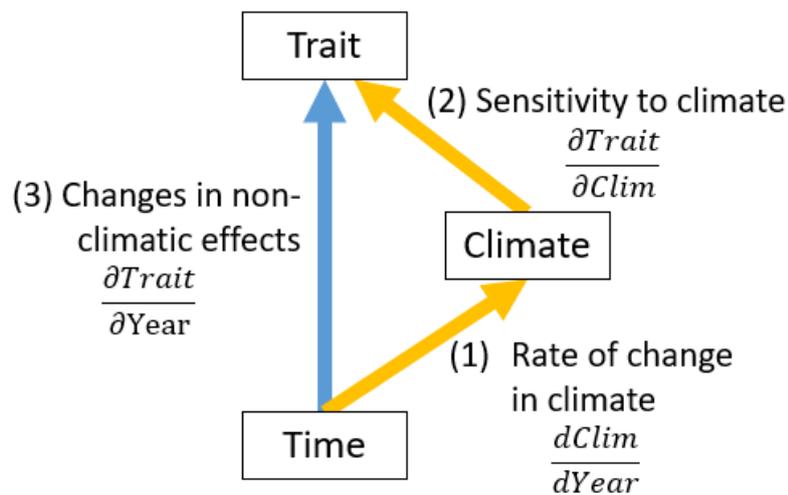
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Many wild populations are showing changes in phenotypic traits. However, the common assumption that such changes are driven by climate change relies on three conditions: that local climate is changing over time, that trait(s) are sensitive to climate variability, and that other causal agents are not also changing. We used long-term datasets on 60 bird species to test these conditions and to quantify the contribution of warming temperatures to changes in three important life-history traits. Across species, approximately half of the magnitude of changes in traits could be attributed to a single temperature window, with averages of 50% for laying date, 40% for body condition and 56% for offspring numbers. Thus, although warming temperatures were a key driver of change, other unknown factors contributed substantially to temporal trends (typically reinforcing change). Further analyses showed that these non-temperature-driven contributions explained most of the inter-specific variation in trait changes.

Introduction

Given the widespread evidence for ongoing temporal change in life-history traits of wild animal and plant populations, a key challenge facing ecology today is to understand the role of our rapidly changing climate in driving these phenotypic changes. Many studies have correlated the responses of traits (such as phenology or reproduction) to climatic variables, which is arguably the most direct means of understanding the sensitivities of species to climate^{1,2}. However, much of the literature simply considers changes in traits over time and makes the implicit assumption that temporal trends reflect responses to climate change; this approach is probably most prevalent in large-scale meta-analyses and comparative studies^{e.g.3-5}. Although the approach has benefits, whether attributing phenotypic change solely or largely to climate change is justifiable is rarely considered, let alone quantitatively tested.

To attribute temporal trends in phenotypic traits to effects of climate change alone, three conditions must be met (Fig. 1): (1) the climate experienced by the population is changing over time; (2) the trait is sensitive to climate variability; and (3) phenotypic change is not due to other causes, i.e. that other non-climatic aspects of the environment with causal effects on the trait are also not changing over time. Even though many studies acknowledge one or more of these conditions when interpreting their results, these three conditions are rarely explicitly checked simultaneously. It therefore remains an open question as to what extent observed trait changes over time are due to climate change, as opposed to being caused by other environmental or evolutionary drivers that are concurrently changing. There is thus a need for a *quantitative* decomposition of the relative importance of temperature versus other causes of temporal trends, and how this differs among species and traits.



52

53 **Figure 1 The components of trait change over time.** The combined strengths of (1) the rate of
 54 change in climate and (2) the focal trait's sensitivity to climate, determine a 'climate pathway', or the
 55 change in the trait over time due to climate. The combined impact of both the climate pathway (1,2)
 56 and (3) the non-climatic effects determines the total change in the trait over time. This path-diagram
 57 shows a visual representation of the structural equation model used and how the terminology in
 58 Equation 1 relate, where we use 'd' and '∂' to distinguish full and partial regression coefficients,
 59 respectively.

60 The three conditions needed to attribute trait changes over time to climate will not necessarily always
 61 be met. Firstly, although changes in the global climate system are unequivocal⁶, the rate of climate
 62 change (Fig 1 component 1) varies seasonally, among locations, and may be absent over short time
 63 periods⁷. Traits may be climate sensitive, but if there is no change in climate over the study period
 64 then temporal trends in traits will be independent of climate. For example, breeding time of British
 65 ring ouzels (*Turdus torquatus*) advances in wetter springs, but precipitation has not changed over the
 66 study period, and therefore nor has breeding time⁸. Secondly, even if organisms experience high rates
 67 of climate change, climate will not drive temporal trends if traits are insensitive or only mildly sensitive
 68 to climate (Fig 1 component 2). For instance, Robinson et al.⁹ found that juvenile survival was
 69 insensitive to climate in 5 out of 10 passerine species. Third, non-climatic factors that drive trait
 70 change can also change over time (Fig 1 component 3). These could include changes in habitat loss,
 71 pollution, spread of invasive species or diseases, loss of keystone species or overexploitation¹⁰⁻¹⁵. The
 72 diversity of human impacts on wild populations implies that attributing changes over time to a single
 73 causal driver may be overly simplistic, even if that single driver is as prominent as climate change.

74 We also have little understanding of how the contribution of climatic and non-climatic factors to
 75 phenotypic change differs among traits. We consider here three traits that have received much
 76 attention in studies of wild animals, and have long-term datasets: reproductive timing, body condition,

77 and reproductive success. Timing of reproduction can be influenced not only by temperature, but also
78 large-scale changes in land use, urban expansion, or nutritional state linked to, for example, habitat
79 degradation or population density^{16,17}. Body condition is sensitive to changes in food availability,
80 predation, selective harvesting and habitat degradation^{2,18,19}. There are also many non-climatic
81 variables that are known to impact reproductive success such as predation, parasitism or diseases²⁰.
82 Despite these non-climatic effects being known to be important, we currently have little
83 understanding of how strongly they contribute to temporal trends or how this varies for different
84 traits in wild populations, mainly because they are challenging to quantifying. It is also not clear
85 whether non-climatic factors generate trait change in the same direction as those of climate change,
86 reinforcing its effects^{12,21}, or if they instead counteract them^{15,22}.

87 Using two long-term datasets on common bird species from the United Kingdom and the Netherlands
88 for three important life-history traits (laying date, body condition, and offspring productivity), we
89 investigate to what extent changes over time can be assumed to be due to increasing temperatures,
90 a key component of climate change. Therefore, we first identify the temperature windows (periods)
91 that best describe associations between traits and temperature. We then use structural equation
92 modelling to quantify the conditions needed to attribute trait changes over time to climate: the rate
93 of change of temperature, the sensitivity of traits to temperature, and the rate of change in traits due
94 to other unknown drivers that are changing concurrently. Finally, we ask three questions: (1) what
95 proportion of trait changes over time are due to temperature, (2) are the combined effects of
96 temperature and other factors counteracted or reinforced, and (3) does the contribution of
97 temperature vary among different traits and species.

98 **Methods**

99 **Biological Data**

100 To get a general understanding of the extent that changes over time can be assumed to be due to
101 warming temperatures, we looked at three commonly studied traits: the timing of egg laying ('laying
102 date'), body condition and the number of fledglings produced per breeding attempt/brood (termed
103 FPBA, a standard measure of breeding success²³). We used two long-term datasets on common bird
104 species, one from the United Kingdom (UK) and another from the Netherlands (NL). Laying date and
105 FPBA were calculated from the dataset from the UK, which consisted of records of 35 common British
106 bird species over 48 years recorded as part of the British Trust for Ornithology's Nest Record Scheme
107 ²⁴ (1966–2013; see Table S1 for sample sizes; British Trust for Ornithology 2015). Body condition was
108 calculated from the dataset from the Netherlands, which consisted of ringing records for 47 common
109 bird species recorded as part of the Dutch Constant Effort Site (CES) program over 21 years (1994-

110 2014; See Table S2 for sample sizes). Due to data availability, the UK dataset consisted of national
111 averages for each species, while the NL dataset consisted of data from multiple sites for each species
112 (range 39-68 sites; see Fig. S1 for map and Table S1 for site details).

113 For both laying date and FPBA, we used annual mean estimates and their standard errors; these data
114 thus consisted of a single estimate per species per year, for both traits (35 species x 48 years= 1680
115 samples). Laying dates were recorded from March to July and were derived by back-calculating from
116 the date and stage (still egg-laying, incubating, hatchling of certain age) of when the nest was found.
117 FPBA estimates were derived from maximum recorded brood size and egg and chick stage nest failure
118 rates in each year (for details see²⁵). As a result, partial brood losses were not taken into account and
119 so breeding success could be underestimated. However, we had no reason to assume that this
120 underestimation is dependent on the climate in any given year or that it has changed over time.

121 We calculated the average adult body condition per species per site per year and its standard error
122 (i.e. population annual averages based on 160,550 captures; see Appendix for details). From the 13th
123 April until the 14th August every year birds were captured, and body mass (grams), wing length
124 (maximum chord measurement²⁶), sex and age-class (juvenile or adult) were all recorded²⁷. Birds were
125 considered adults after their first calendar year in all species. We calculated body condition as the
126 residuals of body mass on size (wing length), while correcting for age, sex and moment of capture
127 (Appendix S1). To make body condition comparable across species of different sizes, we expressed
128 changes in body condition as a percentage relative to a species' mean body mass.

129 **Climate Data**

130 We used daily mean temperature records from the Central England Temperature dataset (Parker et
131 al. 1992) and from the Royal Netherlands Meteorological Institute (KNMI; www.knmi.nl). As we used
132 only single laying date and FPBA estimates for the whole of the United Kingdom (rather than site-level
133 estimates), we used a single measure of climate taken from the Central England Temperature dataset.
134 Dutch temperature data from 37 weather stations across the Netherlands were used, with biological
135 data from each Dutch CES site matched with the closest weather station (mean distance 17 km; Table
136 S3).

137 **Statistical Analysis**

138 **Climate Windows**

139 We performed 'sliding window' analyses for each species and trait (laying date, body condition and
140 FPBA) to identify the time period in each year during which mean temperature best explained the
141 variation in annual trait values for each species. Using the R package *climwin*²⁸, we systematically
142 explored all possible combinations of consecutive weeks for the previous two years (from the 1st and

143 15th of August for the UK and NL datasets, respectively) to identify the ‘best’ possible temperature
144 window. Consequently, a mean annual trait value from 2009 in the UK would consider weather over
145 the dates 01/08/2007-01/08/2009. This meant that potential climate windows could differ in their
146 periods across species, for instance from recent spring temperatures to previous year conditions. All
147 analyses fitted linear temperature relationships and assumed Gaussian distributions for the response
148 variables. For all three response variables, the *climwin* analysis weighted values by the inverse of the
149 standard errors of the estimates, such that uncertain estimates contributed less. We selected the best
150 model based on Akaike’s Information Criterion modified for small samples (AICc²⁹).

151 When testing so many climate window models, the chances of spurious results are high¹.
152 Randomisation techniques were therefore used to assess the likelihood that the best time window
153 might occur by chance²⁸. For each species we performed 50 randomisations using the *randwin*
154 function and calculated the chance that the best window was a true positive using the inbuilt function
155 *pvalue* within *climwin* ($P_{\text{true positive}}=1-P_c$, see²⁸). We considered there to be a temperature signal present
156 if the best window had more than a 50% chance that it was a true positive. Species were therefore
157 categorised as either temperature sensitive or insensitive depending on whether a reliable
158 temperature window could be identified.

159 Although our timeseries are at least two decades long, species with smaller sample sizes could still be
160 more likely to be categorised as insensitive. Therefore, we conducted a generalised linear model with
161 binary errors with the average number of individuals per site per year as the explanatory variable and
162 temperature sensitivity (sensitive or insensitive) as the response variable. Our ability to detect a
163 climate window did not depend on sample size for any of the three traits (Table S6, Fig S7).

164 *Structural Equation Models*

165 After identifying the climate windows for which temperature explained most variation in the traits for
166 each species, we used structural equation models (SEMs) to quantify the importance of temperature
167 in mediating trait changes over time. For each species that was found to be temperature sensitive, we
168 constructed a structural equation model using the R-package *piecewiseSEM*³⁰ (See appendix for R
169 code). Figure 1 shows the path-diagram of the SEM, with three individual path estimates being
170 calculated: the effect of year on temperature, the effect of temperature on the trait and the direct
171 effect of year on the trait. The association between year and trait was therefore decomposed into two
172 pathways, the ‘Temperature Pathway’ which is the indirect effect on the trait mediated by
173 temperature (i.e. changes over time due to the effects of temperature; Fig 1 components 1 & 2) and
174 the ‘Other Pathway’ which is the direct effect on the trait due to all other drivers (i.e. *not due* to the
175 effects of the identified temperature window; Fig 1 component 3)³¹. By assessing the partial regression

176 of a trait on both temperature and year, we effectively ask the question whether temperature explains
 177 temporal trait variation *beyond* any shared directional temporal trends in trait and temperature (i.e.
 178 do year-to-year fluctuations around any shared temporal trend also covary?). Because the Other
 179 Pathway captures the change in the trait over time unrelated to the identified temperature window,
 180 it effectively incorporates effects of other drivers of trait change that have changed directionally over
 181 time. The Other pathway is thus likely composed of many drivers. Although we refer to the first
 182 pathway as the ‘Temperature Pathway’, we note there could in theory also be additional effects of
 183 temperature in other window periods outside of the ‘best’ windows selected in our *climwin* analysis
 184 that would contribute to the ‘Other Pathway’.

185 Temperature was mean centred for each species to ensure that the relationships would reflect within-
 186 population associations³², all response variables had Gaussian distributions and were weighted by the
 187 inverse of the standard error. Species for which there was no evidence of a reliable temperature
 188 window (‘insensitive’ species) were excluded from SEM analyses.

189 Our model was ‘saturated’ as all path estimates were needed to answer our questions³¹. This meant
 190 that the usual model fit statistics could not be calculated. In order to check that the estimates from
 191 our SEMs were likely to be reasonable, we checked the fits of each of the individual path estimates
 192 and made sure the residuals were normally distributed, and the standard errors were not extremely
 193 large or close to zero. All models satisfied these assumptions.

194 *Temperature and Total Pathways*

195 The Temperature and Total Pathways for each species and trait were calculated from the three
 196 individual path estimates previously calculated in each SEM (Fig 1 components 1, 2 & 3). Following the
 197 rules of path tracing³³, the Total Pathway — or the total change in a trait over time — is determined
 198 by each of the underlying linear relationships between year, trait and climate³⁴:

$$199 \quad \frac{dT_{\text{trait}}}{d\text{Year}} = \frac{dT_{\text{temp}}}{d\text{Year}} * \frac{\partial T_{\text{trait}}}{\partial T_{\text{temp}}} + \frac{\partial T_{\text{trait}}}{\partial \text{Year}} \quad (\text{eq. 1})$$

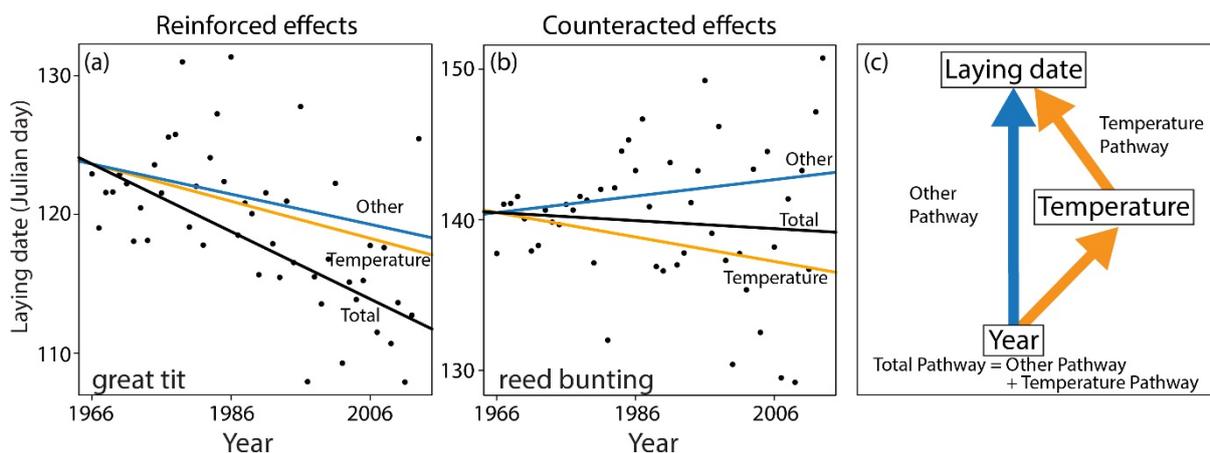
200 (where we use ‘d’ and ‘∂’ to distinguish full and partial regression coefficients, respectively). Equation
 201 1 could be read as the Total Pathway ($\frac{dT_{\text{trait}}}{d\text{Year}}$) being equal to the sum of the Temperature Pathway
 202 ($\frac{dT_{\text{temp}}}{d\text{Year}} * \frac{\partial T_{\text{trait}}}{\partial T_{\text{temp}}}$) and the Other Pathway ($\frac{\partial T_{\text{trait}}}{\partial \text{Year}}$). Where, the Temperature Pathway was calculated as
 203 the product of the effect of year on temperature ($\frac{dT_{\text{temp}}}{d\text{Year}}$) with the effect of temperature on the trait
 204 ($\frac{\partial T_{\text{trait}}}{\partial T_{\text{temp}}}$) (Fig 1 components 1 & 2³¹). As the individual path coefficients from the SEM each have
 205 estimates of associated uncertainty, we applied a bootstrapping technique to calculate 95%
 206 confidence intervals for the compound Temperature and Total Pathways (Appendix 1).

207 **Percentage of change over time explained by temperature**

208 For each species and trait, we calculated the percentage of change over time due to the Temperature
 209 Pathway as:

210
$$\%trend\ due\ to\ temperature = \frac{|Temperature\ Pathway|}{|Other\ Pathway| + |Temperature\ Pathway|} * 100 \quad (eq. 2)$$

211 where |..| denotes the absolute value. Equation 2 denotes the percent contribution of the
 212 Temperature Pathway to the Total Pathway, irrespective of sign or counteracting effects. For example,
 213 if a species had a Total Path estimate of a rate of change in laying date of 4 days per year, a
 214 Temperature Path estimate of 2 days per year, and an Other Path estimate of 2 days per year, then
 215 the Temperature Pathway explains 50% of the total change. If there are counteracting effects, where
 216 the Total Path estimate is zero days per year, the Temperature Path estimate is -1 days per year and
 217 the Other Path estimate is +1 days per year, then the Temperature Pathway would again explain 50%
 218 of the total change. Thus, our metric of eq. 2 is insensitive to the sign of the single pathways and the
 219 magnitude of the Total Pathway, see also Fig. 2 for a graphical example on the great tit and reed
 220 bunting data-sets from the UK. The percent contribution of the Temperature Pathway will be
 221 underestimated due to any error in the estimates of the temperature indices (temperatures collected
 222 at weather stations may differ from the temperatures experience by birds at their study sites), which
 223 will lead to regression dilution³⁵. Consequently, the estimates of the Temperature Path contribution
 224 will be lower than in reality, and the estimate of the Other Pathway will increase correspondingly (as
 225 the two sum to produce the total change). In summary, our estimate of the Temperature Pathway
 226 contribution will be a conservative measure.



227
 228 **Figure 2 Example diagrams illustrating temporal trends in lay date and the contribution of the**
 229 **different pathways.** Points represent the average laying date in each year. In (a) we show a real
 230 example of the reinforced effects in great tits in the UK, with negative slopes for both the
 231 Temperature Pathway (orange) and the Other Pathway (blue), resulting in a stronger overall change
 232 in laying date over time (i.e. the Total Pathway). Plot (b) shows a real example of counteracted

233 effects in reed buntings in the UK, with a negative slope for the Temperature Pathway and a positive
234 slope for the Other Pathway, resulting in a weaker overall change in laying date over time (i.e. the
235 Total Pathway). Plot (c) shows how the slopes in (a) and (b) relate to the structural equation model.

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Results

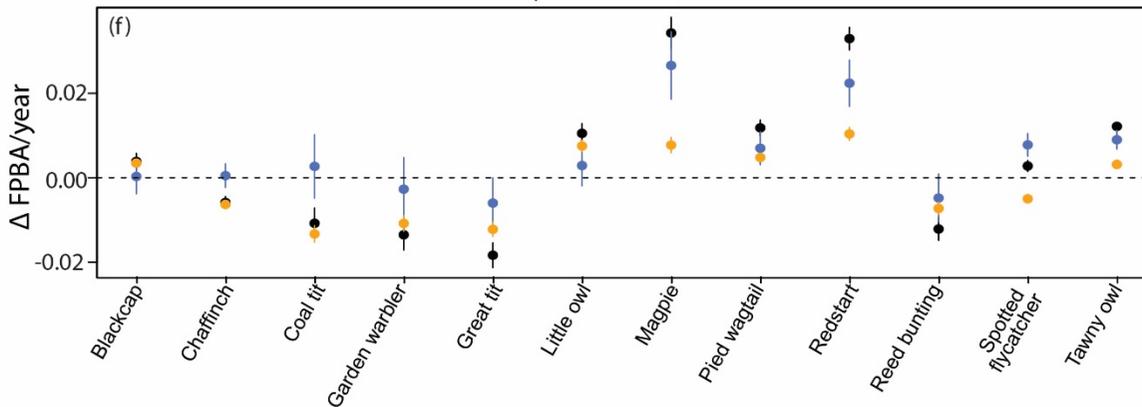
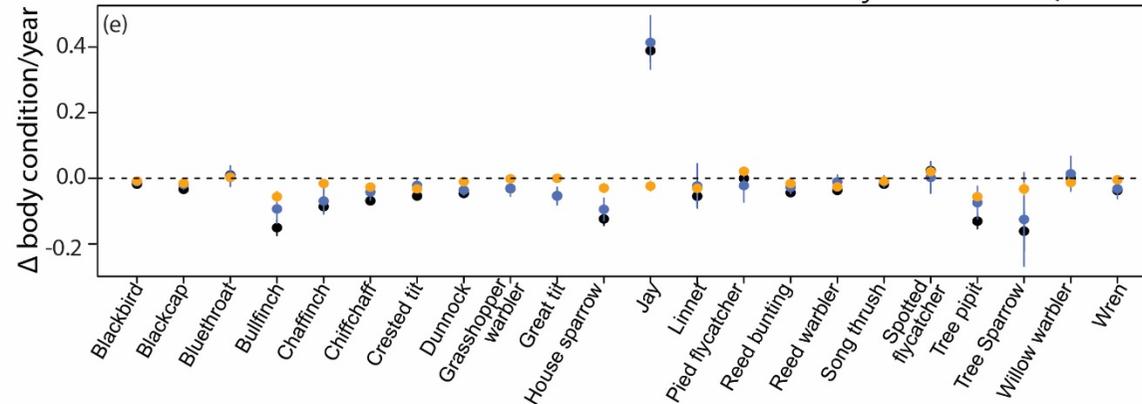
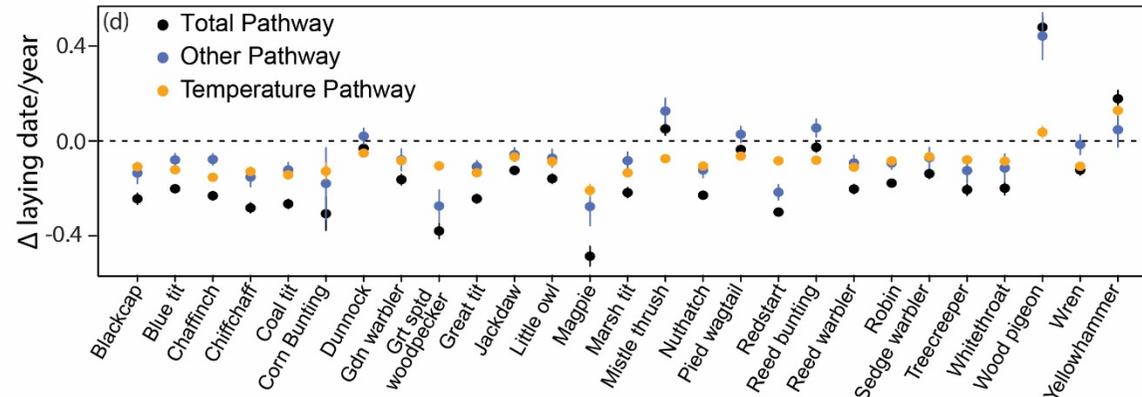
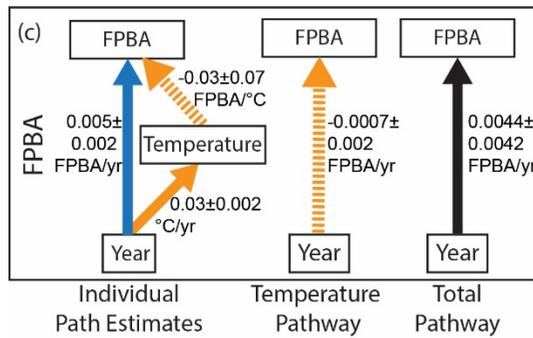
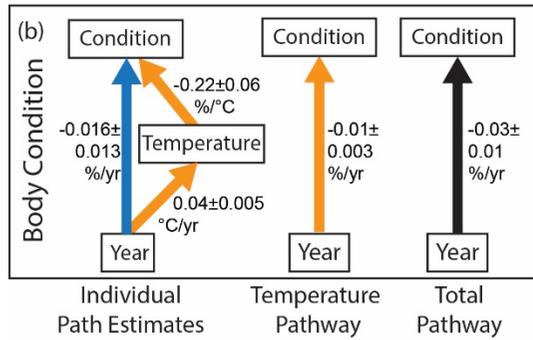
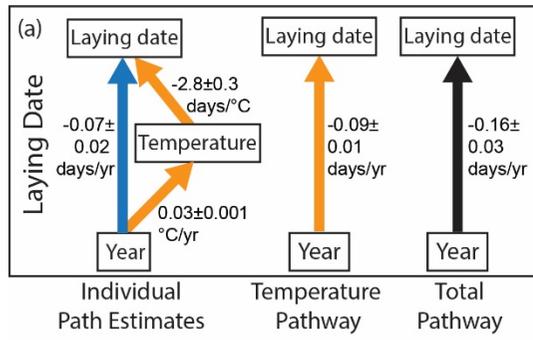
237 Conditions for attributing trait changes to climate

238 To test whether temporal trends can be attributed to warming temperatures, we decomposed trait
239 changes into the three key underlying conditions: change in temperature over time, sensitivity of traits
240 to temperature and impacts of other drivers over time.

241 In support of the first condition, mean temperature (during the windows over which the trait was
242 sensitive) increased over time in both countries over the study period (Fig 3a-c). The second condition
243 was not always met, as traits were not always sensitive to temperature. Laying date was sensitive to
244 temperature in 77% of species (27/35 species in the UK dataset), with the relevant temperature
245 windows occurring around March-May in spring (Figure S5, Table S4). Body condition was sensitive to
246 temperature in 47% of species (22/47 species in the Netherlands dataset), with many temperature
247 windows occurring around early May to mid-July in spring-early summer (Table S5). FPBA was sensitive
248 to temperature in 34% of species (12/35 UK species; Table S4). For the temperature-sensitive species,
249 warming was associated with advances in laying date (2.3 days/°C on average; Fig 3a), decreases in
250 body condition (0.22% /°C on average; Fig 3b), and highly variable effects on FPBA (decreased for 6
251 species and increased for the other 6 species such that there was no change on average; FigS4b).

252 For the third condition, effects other than the identified temperature window were often associated
253 with traits. On average, birds significantly advanced laying by 0.07 ± 0.02 days/year and FBPA increased
254 by 0.005 ± 0.002 fledglings/year due to other effects changing over time (the 'Other Pathway'; Fig 3a,c).
255 Body condition did not show a clear trait change due to other effects (Fig 3c), but this was mainly
256 caused by one species (Jays) showing a strong change in the direction opposite to almost all other
257 species showing decreasing body condition (fig. 3b).

258

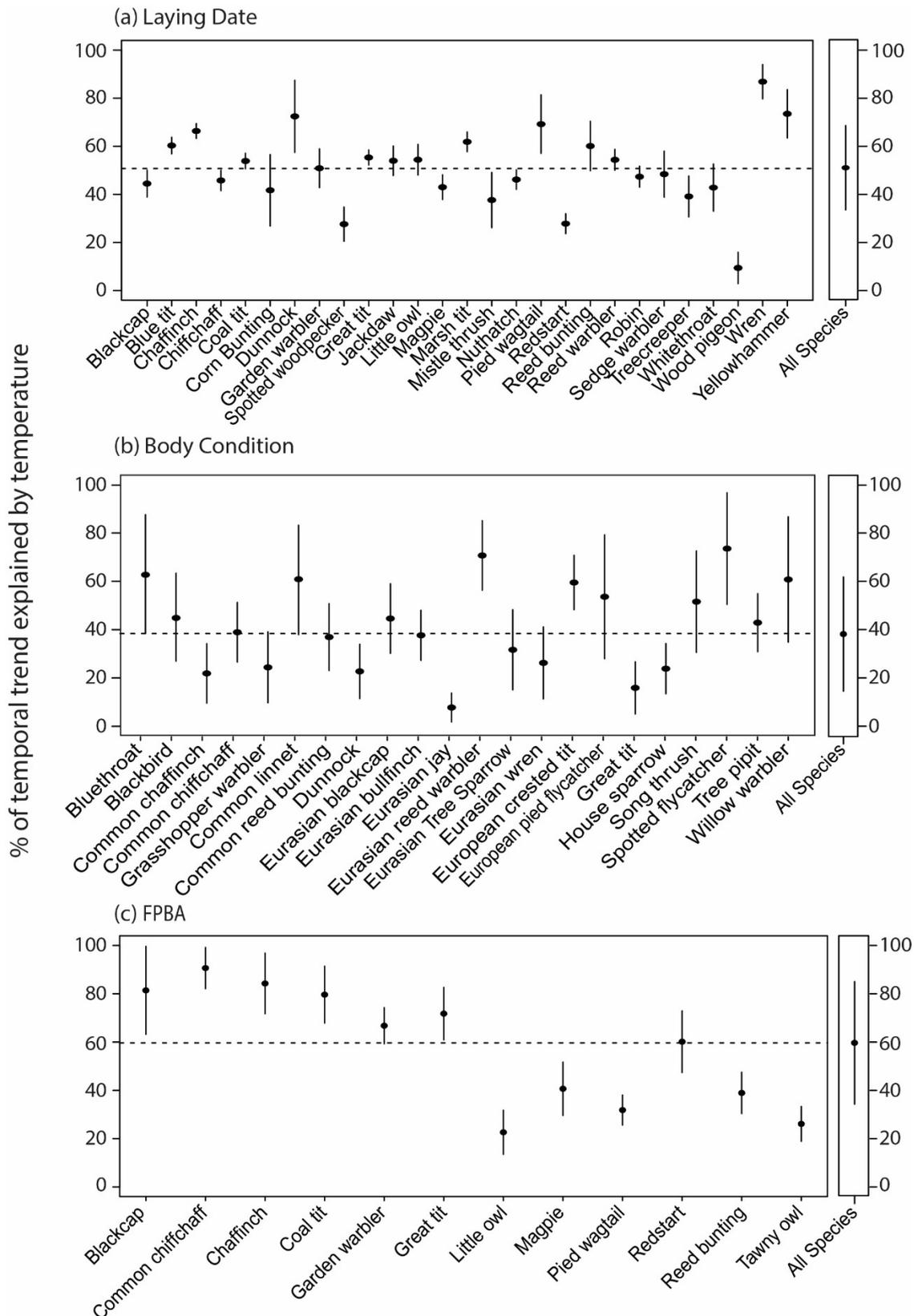


260 **Figure 3 Estimates of path coefficients averaged across species and displayed for each species.** The
261 plots in the left column (a-c) show the graphical representations of the structural equation models
262 and the averaged path estimates (\pm standard error) across all species found to be sensitive to
263 temperature. The leftmost blue and yellow arrows show the full SEM and the individual path estimates
264 for each pathway, while the middle yellow arrow shows the change in trait over time due to
265 temperature (the Temperature Pathway, calculated as the product of the year-to-temperature and
266 the temperature-to-trait path estimates). The rightmost black arrow shows the total change in the
267 trait over time due to all variables, and is calculated as the Temperature Pathway summed with the
268 Other Pathway. Solid arrows indicate the 95% confidence interval did not cross zero, while the dashed
269 arrows indicate it did cross zero. The plots in the right column (d-f) show the path estimates (\pm SEs)
270 for the Total (black), Temperature (yellow) and Other (blue) Pathways. In general, the Temperature
271 Pathway coefficients varied less across species than the Other and Total Pathways. In most cases, the
272 Total path estimate was larger than the two others because the Temperature and Other Pathways
273 reinforced one another. However in some cases, the Total Pathway was closer to zero when the
274 Temperature and Other Pathways counteracted each other's effects.

275 **Temperature-driven trait change**

276 On average across the three traits, half (49%) of the changes in traits over time was due to the
277 Temperature Pathway. There was some variation among the traits, with an average of 50% of
278 temporal changes in lay date attributed to the temperature window, an average of 40% for body
279 condition and an average of 56% for FPBA (Fig 4). However, there were large differences among
280 species in the percentage explained, with values ranging from 9% to 86% for lay date (Fig 4a), from
281 8% to 74% for body condition (Fig 4b) and from 23% to 91% for FPBA (Fig 4c).

282 In most cases the Temperature and Other Pathways had the same sign and reinforced each other (85%
283 for laying date, 77% for body condition and 75% for FPBA; Fig 3d-f). Consequently, the total changes
284 in traits over time were mostly greater than the changes due to temperature alone.



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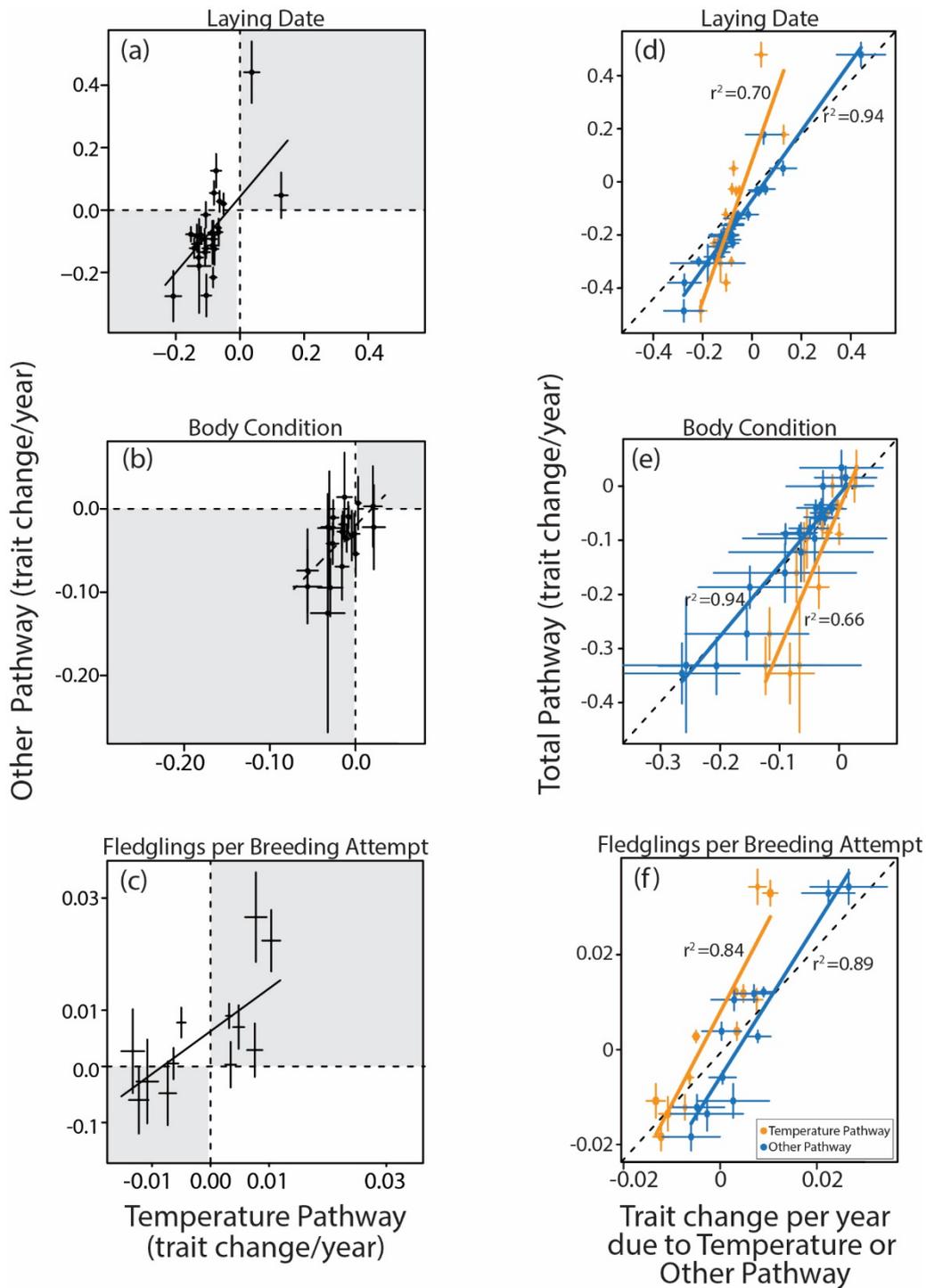
286 **Figure 4 Percentage of temporal trait trends due to increasing temperature.** Percentage of the
 287 trend in life-history traits over time that is due to the Temperature Pathway for each of the three
 288 traits across all species. The separate value listed as 'All Species' shows the average value across all
 289 species for that trait and the horizontal dotted line shows this same average for reference. Error bars
 290 reflect 95% confidence intervals.

291 Interspecific variation

292 There was a significant difference in the changes in laying date over time between temperature-
293 sensitive versus insensitive species. Temperature sensitive species advanced their laying dates by
294 three times as much as insensitive species on average (-0.15 ± 0.04 SE days/year sensitive vs. 0.05 ± 0.06
295 SE days/year insensitive; Fig S6a; Linear regression with Total path coefficient as response and
296 temperature sensitivity [sensitive/insensitive] as the explanatory variable $df=33$, $p=0.008$). However,
297 there were no significant differences in trait changes over time between temperature-sensitive versus
298 -insensitive species for body condition (-0.060 ± 0.049 SE days/year insensitive vs. 0.010 ± 0.056 SE
299 days/year sensitive) or FPBA (0.006 ± 0.003 SE days/year insensitive vs. 0.003 ± 0.004 SE days/year
300 sensitive) (Fig S6b & c).

301 Of the temperature-sensitive species, the Temperature Pathway and Other Pathway estimates were
302 positively correlated for laying date ($r=0.64$ 95% CI=0.35, 0.82, $n=27$) and FPBA ($r=0.72$ 95% CI=0.24,
303 0.91, $n=12$), but not for body condition ($r=0.13$ 95% CI=-0.31, 0.52, $n=22$) (Fig 5a-c).

304 Responses to temperature were more consistent compared to responses to other effects, which
305 varied substantially across species. Variation *among* species in the total trait change over time (due to
306 both temperature and other effects) appeared to be mainly due to the varying effects of the Other
307 Pathway, even though temperature explained on average about half of the total temporal change
308 *within* a species (Fig 3d-f). Specifically, for all traits, the Other Pathway better explained variation in
309 the total change in trait over time among species ($r^2_{\text{Laydate}}=0.94$, $r^2_{\text{Condition}}=0.94$, $r^2_{\text{FPBA}}=0.89$) than the
310 Temperature Pathway ($r^2_{\text{Laydate}}=0.70$, $r^2_{\text{Condition}}=0.66$, $r^2_{\text{FPBA}}=0.84$; Fig. 5d-f).



311

312 **Figure 5 Interspecific comparison of path estimates.** The left panels (a-c) show the correlation
 313 between the Temperature and the Other Pathway for all temperature-sensitive species, where each
 314 point represents a species and bars showing 95% confidence intervals. The dark shaded areas indicate
 315 when the Temperature and Other Pathways had reinforced effects. The right panel (d-f) shows the
 316 relationships between the Total change in trait over time (calculated as the Temperature Pathway
 317 summed with the Other Pathway) compared to the change over time due to 'Temperature' (yellow)
 318 and 'Other' (blue) Pathway. The x-axis is the path estimate for either the Temperature or Other
 319 Pathway. The dotted diagonal $Y=X$ is plotted to emphasize that points that fall closer to this line are
 320 more similar to the Total Pathway.

Discussion

321
322 The notion that changes in traits through time reflect responses to climate warming relies on three
323 conditions being met: climatic conditions are changing, traits are sensitive to climate, and no
324 alternative drivers of change occur. By using two long-term datasets on three life-history traits in
325 common European bird species, we show that (1) temperatures generally increased over time, (2)
326 traits were not always sensitive to temperature and (3) there were additional temporal trends in traits
327 unrelated to temperature. Our results can be viewed as both glass-half-full and glass-half-empty
328 scenarios. The fact that, on average, half of trait changes over time could be attributed to a single
329 temperature window across all species is remarkable for any ecological study, and clearly underlines
330 the impact that global warming has on natural populations. However, our analysis shows that
331 temporal trends in traits should not be solely ascribed to increasing temperature. The non-
332 temperature effects mostly reinforced temperature effects and differences in temporal trends among
333 species were more likely to be due to non-temperature factors than warming, as temperature
334 impacted species fairly consistently. This suggests that comparative studies should be cautious of
335 attributing differences in temporal trends to underlying species differences in sensitivity or exposure
336 to climate change.

337 Temporal trends predominantly, but not solely due to warming

338 The Temperature Pathway explained about half (49%) of temporal changes across all traits and
339 species. This suggests that temperature is likely the single most important contributor to temporal
340 trends given that the Other Pathway is likely comprised of many factors (such as habitat degradation
341 or predation levels), while the Temperature Pathway is driven by one single factor. Yet, other factors
342 were also associated with trait changes over time, suggesting that other drivers outside of our
343 temperature windows must also be influencing traits in European birds. Parmesan & Yohe³ argue that,
344 although competing explanations in the form of non-climatic causal agents could have impacts, it is
345 unlikely that such factors would produce a consistent pattern of impact over space and time. Yet our
346 results, and those of Crick & Sparks¹⁶ who found that only 37% of temporal trends in phenology could
347 be statistically accounted for by changes in spring temperature and rainfall (though their paper does
348 not explain how they arrived at this percentage), suggest that trends over time can be quite strongly
349 determined by non-temperature effects. Furthermore, we found that many species were insensitive
350 to temperature, suggesting that any trait changes over time in these species were solely due to non-
351 climatic effects, or other unidentified climatic effects (i.e. rainfall).

352 The finding that changes in temperature 'only' contributed on average 49% to changes in laying date
353 could be viewed as somewhat unexpected. Many studies have shown that laying date is closely

354 associated with mean spring temperatures^{16,36–38}. This relationship is considered to be predominantly
355 driven by the need to reduce mismatches with their food supplies, whose timing of peak abundance
356 vary with temperature^{37,39}. However, because the total change in laying date was substantially earlier
357 than would be expected due to increased temperatures alone, other climatic (rainfall³⁸) or non-
358 climatic factors (urbanisation, land-use^{16,17,40}) may play a stronger role than previously thought and
359 deserve more attention.

360 Increasing temperature was also the main driver for changes in body condition and FPBA (offspring
361 productivity), contributing on average 40% and 56% to temporal changes, respectively. Yet, changes
362 in factors other than increasing temperatures still contributed substantially to trends in FPBA and body
363 condition over time. Although it is becoming clearer that body condition and mass are impacted by
364 warming temperatures^{34,41–43}, our understanding of the mechanisms driving temporal changes are still
365 limited⁴⁴. Similarly, warming temperatures can influence offspring success via heat stress on young or
366 indirectly affect resources²¹, yet many other variables are known to be important including predation,
367 disease²⁰ and rainfall²¹. Future studies are now needed to confirm whether this dominant role of
368 temperature is a general pattern in other taxa, traits and regions. Our simple quantitative framework
369 provides a straightforward way to perform such comparative studies with the main prerequisite being
370 long time series on traits (as our framework does not rely on data of potential other drivers).

371 Interspecific variation in trait change

372 Interspecific variation in trait changes over time depended more on the impact of non-temperature
373 drivers, rather than reflecting thermal sensitivity. Interspecific variation was better explained by the
374 Other Pathway than the Temperature Pathway, largely because of considerable variation in the
375 sensitivity of traits to non-temperature effects across species (Fig 5). For instance, changes in laying
376 date from warming were fairly consistent across species (Fig 3d), while the total change in laying date
377 differed substantially across species due to non-temperature factors. Part of this high interspecific
378 variability might be due to the Other Pathway being comprised of multiple drivers. Different drivers
379 might act upon species differently depending on their sensitivities. For example, increased
380 urbanisation might cause earlier egg laying in some species (e.g. magpie¹⁶), while rural species may be
381 more affected by agricultural changes.

382 Effects of temperature mostly reinforced by other effects

383 The effects of increasing temperatures on traits were reinforced by the Other Pathway in 82% of cases,
384 suggesting that ‘disturbance-sensitive’ species may be sensitive to both global warming as well as
385 various (unknown) environmental drivers. Other studies on population dynamics and biodiversity
386 show combined non-climatic and climatic effects increased overall species declines^{12,45}. Our results

387 thus echo the idea of a ‘deadly anthropogenic cocktail’ of climate change and other effects like habitat
388 destruction^{11,45,46}. Reinforcing effects are important to recognise because if changes over time are
389 assumed to reflect effects of warming (as in most large-scale meta-analyses), they would be
390 overestimated. Additionally, counteracted effects were not uncommon (18% of cases), where the
391 effects of increasing temperatures were dampened or buffered by other factors. Several single species
392 studies on population growth have shown that counteracting effects occur^{15,47}, suggesting that
393 identifying these other factors could improve management actions to help buffer the effects of climate
394 change.

395 [Quantitative framework for estimating contributions to change](#)

396 Our simple framework to decompose the contribution of temperature to phenotypic change is
397 conceptually similar to methods used to account for shared trends (i.e. year-detrending⁴⁸), but our
398 multivariate structural equation model also specifically allows for decomposing the contribution of
399 climatic and other pathways on the trait change over time.

400 Several decisions were made that could be important when interpreting results. Firstly, because we
401 selected only the best average temperature window, our temperature measure is a proxy of global
402 warming and is thus a minimum estimate of the impact of climate change more generally. However,
403 we have shown that this proxy is potentially the single most important contributor to trait changes
404 over time. Secondly, this means that we compare temperature across different periods which may
405 have different underlying mechanisms for different species. Here, we were not primarily interested in
406 the mechanisms, but instead focused on identifying correlations. Thirdly, we compared two datasets
407 with different scales of information. The national UK temperatures are potentially a poorer proxy of
408 local temperatures. A consequence of having less reliable temperature data could be weaker
409 estimates of climate sensitivity due to regression dilution, but we note that temperatures are usually
410 strongly spatially autocorrelated.

411 [Implications for comparative climate change ecology](#)

412 Our study illustrates that although increasing temperatures contribute greatly to changes in life-
413 history traits, temporal trends cannot be assumed to be due solely to the effects of warming
414 temperatures. Because temperature-unrelated factors contribute to trends over time and differences
415 in trends may more reflect a species sensitivity and exposure to non-temperature drivers, we caution
416 whether studies should be considering trends over time to be solely due to global warming. As
417 comparative studies typically aim to identify species characteristics that make some species more
418 vulnerable to climate change, focussing on trend data thus runs the risk of identifying the species
419 characteristics that make them either sensitive to non-climatic drivers, or to environmental change in

420 general. Clearly, for identifying the species most at risk from climate change, and for developing
421 predictive models and appropriate conservation management strategies it is important to attribute
422 changes to the correct drivers^{3,49}. We acknowledge the challenges in quantifying climatic sensitivity
423 directly for multiple species, that meta-analyses rely on information available in the literature (mostly
424 temporal trends) and climate sensitivities are quantified using various methods and different climate
425 variables are hard to compare⁵⁰. Further studies are needed that decompose the contributions of
426 climate to trait changes to help identify general patterns in other taxa, traits and regions.
427 Decomposing changes over time due to other specific climate variables such as rain and humidity, and
428 non-climatic variables such as pollution or habitat fragmentation, would substantially improve our
429 understanding of their contributions to temporal trends. Our framework provides a much-needed
430 quantitative means to assess the relative contributions of different drivers to change.

431 References

- 432 1. van de Pol, M. *et al.* Identifying the best climatic predictors in ecology and evolution.
433 *Methods Ecol. Evol.* **7**, 1246–1257 (2016).
- 434 2. Salewski, V., Hochachka, W. M. & Fiedler, W. Global warming and Bergmann’s rule: do central
435 European passerines adjust their body size to rising temperatures? *Oecologia* **162**, 247–60
436 (2010).
- 437 3. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across
438 natural systems. *Nature* **421**, 37–42 (2003).
- 439 4. Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nat. Clim. Chang.* **3**,
440 919–925 (2013).
- 441 5. Thackeray, S. J. *et al.* Trophic level asynchrony in rates of phenological change for marine,
442 freshwater and terrestrial environments. *Glob. Chang. Biol.* **16**, 3304–3313 (2010).
- 443 6. IPCC. CLIMATE CHANGE 2014 Synthesis Report Summary for Policymakers. (2014).
- 444 7. Buckley, L. B. & Kingsolver, J. G. Functional and Phylogenetic Approaches to Forecasting
445 Species’ Responses to Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **43**, 205–226 (2012).
- 446 8. BEALE, C. M. *et al.* Climate change may account for the decline in British ring ouzels *Turdus*
447 *torquatus*. *J. Anim. Ecol.* **75**, 826–835 (2006).
- 448 9. Robinson, R. A., Baillie, S. R. & Crick, H. Q. P. Weather-dependent survival: Implications of
449 climate change for passerine population processes. *Ibis (Lond. 1859)*. **149**, 357–364 (2007).
- 450 10. Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. Quantifying Threats to
451 Imperiled Species in the United States. *Bioscience* **48**, 607–615 (1998).
- 452 11. Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. Synergies among extinction drivers under
453 global change. *Trends Ecol. Evol.* **23**, 453–460 (2008).
- 454 12. Mora, C., Metzger, R., Rollo, A. & Myers, R. A. Experimental simulations about the effects of
455 overexploitation and habitat fragmentation on populations facing environmental warming.

- 456 *Proc. R. Soc. B Biol. Sci.* **274**, 1023 LP – 1028 (2007).
- 457 13. Edinger, E. N., Jompa, J., Limmon, G. V, Widjatmoko, W. & Risk, M. J. Reef degradation and
458 coral biodiversity in indonesia: Effects of land-based pollution, destructive fishing practices
459 and changes over time. *Mar. Pollut. Bull.* **36**, 617–630 (1998).
- 460 14. Spooner, F. E. B., Pearson, R. G. & Freeman, R. Rapid warming is associated with population
461 decline among terrestrial birds and mammals globally. *Glob. Chang. Biol.* **24**, 4521–4531
462 (2018).
- 463 15. Stopher, K. V, Bento, A. I., Clutton-Brock, T. H., Pemberton, J. M. & Kruuk, L. E. B. Multiple
464 pathways mediate the effects of climate change on maternal reproductive traits in a red deer
465 population. *Ecology* **95**, 3124–3138 (2014).
- 466 16. Crick, H. Q. P. & Sparks, T. H. Climate change related to egg-laying trends. *Nature* **399**, 423
467 (1999).
- 468 17. Drent, R. H. & Daan, S. The Prudent Parent: Energetic Adjustments in Avian Breeding. *Ardea*
469 **38–90**, 225–252 (2002).
- 470 18. Lima, S. L. Predation Risk and Unpredictable Feeding Conditions: Determinants of Body Mass
471 in Birds. *Ecology* **67**, 377–385 (1986).
- 472 19. Garel, M. *et al.* SELECTIVE HARVESTING AND HABITAT LOSS PRODUCE LONG-TERM LIFE
473 HISTORY CHANGES IN A MOUFLON POPULATION. *Ecol. Appl.* **17**, 1607–1618 (2007).
- 474 20. Best, L. B. & Stauffer, F. Factors Affecting Nesting Success in Riparian Bird Communities.
475 *Condor* **82**, 149–158 (1980).
- 476 21. Becker, M. E. & Weisberg, P. J. Synergistic effects of spring temperatures and land cover on
477 nest survival of urban birds. *Condor* **117**, 18–30 (2014).
- 478 22. Radinger, J. *et al.* Synergistic and antagonistic interactions of future land use and climate
479 change on river fish assemblages. *Glob. Chang. Biol.* **22**, 1505–1522 (2016).
- 480 23. Baillie, S. R. *et al.* BirdTrends 2014: trends in numbers, breeding success and survival for UK
481 breeding birds. *Res. Rep. 662. BTO, Thetford. <http://www.bto.org/birdtrends>. (2014).*
- 482 24. BTO. British Trust for Ornithology. Available at: [http:// www.bto.org/](http://www.bto.org/). Last accessed 23
483 February 2020. (2020).
- 484 25. Crick, H. Q. P., Baillie, S. R. & Leech, D. I. The UK Nest Record Scheme: its value for science
485 and conservation: Capsule A review of its methodology, analytical procedures and uses. *Bird*
486 *Study* **50**, 254–270 (2003).
- 487 26. Svensson, L. *Identification guide to European passerines.* (1992).
- 488 27. Robinson, R. A., Julliard, R. & Saracco, J. F. Constant effort: Studying avian population
489 processes using standardised ringing. *Ring. Migr.* **24**, 199–204 (2009).
- 490 28. Bailey, L. D. & van de Pol, M. climwin: An R Toolbox for Climate Window Analysis. *PLoS One*
491 **11**, e0167980 (2016).
- 492 29. Burnham, K. & Anderson, D. *Model selection and multimodel inference.* (Springer, 2002).
- 493 30. Lefcheck, J. S. *piecewiseSEM* : Piecewise structural equation modelling in r for ecology,

- 494 evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
- 495 31. Grace, J. B. *Structural Equation Modeling and Natural Systems*. (Cambridge University Press,
496 2006).
- 497 32. van de Pol, M. & Wright, J. A simple method for distinguishing within- versus between-
498 subject effects using mixed models. *Anim. Behav.* **77**, 753–758 (2009).
- 499 33. Wright, S. The Method of Path Coefficients. *Ann. Math. Stat.* **5**, 161–215 (1934).
- 500 34. McLean, N., van der Jeugd, H. P. & van de Pol, M. High intra-specific variation in avian body
501 condition responses to climate limits generalisation across species. *PLoS One* **13**, e0192401
502 (2018).
- 503 35. Spearman, C. The Proof and Measurement of Association between Two Things. *Am. J.*
504 *Psychol.* **100**, 441–471 (1987).
- 505 36. Charmantier, A. *et al.* Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild
506 Bird Population. *Science (80-.)*. **320**, 800–803 (2008).
- 507 37. Visser, M. E. & Both, C. Shifts in phenology due to global climate change: the need for a
508 yardstick. *Proc. R. Soc. B Biol. Sci.* **272**, 2561–2569 (2005).
- 509 38. Both, C., Piersma, T. & Roodbergen, S. P. Climatic change explains much of the 20th century
510 advance in laying date of Northern Lapwing *Vanellus vanellus* in The Netherlands. *ARDEA* **93**,
511 79–88 (2005).
- 512 39. Both, C. Food availability, mistiming, and climatic change. in *Effects of Climate Change on*
513 *Birds* (eds. Moller, A. P., Fiedler, W. & Berthold, P.) (Oxford University Press, 2010).
- 514 40. Low, M., Arlt, D., Pärt, T. & Öberg, M. Delayed timing of breeding as a cost of reproduction. *J.*
515 *Avian Biol.* **46**, 325–331 (2015).
- 516 41. Gardner, J. L., Amano, T., Sutherland, W. J. & Clayton, M. Individual and demographic
517 consequences of reduced body condition following repeated exposure to high temperatures.
518 *Ecol.* **97**, 786–795 (2016).
- 519 42. Paquette, S. R., Pelletier, F., Garant, D. & Bélisle, M. Severe recent decrease of adult body
520 mass in a declining insectivorous bird population. *Proc. R. Soc. B Biol. Sci.* **281**, 20140649-
521 (2014).
- 522 43. Ozgul, A. *et al.* Coupled dynamics of body mass and population growth in response to
523 environmental change. *Nature* **466**, 482–485 (2010).
- 524 44. McLean, N. M., van der Jeugd, H. P., van Turnhout, C. A. M., Lefcheck, J. S. & van de Pol, M.
525 Reduced avian body condition due to global warming has little reproductive or population
526 consequences. *Oikos* **129**, 714–730 (2020).
- 527 45. Mantyka-pringle, C. S., Martin, T. G. & Rhodes, J. R. Interactions between climate and habitat
528 loss effects on biodiversity: a systematic review and meta-analysis. *Glob. Chang. Biol.* **18**,
529 1239–1252 (2012).
- 530 46. Travis, J. M. J. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc.*
531 *R. Soc. B Biol. Sci.* **270**, 467–473 (2003).
- 532 47. Cleasby, I. R. *et al.* Climatic conditions produce contrasting influences on demographic traits

- 533 in a long-distance Arctic migrant. *J. Anim. Ecol.* **86**, 285–295 (2016).
- 534 48. Iler, A. M., Inouye, D. W., Schmidt, N. M. & Høye, T. T. Detrending phenological time series
535 improves climate–phenology analyses and reveals evidence of plasticity. *Ecology* **98**, 647–655
536 (2017).
- 537 49. Wright, L. J. *et al.* Importance of climatic and environmental change in the demography of a
538 multi-brooded passerine, the woodlark *Lullula arborea*. *J. Anim. Ecol.* **78**, 1191–1202 (2009).
- 539 50. van de Pol, M. & Bailey, L. D. Quantifying the climatic sensitivity of individuals, populations,
540 and species. in *Effects of Climate Change on Birds* (Oxford University Press, 2019).
541 doi:10.1093/oso/9780198824268.003.0005
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Figures

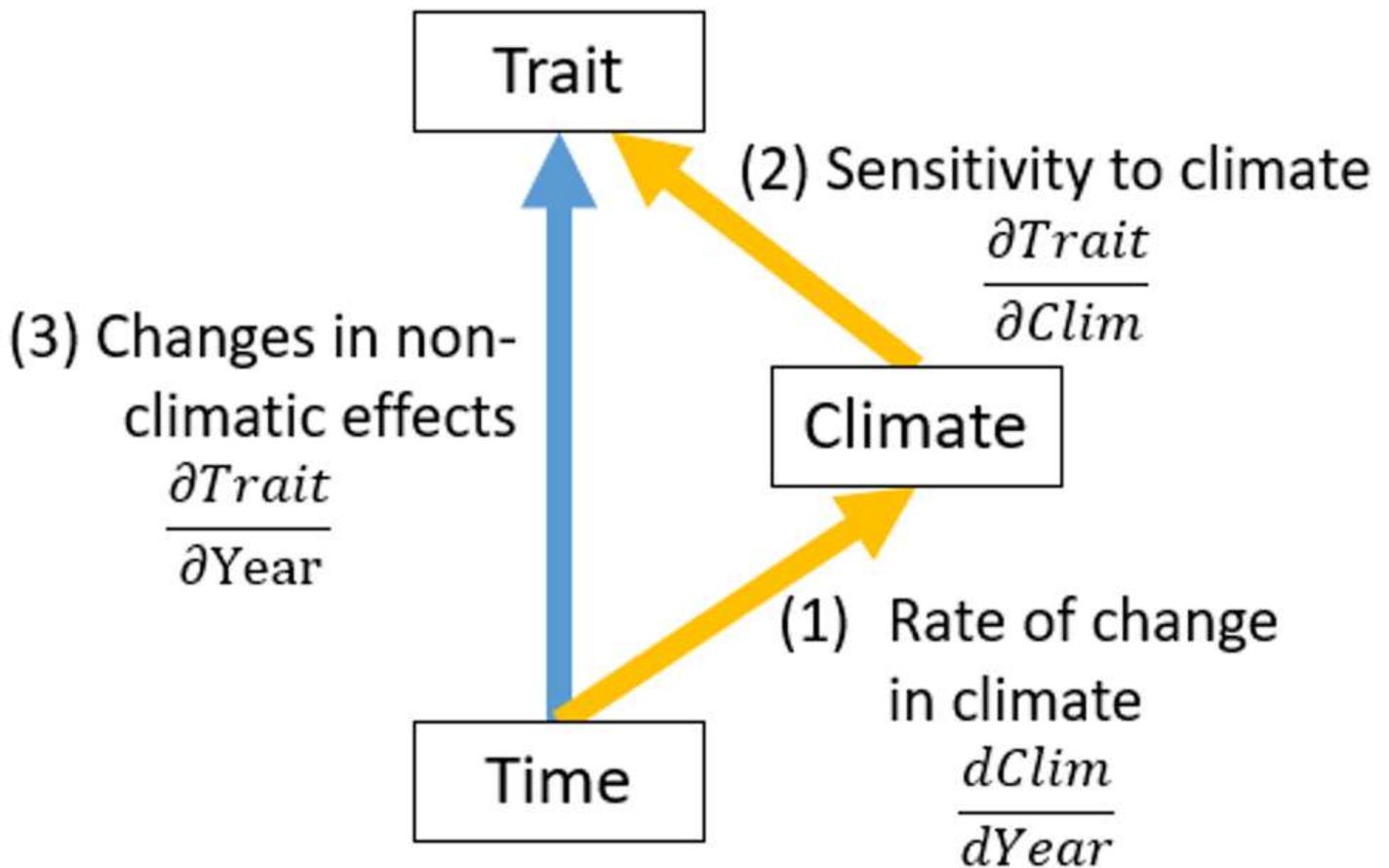


Figure 1

The components of trait change over time. The combined strengths of (1) the rate of change in climate and (2) the focal trait's sensitivity to climate, determine a 'climate pathway', or the change in the trait over time due to climate. The combined impact of both the climate pathway (1,2) and (3) the non-climatic effects determines the total change in the trait over time. This path-diagram shows a visual representation of the structural equation model used and how the terminology in Equation 1 relate, where we use 'd' and '∂' to distinguish full and partial regression coefficients, respectively.

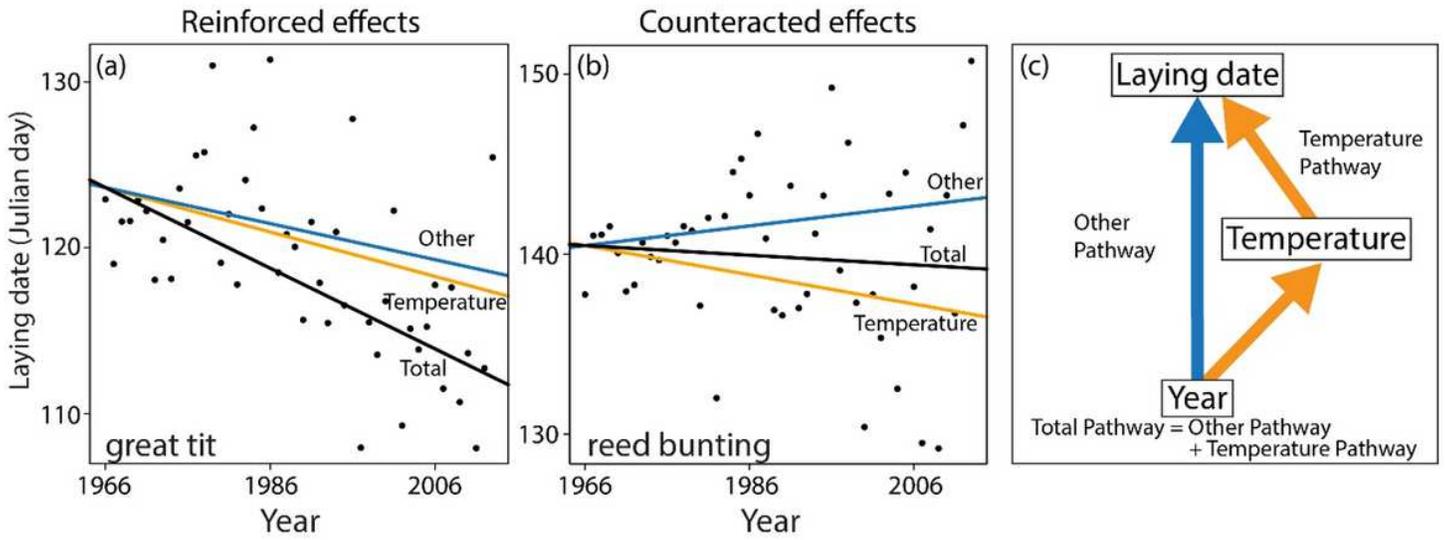


Figure 2

Example diagrams illustrating temporal trends in lay date and the contribution of the different pathways. Points represent the average laying date in each year. In (a) we show a real example of the reinforced effects in great tits in the UK, with negative slopes for both the Temperature Pathway (orange) and the Other Pathway (blue), resulting in a stronger overall change in laying date over time (i.e. the Total Pathway). Plot (b) shows a real example of counteracted effects in reed buntings in the UK, with a negative slope for the Temperature Pathway and a positive slope for the Other Pathway, resulting in a weaker overall change in laying date over time (i.e. the Total Pathway). Plot (c) shows how the slopes in (a) and (b) relate to the structural equation model.

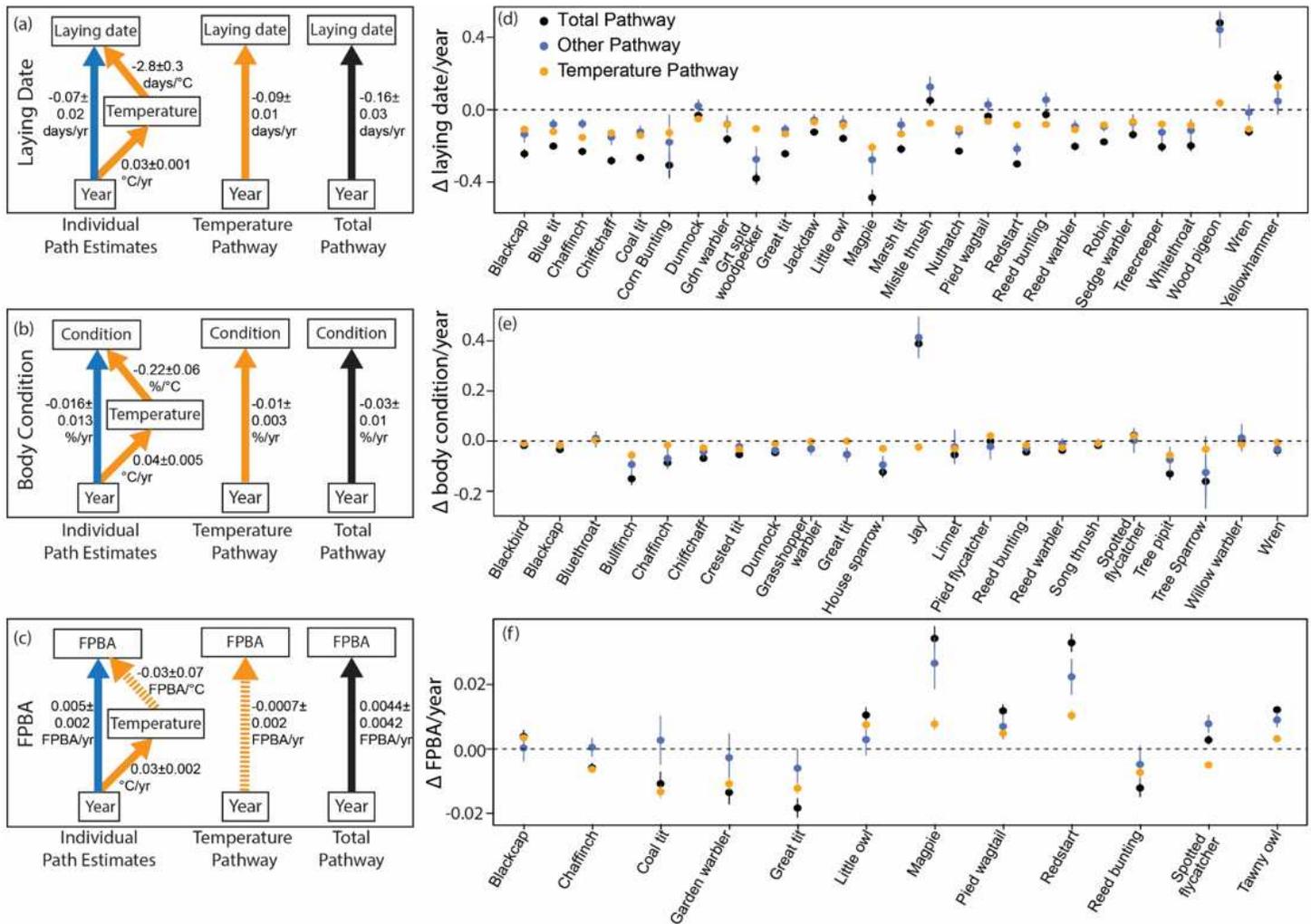


Figure 3

Estimates of path coefficients averaged across species and displayed for each species. The plots in the left column (a-c) show the graphical representations of the structural equation models and the averaged path estimates (\pm standard error) across all species found to be sensitive to temperature. The leftmost blue and yellow arrows show the full SEM and the individual path estimates for each pathway, while the middle yellow arrow shows the change in trait over time due to temperature (the Temperature Pathway, calculated as the product of the year-to-temperature and the temperature-to-trait path estimates). The rightmost black arrow shows the total change in the trait over time due to all variables, and is calculated as the Temperature Pathway summed with the Other Pathway. Solid arrows indicate the 95% confidence interval did not cross zero, while the dashed arrows indicate it did cross zero. The plots in the right column (d-f) show the path estimates (\pm SEs) for the Total (black), Temperature (yellow) and Other (blue) Pathways. In general, the Temperature Pathway coefficients varied less across species than the Other and Total Pathways. In most cases, the Total path estimate was larger than the two others because the Temperature and Other Pathways reinforced one another. However in some cases, the Total Pathway was closer to zero when the Temperature and Other Pathways counteracted each other's effects.

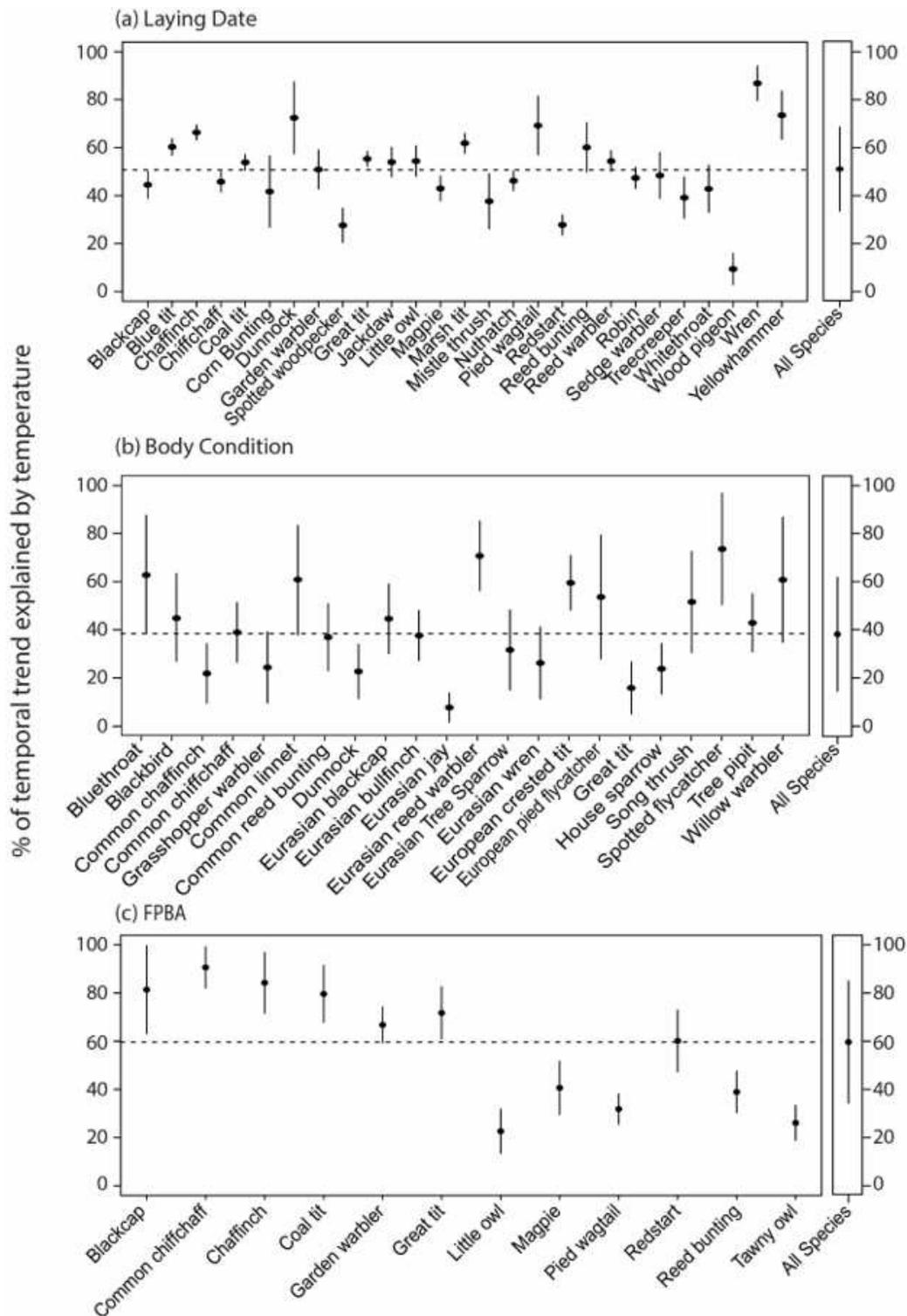


Figure 4

Percentage of temporal trait trends due to increasing temperature. Percentage of the trend in life-history traits over time that is due to the Temperature Pathway for each of the three traits across all species. The separate value listed as 'All Species' shows the average value across all species for that trait and the horizontal dotted line shows this same average for reference. Error bars reflect 95% confidence intervals.

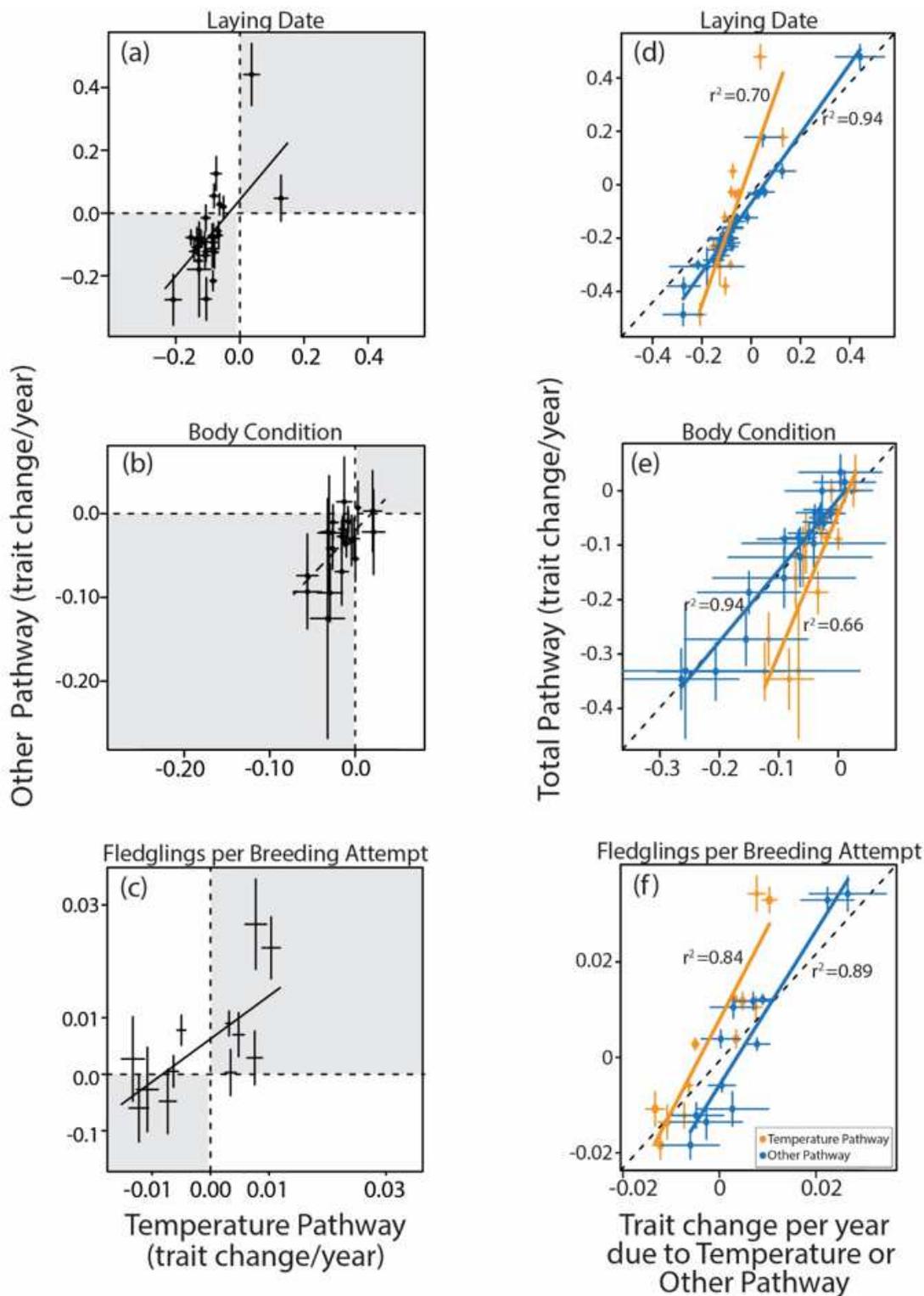


Figure 5

Interspecific comparison of path estimates. The left panels (a-c) show the correlation between the Temperature and the Other Pathway for all temperature-sensitive species, where each point represents a species and bars showing 95% confidence intervals. The dark shaded areas indicate when the Temperature and Other Pathways had reinforced effects. The right panel (d-f) shows the relationships between the Total change in trait over time (calculated as the Temperature Pathway summed with the

Other Pathway) compared to the change over time due to 'Temperature' (yellow) and 'Other' (blue) Pathway. The x-axis is the path estimate for either the Temperature or Other Pathway. The dotted diagonal $Y=X$ is plotted to emphasize that points that fall closer to this line are more similar to the Total Pathway.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Appendix.doc](#)