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1 Warming temperatures drive at least half of the magnitude of long-term
2 trait changes in European birds

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Abstract

24
25 Many wild populations are experiencing temporal changes in life-history and other phenotypic traits,
26 and these changes are frequently assumed to be driven by climate change rather than non-climatic
27 drivers. However, this assumption relies on three conditions: that local climate is changing, traits are
28 sensitive to climate variability, and other drivers are not also changing over time. Although many
29 studies acknowledge one or more of these conditions, all three are rarely checked simultaneously.
30 Consequently, the relative contribution of climate change to trait change, and the variance of this
31 contribution across traits and species, remain unclear. We used long-term datasets on 60 bird species
32 in Europe to test the three conditions in laying date, offspring number and body condition, and used
33 a method that quantifies the contribution of warming temperatures to changes in traits relative to
34 other effects. Across species, approximately half of the magnitude of changes in traits could be
35 attributed to rising mean temperature, suggesting that increasing temperatures are likely the single
36 most important contributor to temporal trends and emphasises the impact that global warming is
37 having on natural populations. There were also substantial non-temperature-related temporal trends
38 (presumably due to other changes such as urbanisation), which generally caused trait change in the
39 same direction as warming. Attributing temporal trends solely to warming thus overestimates the
40 impact of warming. Furthermore, contributions from non-temperature drivers explained most of the
41 inter-specific variation in trait changes, raising concerns about comparative studies that attribute
42 differences in temporal trends to species differences in climate-change sensitivity.

Significance Statement

43
44 Climate change is impacting wild populations, but its relative importance compared to other causes
45 of change is still unclear. Many studies assume that changes in traits primarily reflect effects of climate
46 change, but this assumption is rarely tested. We show that in European birds, global warming was
47 likely the single most important contributor to temporal trends in laying date, body condition and
48 offspring number. However, non-temperature factors were also important and acted in the same

49 direction, implying that attributing temporal trends solely to rising temperatures overestimates the
50 impact of climate warming. Differences among species in the amount of trait change were
51 predominantly determined by these non-temperature effects, suggesting that species differences are
52 not due to variation in sensitivity to temperature.

53 Introduction

54 Given the widespread evidence for ongoing temporal changes in traits of wild animal and plant
55 populations, a key challenge facing ecology today is to understand the role of the rapidly-changing
56 climate in driving these changes. Many studies have correlated temporal variation in phenotypic traits,
57 such as phenology, morpho-physiology and life-history (offspring number, survival/longevity), with
58 changes in climatic variables, which is arguably the most direct means of understanding species'
59 sensitivities to climate (see ¹ for review of approaches). However, much of the literature simply
60 considers changes in climate-sensitive traits over time – as such information is most widely available
61 – and makes the implicit assumption that temporal trends largely reflect responses to climate change.
62 This approach is probably most prevalent in large-scale meta-analyses and comparative studies^{e.g.2-4}.
63 Although it has its merits, whether attributing trait change solely or largely to effects of climate change
64 is justifiable is rarely considered, let alone quantitatively tested.

65 To attribute temporal trends in traits to effects of climate change alone, three conditions must be met
66 (Fig 1a): (1) the climate experienced by the population is changing over time; (2) the trait is sensitive
67 to climate variability (i.e. the mean population value of a trait covaries with a climate variable across
68 years, likely reflecting the average phenotypically plastic response of all individuals, a micro-
69 evolutionary response or changes to the population composition⁵); and (3) phenotypic change is not
70 due to other causes/stressors, i.e. that other non-climatic aspects of the environment with causal
71 effects on the trait are also not changing over time. Even though many studies acknowledge one or
72 more of these conditions when interpreting their results, these three conditions are rarely explicitly
73 checked simultaneously. It therefore remains an open question as to what extent observed trait
74 changes over time are due to climate change, as opposed to being caused primarily by other
75 environmental drivers that are concurrently changing. There is thus a need for a *quantitative*
76 decomposition of the relative importance of temperature versus other causes of temporal trends, and
77 how this differs among species and traits.

78 The three conditions needed to attribute trait changes over time to climate will not necessarily always
79 be met. Firstly, although changes in the global climate system are unequivocal⁶, the rate of change in

80 particular aspects of climate (Fig 1a component 1) will vary seasonally and geographically, and may
81 even be absent over short study periods⁷. Traits may be climate sensitive, but if there is no directional
82 change in climate over the study period then temporal trends in traits are not being driven by climate.
83 For example, breeding advanced in wetter springs for British ring ouzels (*Turdus torquatus*), but
84 precipitation had not increased or decreased over the study period (only annual variation with no
85 temporal trend), and therefore breeding time did not become earlier in recent years either⁸. Secondly,
86 even if organisms experience high rates of climate change, climate will not drive temporal trends if
87 traits are insensitive or only mildly sensitive to climate (Fig 1a component 2). For instance, Robinson
88 et al.⁹ found that juvenile survival was insensitive to climate in 5 of 10 British bird species. Third, non-
89 climatic factors that drive trait change can also change over time (Fig 1a component 3). These could
90 include changes in urbanisation, habitat loss, pollution, invasive species, diseases, loss of keystone
91 species or overexploitation¹⁰⁻¹⁵. The diversity of human impacts on wild populations implies that
92 attributing changes over time to a single causal driver may be overly simplistic, even if that single
93 driver is as prominent as climate change.

94 To date, we have little understanding of how the contribution of climatic and non-climatic factors to
95 phenotypic change differs among traits. We consider three traits that have received much attention
96 in studies of wild animals, and for which long-term datasets are available: reproductive timing, body
97 condition, and offspring number. Timing of reproduction can be influenced not only by temperature,
98 but also by large-scale changes in land use, urban expansion, or nutritional state linked to habitat
99 degradation or population density^{16,17}. Changes in morpho-physiology (body condition, mass, size)
100 have been coined as one of the major responses to climate across the globe^{18,19}. Hotter temperatures
101 are often associated with decreased body mass or condition²⁰⁻²³, although it is still unclear whether
102 this is a detrimental consequence from poorer foraging or heat stress, or if it provides some advantage
103 through lowered energy expenditure or improved agility²⁴. Body condition is also sensitive to non-
104 climatic factors like changes in food availability, predation, selective harvesting and habitat
105 degradation²⁵⁻²⁷. Offspring number can be influenced by warming temperatures via heat stress
106 directly affecting young or indirectly affecting resources²⁸, yet many non-climatic variables are also
107 known to impact this trait, such as predation, parasitism or diseases²⁹. However, despite both climatic
108 and non-climatic stressors being known to be important for all these traits, we currently have little
109 understanding of how strongly they contribute to temporal trends, or how the contributions vary for
110 different traits in wild populations, mainly because they are challenging to quantify. It is also not clear
111 whether non-climatic factors generate trait change in the same direction as those of climate change,
112 reinforcing its effects^{12,28}, or if they instead counteract them^{15,30}.

113 Using two long-term datasets on 60 common bird species from the United Kingdom and the
114 Netherlands for the three traits of laying date, body condition, and offspring productivity, we
115 investigate here to what extent changes over time can be assumed to be due to increasing mean
116 temperatures, a key component of, and our index for, climate warming. Therefore, we first identify
117 the temperature periods (or ‘windows’) that best describe associations between traits and
118 temperature. We present a method based on path analysis³¹ that can quantify the parameters
119 involved in attributing trait changes over time to climate: the rate of change of temperature, the
120 sensitivity of traits to temperature, and the rate of change in traits due to other unknown drivers that
121 are changing concurrently. Finally, using our simple method we answer three questions: of those
122 species sensitive to temperature, (1) what proportion of trait changes over time are due to warming?
123 (2) do the effects of warming and other drivers counteract or reinforce each other? and (3) does the
124 contribution of warming vary among different traits and species?

125 Methods

126 Data

127 To quantify the extent of trait changes attributable to warming temperatures, we analysed the timing
128 of egg laying (‘laying date’), body condition, and the number of fledglings produced per breeding
129 attempt (‘offspring number’). We used two long-term datasets on common bird species, one from the
130 United Kingdom (UK) and one from the Netherlands (NL).

131 The dataset from the UK was part of the British Trust for Ornithology’s Nest Record Scheme³², which
132 was used to investigate laying date and offspring number (36 species, 1966–2019; Table S1). Data are
133 not collected at distinct sites, but rather are opportunistic throughout the region. We grouped the UK
134 data into three latitudinal bands (Appendix Fig S2) and calculated annual averages and standard errors
135 within these to account for possible latitudinal gradients (Appendix Fig S2). The UK data therefore
136 consisted of an estimate of the average value for each species in each year for each of the three
137 latitudinal bands, for each trait (35 species, 54 years and 3 bands, giving 5,185 laying date and 5,222
138 offspring number estimates). We used daily mean temperature records from the European Climate
139 Assessment and Dataset³³ for the UK. Temperature was averaged within the three latitudinal bands
140 to account for any latitudinal differences in climate windows (see Appendix for details).

141 The dataset from the NL was part of the site-specific Dutch Constant Effort Site (CES) program
142 (collected from April-August), and was used to analyse changes in body condition (47 species, 86 sites,
143 1994-2014; Table S2). Adult body condition was calculated as the residuals from the linear regression
144 of body mass on wing length, age, sex and capture timing for each individual. Average adult body
145 condition was then calculated per species per site per year and its standard error (i.e. population

146 annual averages based on 193,028 individual captures from 47 species, 86 sites and 30 years, giving
147 11,568 average condition estimates; see Appendix for details). We used daily mean temperature
148 records from the Royal Netherlands Meteorological Institute for NL (see Appendix for details).

149 **Statistical Analysis**

150 ***Climate Windows***

151 We performed 'sliding window' analyses to identify the time period during which mean temperature
152 best explained the variation in annual trait values for each trait and species. Thus, we used the mean
153 temperature within the relevant time window as our index for global warming. To identify this 'best'
154 possible temperature window, we used the R package *climwin*³⁴ and systematically explored all
155 possible combinations of consecutive weeks for the previous two years. Consequently, species'
156 climate windows can differ in both duration and timing, for instance ranging from periods in recent
157 springs to periods in the previous year (Fig S3). For the UK specifically, the best temperature window
158 was identified for each of the three latitudinal bands to account for any latitudinal differences in
159 climate windows (see Appendix for details). The NL data were not broken up by latitude, and so the
160 best temperature window identified was for each species across the whole (small) country. All
161 analyses fitted linear temperature relationships and assumed Gaussian distributions for the response
162 variables.

163 When testing so many climate window models, the chances of spurious results are high¹.
164 Randomisation techniques were used to assess the likelihood that the best window occurred by
165 chance³⁴. Species were categorised as either temperature 'sensitive' or 'insensitive' depending on
166 whether a reliable temperature window could be identified (see Appendix for details). Although our
167 time series are at least two decades long, species with smaller sample sizes could still be more likely
168 to be categorised as insensitive. However, we checked that the ability to detect a climate window did
169 not depend on sample size for any traits (see Appendix, Table S6).

170 ***Path analysis using Structural Equation Models***

171 We used path analyses within structural equation models (SEMs) to quantify the importance of
172 temperature in mediating trait changes over time³¹. SEMs are a generalisation of path models that
173 *inter alia* allow for the inclusion of random effects. We constructed a SEM for each species that was
174 found to be temperature sensitive. Figure 1a shows the path-diagram of the SEM, with three individual
175 path estimates being calculated: (1) the effect of year on temperature, (2) the effect of temperature
176 on the trait, and (3) the direct effect of year on the trait. We used the R-package *piecewiseSEM*³⁵ (see
177 Appendix for code). Temperature was mean centred for each species to ensure that the relationships
178 would reflect within-population associations³⁶, and all response variables had Gaussian distributions

179 and were weighted by the inverse of the standard error to account for differences in precision within
180 time-series. Site (for the NL) or band (for the UK) were included as a random nested term for each
181 response variable.

182 The association between year and trait was decomposed into two pathways: the ‘Temperature
183 Pathway’ which is the indirect effect on the trait mediated by temperature (i.e. trait changes over time
184 due to the effects of the identified temperature window; Fig 1a components 1 & 2) and the ‘Other
185 Pathway’, which is the direct effect on the trait due to all other drivers (i.e. *not due* to the effects of
186 mean temperature — instead, any other effects such as habitat degradation ; Fig 1a component 3)³⁷.
187 Consequently, the Temperature Pathway gives the change in trait due to increasing mean
188 temperature per year, and the Other Pathway gives the change in trait over time due to non-
189 temperature drivers.

190 This method isolates temperature effects from other covarying impacts similarly changing over time.
191 Because the Other Pathway captures changes over time unrelated to the temperature window, it
192 separates out the effects of all other, non-temperature drivers of trait change over time from the
193 Temperature Pathway. By assessing the partial regression of a trait on both temperature and year, we
194 effectively ask the question whether temperature explains temporal trait variation *beyond* any shared
195 directional temporal trends in trait and temperature³⁸. The Other Pathway is likely composed of many
196 drivers. Theoretically, there could also be effects of temperature from other window periods outside
197 of the ‘best’ windows selected that would contribute to the Other Pathway (see Discussion), but we
198 assumed that multiple uncorrelated temperature signals are rare and therefore did not consider them
199 separately.

200 Our model was ‘saturated’ as all path estimates were needed to answer our questions. This meant
201 that the usual model fit statistics could not be calculated³⁷. To check that the estimates from our SEMs
202 were likely to be reasonable, we checked the fits of each of the individual path estimates and made
203 sure the residuals were normally distributed, and the standard errors were not extremely large or
204 close to zero. All models satisfied these assumptions.

205 *Temperature and Total Pathway Calculations*

206 The Temperature and Total Pathways for each SEM were calculated from the three individual path
207 estimates (Fig 1a components 1, 2 & 3). Following the rules of path tracing³¹, the Total Pathway — or
208 the total change in a trait over time — is determined by each of the underlying linear relationships
209 between year, trait and climate²³:

$$210 \quad \text{Total Pathway} = \text{Temperature Pathway} + \text{Other Pathway}$$

211
$$\frac{dT_{\text{trait}}}{d\text{Year}} = \frac{dT_{\text{emp}}}{d\text{Year}} * \frac{\partial T_{\text{trait}}}{\partial T_{\text{emp}}} + \frac{\partial T_r}{\partial \text{Year}} \quad (\text{eq. 1})$$

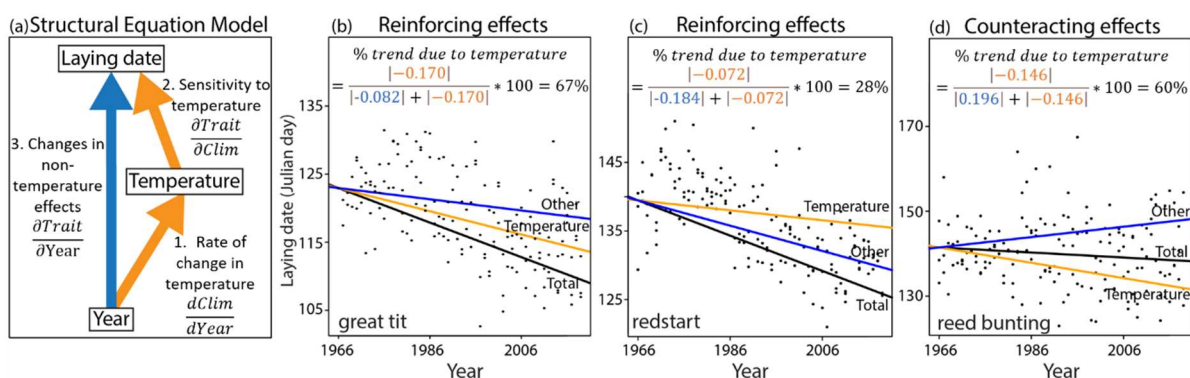
212 (where we use 'd' and '∂' to distinguish full and partial regression coefficients, respectively). The Total
 213 Pathway ($\frac{dT_{\text{trait}}}{d\text{Year}}$) is equal to the sum of the Temperature Pathway ($\frac{dT_{\text{emp}}}{d\text{Year}} * \frac{\partial T_{\text{trait}}}{\partial T_{\text{emp}}}$) and the Other
 214 Pathway ($\frac{\partial T_r}{\partial \text{Year}}$). The Temperature Pathway was calculated as the product of the effect of year on
 215 temperature ($\frac{dT_{\text{emp}}}{d\text{Year}}$) with the effect of temperature on trait ($\frac{\partial T_{\text{trait}}}{\partial T_{\text{emp}}}$) (Fig 1a components 1 & 2³⁷). We
 216 classify species where the Temperature and Other Pathways are in the same direction (Fig 1b) as
 217 'reinforced effects' and in opposite directions (Fig. 1c) as 'counteracted effects'. We applied a
 218 bootstrapping technique to calculate 95% confidence intervals for the compound Temperature and
 219 Total Pathways (see Appendix).

220 **Trait change due to warming**

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

223
$$\% \text{ trend due to warming} = \frac{|\text{Temperature Pathway}|}{|\text{Other Pathway}| + |\text{Temperature Pathway}|} * 100 \quad (\text{eq. 2})$$

224 where |..| denotes the absolute value. Equation 2 denotes the percent contribution of the
 225 Temperature Pathway to the Total Pathway. Because the Temperature Pathway gives the change in
 226 trait due to increasing mean temperature per year, this metric gives the percent trend due to warming
 227 temperatures. Our metric is insensitive to the sign of the single pathways (i.e. allows for comparing
 228 counteracting and reinforcing effects) and the magnitude of the Total Pathway (see Appendix for
 229 rationale). Fig 1(b-d) shows graphical examples.



230
 231 **Figure 1 The components of trait change over time and examples illustrating temporal trends in lay**
 232 **date and the contribution of the different pathways.** In (a) this path-diagram shows a visual
 233 representation of the structural equation model used with terminology as in Equation 1 ('d' and '∂' to
 234 distinguish full and partial regression coefficients, respectively). The combined strengths of (1) the
 235 rate of change in temperature and (2) the trait's sensitivity to temperature, determine a 'temperature

236 pathway', or the change in the trait over time due to temperature. The combined impact of both the
237 temperature pathway (1,2) and (3) the non-temperature ('Other') effects, determines the total change
238 in the trait over time. In (b) we show a real example of reinforcing effects on great tit laying date in
239 the UK, with negative slopes for both the Temperature Pathway (orange) and the Other Pathway
240 (blue), resulting in a stronger overall advance in laying date over time (i.e. the Total Pathway). Plot (c)
241 shows another example of reinforcing effects in redstart laying date but the Temperature Pathway is
242 much weaker than the Other Pathway, and so the percent trend due to temperature is much lower.
243 Plot (d) shows an example of counteracting effects in reed bunting lay date, with a negative slope for
244 the Temperature Pathway and a positive slope for the Other Pathway, resulting in little overall change
245 in laying date over time (i.e. the Total Pathway). The equation for calculating the percentage of the
246 trend over time due to temperature is also displayed. Points represent the average laying date in each
247 year in each of the three latitudinal bands.

248 Results

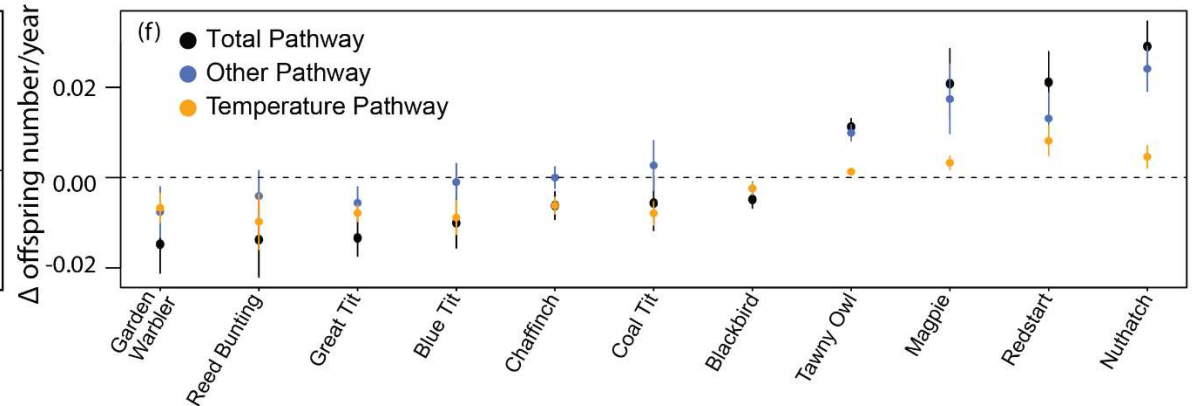
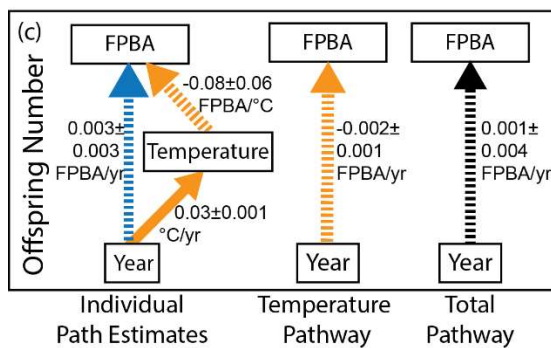
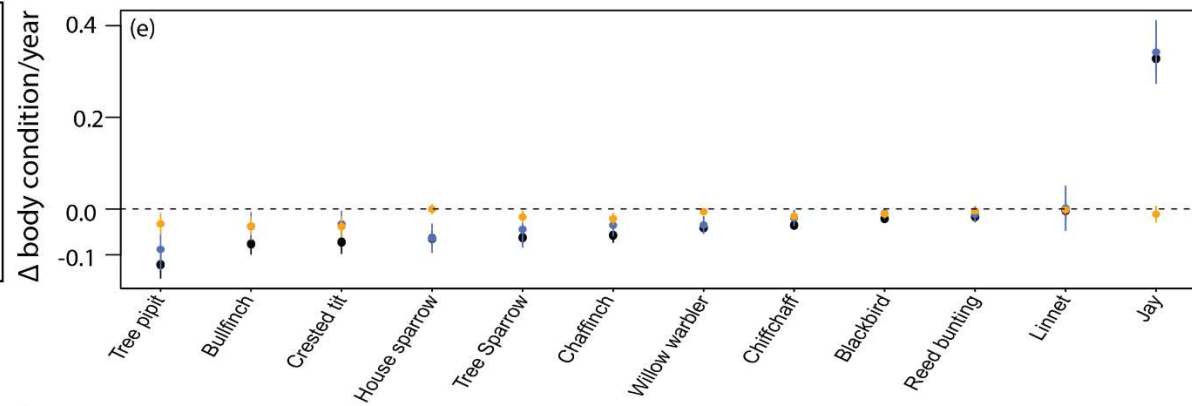
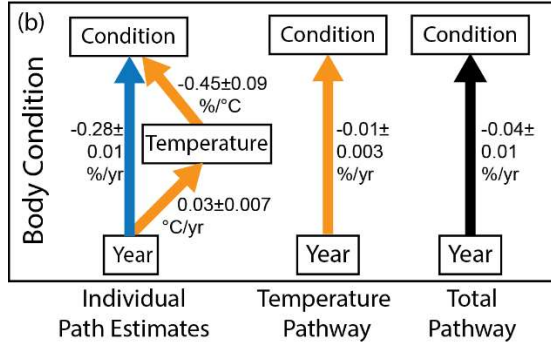
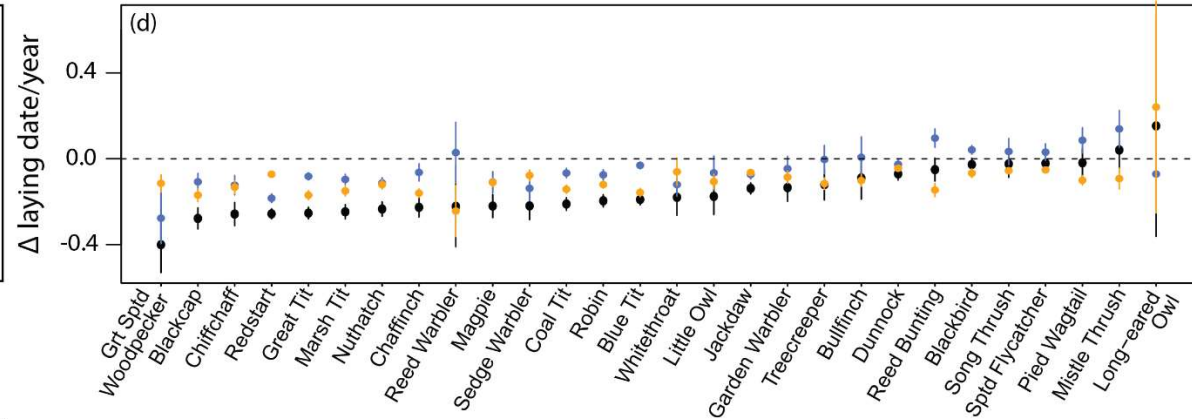
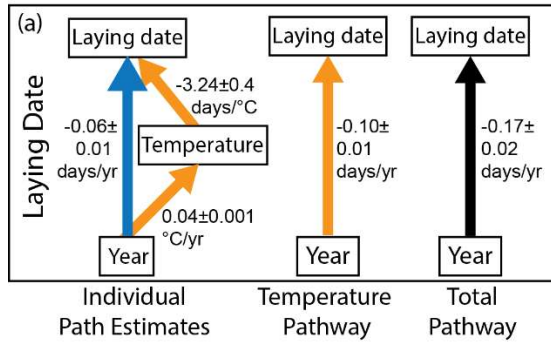
249 Conditions for attributing trait changes to climate

250 To understand whether temporal trends can be attributed to warming temperatures, we tested for
251 the three key underlying conditions: change in temperature over time, sensitivity of traits to
252 temperature, and impacts of other drivers over time. In support of the first condition, mean
253 temperature (during the 'best windows' identified for each species-trait combination) increased over
254 time for all traits and species except three which experienced decreasing mean temperature (3/119;
255 Reed bunting, Blackbird and (just) Chiffchaff for body condition; Figs S5c, S6c & S7c).

256 The degree to which the second condition (trait sensitivity to climate) was met varied across traits.
257 Laying date was sensitive to mean temperature in 86% of species (31/36 species, Table S4), with the
258 relevant temperature windows occurring around March-June in spring (Fig S3). Body condition was
259 sensitive to temperature in 32% of species (15/47 of NL species, Table S5), with many temperature
260 windows occurring around early May to mid-July in spring-early summer in that year and the previous
261 year. Offspring number was sensitive to temperature in 31% of species (11/35 of UK species; Table
262 S4). The three temperature-sensitive species with decreasing temperatures were removed from
263 further analyses, as we were interested in the contribution of warming. For the temperature-sensitive
264 species, warming was associated with advances in laying date (3.2 days/°C on average; Fig 2a),
265 decreases in body condition (0.45%/°C on average; Fig 2b), and highly variable effects on offspring
266 number (negative for 7 species and positive for the other 4 species, such that there was on average
267 no change across species; Fig S7b). Temperature-insensitive species were removed from further

268 analyses, but we note that there were no significant differences in trait changes over time between
269 temperature-sensitive versus -insensitive species (Fig S4).

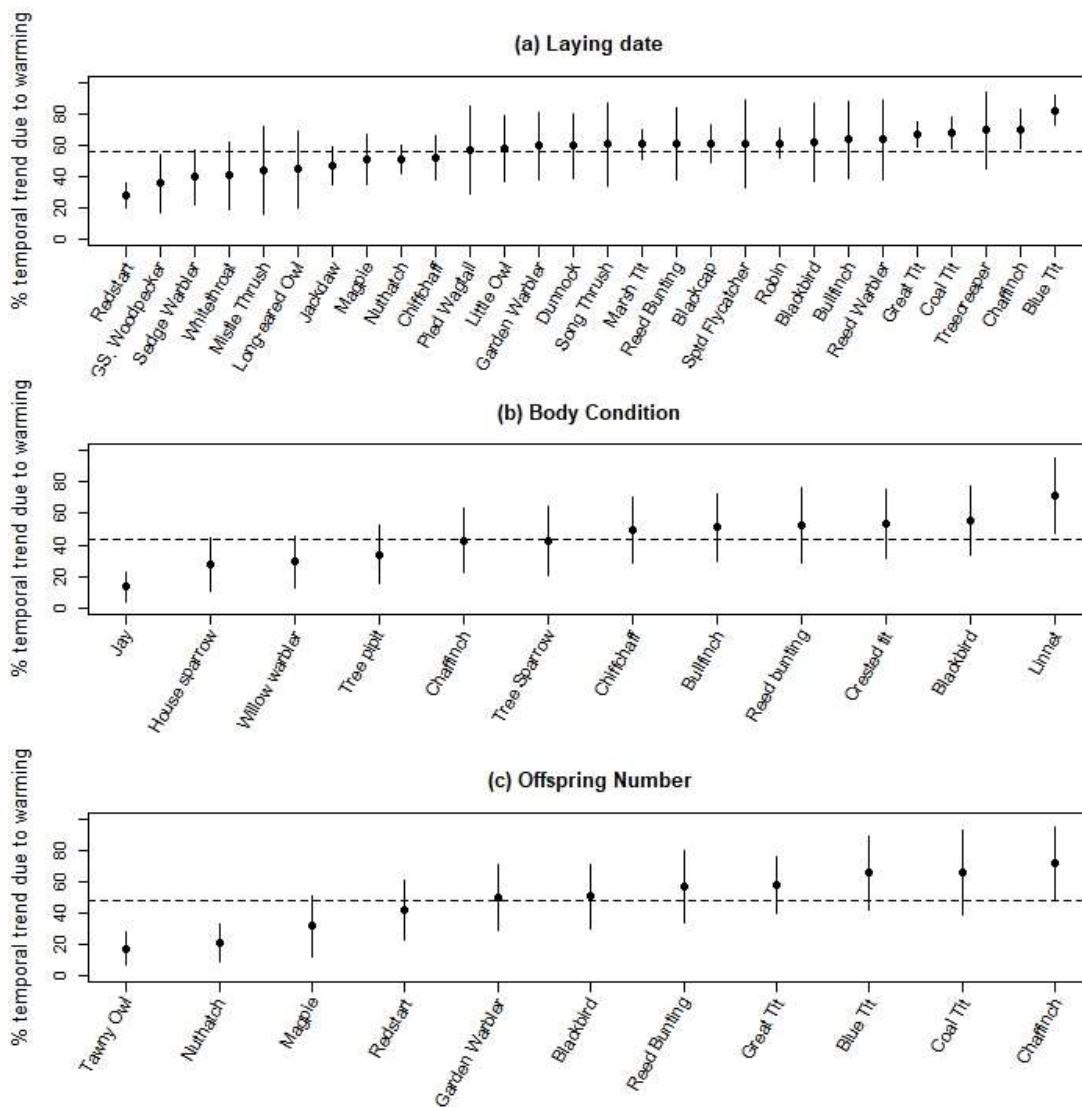
270 For the third condition (no impacts of other drivers over time), trait changes due to effects other than
271 the identified mean temperature window were common and often strong. On average, laying date
272 and body condition had a consistent non-temperature related trend across species that advanced
273 laying date by 0.06 ± 0.01 days/year and decreased body condition by $0.03 \pm 0.007\%$ /year. For offspring
274 number, other effects contributed strongly to temporal trends in individual species, but the
275 direction/sign was not consistent across species (the 'Other Pathway'; Fig 2a-c).



277 **Figure 2 Estimates of path coefficients averaged across species and displayed for each species.** The
278 plots in the left column (a-c) show the graphical representations of the structural equation models
279 and the averaged path estimates (\pm standard error) across all species found to be sensitive to
280 temperature. The leftmost blue and yellow arrows show the full SEM and the individual path estimates
281 for each pathway, while the middle yellow arrow shows the change in trait over time due to
282 temperature (the Temperature Pathway, calculated as the product of the year-to-temperature and
283 the temperature-to-trait path estimates). The rightmost black arrow shows the total change in the
284 trait over time due to all variables, and is calculated as the Temperature Pathway summed with the
285 Other Pathway. Solid arrows indicate the 95% confidence interval did not cross zero, while the dashed
286 arrows indicate it did cross zero. The plots in the right column (d-f) show the path estimates (\pm SEs)
287 for the Total (black), Temperature (yellow) and Other (blue) Pathways for all temperature sensitive
288 species. In general, the Temperature Pathway coefficients varied less across species than the Other
289 and Total Pathways. Note that the Jay has been removed from the average body condition estimates
290 as it was a substantial outlier, although its removal did not change the estimates, but did lower the
291 95% CI.

292 Trait change over time due to warming

293 Across all temperature-sensitive species and traits, over half (52%) of the change in traits over time
294 was due to the Temperature Pathway. However, there was some variation among the traits, with an
295 average of 57% of temporal changes in laying date attributed to the temperature window (Fig 3a), an
296 average of 44% for body condition (Fig 3b), and an average of 48% for offspring number (Fig 3c).



297

298 **Figure 3 Percentage of temporal trait trends due to increasing temperature.** Percentage of the trend
 299 in life-history traits over time that is due to the Temperature Pathway for (a) Laying date (b)
 300 Body Condition and (c) Offspring Number across all species sensitive to temperature. The horizontal dotted
 301 line in each panel shows the average value across all species for that trait. Error bars indicate 95%
 302 confidence intervals.

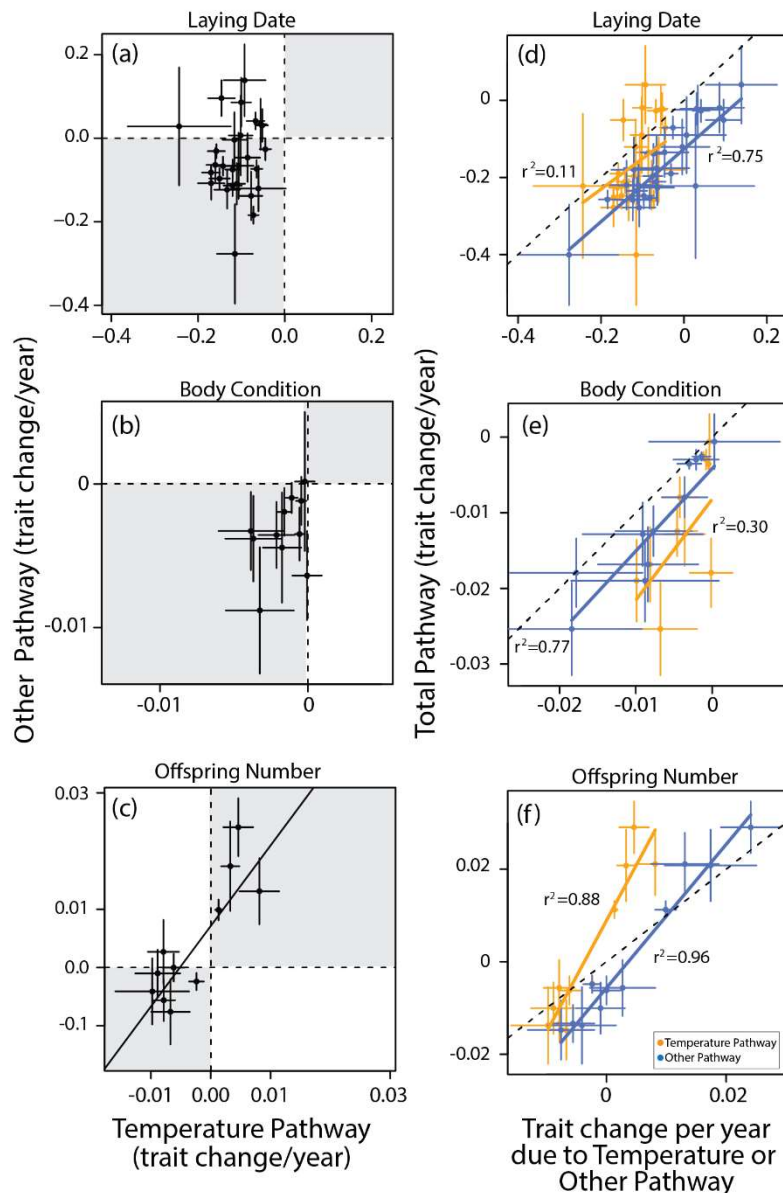
303 Relationship between Temperature and Other Pathways

304 The Temperature and Other Pathways tended to have the same sign and thus reinforced each other
 305 (same sign pathways in 83% of species for body condition, 82% for offspring number, 68% for laying
 306 date; Fig 2d-f). The magnitude of the Temperature and Other Pathway estimates were positively
 307 correlated for offspring number ($r=0.85$ 95% CI=0.51, 0.96, $n=11$), but uncorrelated for body condition
 308 ($r=0.39$ 95% CI=-0.28, 0.80, $n=11$) and laying date ($r=-0.02$ 95% CI=-0.39, 0.35, $n=28$) (Fig 4a-c).

309 Interspecific variation

310 The percentage of the overall trend in a trait attributed to warming differed substantially among
 311 species, with values ranging from 28% to 82% for laying date, from 13% to 71% for body condition,

312 and from 17% to 71% for offspring number (Fig 3). Notably, variation *among* species in the total trait
 313 change over time (the Total Pathway) appeared to be mainly due to variation in the Other Pathway
 314 (explained interspecific variation in Total Pathways by Other Pathway: $r^2_{\text{laydate}}=0.75$, $r^2_{\text{condition}}=0.77$,
 315 $r^2_{\text{offspring}}=0.96$; Fig. 4d-f) rather than in the Temperature Pathway ($r^2_{\text{laydate}}=0.11$, $r^2_{\text{condition}}=0.30$,
 316 $r^2_{\text{offspring}}=0.88$), even though temperature explained on average almost half of the total temporal
 317 change *within* a species (Fig 3). This is likely because changes in traits due to the Temperature Pathway
 318 were more consistent among species compared to changes due to the Other Pathway for all traits.



319

320 **Figure 4 Interspecific comparison of path estimates.** The left panels (a-c) show the correlation
 321 between the Temperature and the Other Pathway for all temperature-sensitive species, where each
 322 point represents a species. The dark shaded areas indicate the Temperature and Other Pathways
 323 having ‘reinforced’ effects. The right panel (d-f) shows the relationships between the Total Pathway
 324 (the change in trait over time, calculated as the Temperature Pathway summed with the Other
 325 Pathway) compared to the change over time due to Temperature (yellow) and Other (blue) Pathways.

326 The x-axis is the path estimate for either the Temperature or Other Pathway. The dotted diagonal $Y=X$
327 is plotted to emphasize that points that fall closer to this line are more similar to the Total Pathway.
328 The long-eared owl was removed from the laying date estimates and figures as it was an outlier with
329 substantial uncertainty surrounding path estimates. Error bars show 95% confidence intervals.

330 Discussion

331 The assumption that changes in phenotypic traits through time reflect responses to climate warming
332 relies on three conditions being met: changing local climate, traits being sensitive to climate, and no
333 alternative drivers of change occurring. By using our simple method with long-term datasets on three
334 traits in 60 common bird species in Europe, we show here that (1) mean temperatures generally
335 increased over time, (2) laying date was sensitive to mean temperature for most species, but
336 sensitivity of body condition and offspring number could only be detected in about a third of the
337 species, and (3) other unknown drivers contributed strongly to temporal trends. On average across all
338 three traits, 44%-57% of trait changes over the past decades could be attributed to warming.
339 Parmesan & Yohe² have argued that, although competing explanations in the form of non-climatic
340 causal agents could have impacts, it is unlikely that such drivers would produce a consistent pattern
341 of impact over space and time. Our study suggests that this proposition, which is also a crucial—but
342 rarely explicitly mentioned—assumption in many other studies, may not generally hold, and that other
343 drivers in addition to temperature change may also have a strong and consistent effect on phenotypic
344 trends. Such a conclusion should possibly not be surprising in a world where humans are rapidly
345 altering the environment in multiple ways, of which anthropogenic climate warming is only one.

346 Importance of global warming for trait change

347 Our analysis thus shows that temporal trends in traits cannot always be solely ascribed to increasing
348 temperature. However, the fact that a single temperature variable can explain around 50% of the
349 temporal trends across all species is remarkable for any ecological study, and clearly underlines the
350 impact that global warming is having on natural populations. Increasing temperatures were still likely
351 the single most important contributor to temporal trends in all traits, even though less than half of
352 temporal trends were due to warming for body condition and offspring number. This is because the
353 Other Pathway is likely comprised of many drivers such as habitat degradation or predation. Despite
354 this, the Other Pathway strongly determined trait changes over time, suggesting that unknown drivers
355 outside of our temperature windows were also heavily influencing these traits in European birds.
356 Furthermore, similar changes in traits over time in species that were insensitive to temperature (i.e.
357 more than half of the bird species considered), were solely due to non-climatic effects, or other
358 climatic effects that were not considered (e.g. rainfall).

359 The total change in laying date was substantially earlier than would be expected due to increased
360 temperatures alone. Many studies have shown that laying date is closely associated with mean spring
361 temperatures^{16,39–41}. This relationship is considered to be predominantly driven by the need to reduce
362 mismatches with their food supplies, whose timing of peak abundance vary with temperature^{40,42}.
363 Consequently, it was somewhat surprising that 43% of changes in laying date over time were due to
364 the Other Pathway. Our study strongly suggests that temperature only tells part of the story for
365 changes in laying date, and that changes in other climatic (e.g. rainfall⁴¹) or non-climatic factors (e.g.
366 urbanisation, land-use^{16,17,43}) may play a more prominent role than previously thought, and hence may
367 deserve more attention.

368 Overall, warming only tells us a part of the story of why these traits are changing. Future work is now
369 needed to determine whether this extends to other species and traits. It will be important to identify
370 the key ecological driver(s) that make up the Other Pathway, and the path analysis method we
371 presented here is amenable to explicitly including additional climatic and non-climatic drivers as
372 alternative mediating pathways to explore this in a quantitative way. Thus, the method used here
373 provides a framework for further work on identifying and quantifying these other ecological drivers.

374 **Reinforcing climatic and non-climatic drivers**

375 We found that attributing trait changes solely to climate warming is not only imprecise, but actually
376 results in systematic overestimation of its impact because temperature effects were mostly reinforced
377 by non-temperature effects for all three traits. Reinforcement among pathways also suggests that
378 species which are sensitive to warming are also sensitive to other changes in the environment, thereby
379 providing support for the idea of ‘disturbance-sensitive’ species (a concept raised in the field of
380 population dynamics and biodiversity^{12,44}) and emphasises that different aspects of global change may
381 accumulate on wildlife. In the case of body condition, trait change due to warming and other drivers
382 typically resulted in lowered body condition, which has previously been suggested as a maladaptive
383 impact of climatic change²⁴. However, for offspring numbers some species increased their productivity
384 while other species decreased their productivity over time due to both pathways, and the positive
385 correlation among both pathways further suggested that there are likely winners and losers among
386 European birds from ongoing environmental change. Additionally, advances in laying date are typically
387 considered plastic responses that should allow species to track temperature-mediated variation in
388 optimum conditions⁴⁵. Our large-scale analysis provides the novel insight that these reinforcements
389 may be common, but whether this is of concern will depend strongly on the ecological context of the
390 trait (directionality of change and whether this is maladaptive or not).

391 Identifying what makes a species sensitive to climate change

392 Among-species differences in temporal trends were driven primarily by drivers other than warming.
393 This appeared to be because warming had a more consistent effect on species compared to non-
394 temperature effects. Non-temperature effects on species varied more, which drove the variation in
395 total trait change over time across species. This implies that comparative studies should be cautious
396 of attributing differences in temporal trends to underlying species differences in sensitivity (or
397 exposure) to climate change, as they may actually more reflect sensitivity to other changes in the
398 environment. For instance, comparative studies typically aim to identify species characteristics (e.g.
399 allometry, longevity, specialization, dispersal capacity) that make some species more vulnerable or
400 sensitive to climate change (potentially including not ‘keeping up’ enough in the case of phenology),
401 but basing these analyses on responses over time runs the risk of identifying species characteristics
402 that make them sensitive to non-climatic drivers. Such potential misidentification is of concern, as
403 species characteristic are increasingly used to extrapolate climate vulnerabilities to data-deficient
404 species to prioritise conservation strategies across taxa and countries^{46–48}. Instead, improving our
405 understanding of exactly which species or habitat characteristics can explain a species’ sensitivity to
406 rising temperatures versus other non-temperature effects will provide a better understanding of
407 species’ vulnerabilities to climatic changes over time. Identifying such species or habitat
408 characteristics will also generate hypotheses about what other non-temperature drivers might be
409 important, and *why* the temperature pathway might be more or less important for different species.

410 Method for estimating contributions to change

411 Our simple quantitative method to decompose the contribution of climate warming to trait change is
412 conceptually similar to statistical methods used to account for shared trends (i.e. year-detrending³⁸).
413 However, our method can decompose the contributions of climatic and other pathways to trait change
414 over time. Thus, we aim to investigate whether it is likely that temperature causes trait variation, or
415 whether instead they are only correlated due to something else changing over time (see Appendix for
416 details). Our key metric ‘percentage of trend due to warming’ should be viewed as a conservative
417 (minimum) estimate for two reasons. Firstly, the strength of the temperature sensitivity—and
418 consequently also of the Temperature Pathway—could be underestimated (biased towards zero) due
419 to measurement error surrounding the temperatures that the birds experience (causing regression
420 dilution). Although temperatures at weather stations will have little measurement error, they can be
421 imperfect proxies of the causal micro-climates that organisms experience at study sites. We note that
422 mean temperatures at the nearest weather station are likely to be highly correlated with the mean
423 temperature at the study site because mean temperatures typically exhibit strong spatial
424 autocorrelation and their proximities were close in both countries due to their high density of weather

425 stations. A second reason for our key metric to be conservative is that we selected only the ‘best’
426 mean temperature window, and thus our temperature measure is only an index of global warming, or
427 climate change more generally. Additional periods in other parts of the year, or other temperature
428 measures (e.g. number of hot days) could also be influential (see Appendix for further discussion).
429 Other dimensions of warming or climate change outside of the temperature windows identified here
430 could be included in the Other Pathway, but only if (i) sensitivity to such alternative aspects of climate
431 change exist, (ii) these climate variables are also changing over time, and (iii) they are uncorrelated to
432 the focal climate aspect (mean temperature here). We have shown that our mean temperature index
433 is likely the single most important contributor to trait changes over time and note that different
434 aspects of climate change are often highly intercorrelated. Our method is amenable to including
435 additional climate variables to explore hypotheses about effects of other variables.

436 Conclusion

437 Although it is clear that warming is having large impacts on natural populations and that rising
438 temperatures appear to be a main driver of changes in traits over time, we have shown here that
439 temporal trends in phenotypic traits cannot always be assumed to be driven entirely by rising
440 temperatures. Identifying the contributions of key climatic and non-climatic drivers to trait changes
441 over time will be vital for developing appropriate conservation management strategies as the specific
442 actions to mitigate impacts or promote adaptation will differ substantially for different drivers^{2,49}. As
443 we increase our understanding of how changes in climate directly impact species and how non-
444 climatic variables simultaneously drive changes, we can better identify those species or populations
445 most at risk from climate change.

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