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1 **Thermal constraints on body size depend on the population position within the species'**
2 **thermal range in temperate songbirds**

3 Nicolas Dubos, Olivier Dehorter, Pierre-Yves Henry, Isabelle Le Viol

4 *Running title:* Temperature effect on size along thermal range

5

6 **ABSTRACT**

7 **Aim** There is mounting evidence that climate warming can induce morphological changes
8 locally, particularly size reduction. However, the direction of thermal stress may differ
9 between climatic regions. We predicted that morphological response to temperature
10 fluctuations should vary throughout species ranges, depending on the local climate. Hot
11 temperature anomalies are expected to induce size reduction in hot regions where species live
12 close to their upper thermal limit, whereas size stasis (or increase) would be expected in cold
13 regions, where species live close to their lower thermal limit.

14 **Location** France (204 sites)

15 **Time period** 2000-2014 springs

16 **Major taxa studied** Songbird species (n = 9)

17 **Methods** We tested whether the effect of temperature anomalies on juvenile body size varied
18 along an 11°C-thermal gradient.

19 **Results** In warmer springs, juveniles were larger overall at the coldest sites, but this effect
20 decreased towards the hottest sites, becoming negative for 2 species.

21 **Main conclusions** Warming should induce body size increases more frequently at the cold
22 edge of species distribution ranges, and rather body size declines at the hot edge. The climate-

23 dependency of the effect of weather fluctuations on body size is still under-acknowledged,
24 and the pattern identified deserves to be investigated over broader climatic gradients and
25 taxonomic coverage. Climate-driven changes in body size are therefore not uniform across
26 climatic regions and within species ranges.

27

28 *Key words:* Bergmann's rule, birds, climate warming, France, temperature anomaly, thermal
29 range, wing length

30

31 INTRODUCTION

32 Although an increasing attention is given to body size change as a response to climate
33 warming (Gardner *et al.*, 2011), this phenomenon is still little documented and its underlying
34 mechanisms are poorly understood. The effects of rising temperatures on animal structural
35 size can be mediated through effects on juvenile growth and size-dependent mortality
36 (Gardner *et al.*, 2014). The original proposal was that body size would decline with warming
37 as a result of the advantage of being smaller under warmer conditions. With a higher surface-
38 volume ratio, smaller individuals can dissipate body heat more efficiently than larger
39 individuals, which is advantageous in warm climates, as stated in Bergmann's rule
40 (Bergmann, 1847). With climate warming, larger individuals would increasingly suffer from
41 hyperthermia, and a size reduction is a possible adaptive response enabling individuals to
42 cope with increasingly warm conditions (Gardner *et al.*, 2011).

43 The application of Bergman's rule to climate warming has received controversial evidence so
44 far (Teplitsky & Millien, 2014). Despite rising temperatures, many species have not exhibited
45 any change in body size over time (Meiri *et al.*, 2009; Kruuk *et al.*, 2015), or the trend was
46 opposite to the prediction, *i.e.* size increase (Björklund *et al.*, 2014; Pérez *et al.*, 2016). This
47 may be related to the complexity of temperature and other climatic impacts on physiology and
48 body size (Gardner *et al.*, 2014). Temperature change can potentially have contradictory
49 effects depending on which biological feature is affected (e.g., body growth *versus* survival),
50 and which aspect of temperature change is regarded (e.g., mean temperature *versus* heat wave
51 frequency). For instance, increasing mean temperatures may impact body growth positively
52 (Gardner *et al.*, 2014), which is contradictory with the proposal of an application of
53 Bergmann's rule to climate warming (*i.e.*, selection for smaller in warmer mean
54 temperatures). Besides, heat waves may select for larger individuals as a result of a lower
55 evaporative water loss, enabling them to better evade dehydration (Gardner *et al.*, 2011).

56 More importantly, the effect of temperature fluctuations probably differs between climatic
57 regions. For instance, the physiological and ecological consequences of annual weather
58 deviation are likely to depend on the average local climatic regime: in cool or cold regions
59 (e.g., Collins *et al.*, 2016; Pérez *et al.*, 2016; Dubos *et al.*, 2018), or during cool periods of the
60 year (e.g., Gardner *et al.*, 2014b), hot temperatures indeed affect body growth positively. In
61 addition, events of extreme heat are also scarcer in temperate climates than in arid systems
62 (Garcia *et al.*, 2014). Observed body size variations are therefore expected to represent the
63 response to fluctuations in average temperatures in temperate climates (Dubos *et al.*, 2018),
64 whereas the influence of extreme hot events is expected to be particularly strong in arid, semi-
65 arid and tropical climates (Holmgren *et al.*, 2016; Gardner *et al.*, 2017). In arid or semi-arid
66 climates, larger individuals are expected to survive heat waves better, presumably because the
67 smallest individuals show higher rates of evaporative water loss, and would be more exposed
68 to dehydration and mortality during heat waves (McKechnie & Wolf, 2010).

69 For the same species, temporal variation in body size can differ between sites (e.g., Meiri *et*
70 *al.*, 2009; Collins *et al.*, 2017; Dubos *et al.*, 2018). Within a species distribution range,
71 populations are likely to have adapted locally to average meteorological conditions (e.g., Both
72 & te Marvelde, 2007). Their response to changes in environmental conditions may therefore
73 differ between the hottest and the coldest parts of their distribution range (Both & te
74 Marvelde, 2007; Socolar *et al.*, 2017). This is the case for population trends of European
75 birds: abundances decline towards the hot edge of their species distribution range, while they
76 increase towards the cold edge (Jiguet *et al.*, 2010). Differential responses to climate change
77 were also observed in avian phenology, with advancements in egg laying near the cold edge
78 but not near the warm one (depending on the species; Both & te Marvelde, 2007). A similar
79 pattern was found in the nesting success of Californian birds, with a positive effect of
80 temperature anomaly towards the cold edge of species distributions, and a negative effect

81 towards the warm edge (Socolar *et al.*, 2017). Individuals living close to the hot edge of their
82 species distribution range are the most threatened by climate warming, because they live close
83 to their upper thermal limit already (Jiguet *et al.*, 2010; Deutsch *et al.* 2008; Tewksbury *et al.*
84 2008; Socolar *et al.*, 2017). Conversely, individuals living at the cold edge are more cold-
85 limited and would even benefit from hot anomalies, as a result of a lower exposure to cold
86 stress (Jiguet *et al.*, 2006). Hence, across thermal ranges, the impact of climate warming on
87 populations is expected to change gradually, and ranges from positive at the cold edge
88 towards negative at the hot edge (Jiguet *et al.*, 2010). The influence of thermal anomalies
89 would therefore depend on the relative position of the population within the distribution
90 range, even within the inner part of species thermal ranges. Although this variation of the
91 effect of temperature anomalies across a species range is now well acknowledged for
92 population trends (Jiguet *et al.*, 2010), to our knowledge, it has not yet been investigated on
93 body size responses to temperature changes.

94 Contrasting effects of temperature increase on body size across the thermal range are expected
95 to occur through two main mechanisms: (i) direct, thermoregulatory costs, and (ii) indirect,
96 ecological effects through ecosystem productivity (Yom-Tov & Geffen, 2011) and temporally
97 mismatched predator-prey interactions (Husby *et al.*, 2011). Firstly, the ability to
98 thermoregulate depends on morphology, and the thermal constraint affecting morphology is
99 expected to depend on the local climate. For instance, in song sparrows (*Melospiza melodia*),
100 selection for heat retention was found to prevail in a continental climate during winter
101 (Danner & Greenberg 2015), while for the same species, it was driven by heat dissipation in a
102 Mediterranean climate during summer (Greenberg *et al.*, 2012). In this case, the differential
103 morphological change affecting thermoregulation was applied to bill size. However, this
104 should also apply to structural size, as heat loss/conservation can depend on the size of body
105 appendices (e.g., Allen's rule; Allen, 1877) as well as on structural size (e.g., Bergmann's

106 rule). In cold or cool regions (e.g., temperate to polar), individuals may be larger in warmer
107 years (Collins *et al.*, 2016; Pérez *et al.*, 2016; Dubos *et al.*, 2018) when the cold constraint on
108 growth is alleviated. Tissue growth increases with temperature in two ways: by accelerating
109 biochemical reactions and metabolism (Gillooly *et al.*, 2001), and by reducing the allocation
110 of energy used for body heat maintenance (Kendeigh, 1969), so this energy can be reallocated
111 to growth (Gillooly *et al.*, 2001; Dawson *et al.*, 2005). Nestling growth may also be indirectly
112 facilitated by warmer temperatures through the reduced thermoregulatory load for parents:
113 parents can spend more time foraging to provision nestlings with food, and less time at the
114 nest to maintain them warm (e.g., Socolar *et al.*, 2017). In warmer regions (e.g., dry tropical
115 and Mediterranean), the risk that a temperature increase reaches detrimental or sub-lethal
116 levels is higher (Khaliq *et al.*, 2014). Larger individuals may suffer more from increasing
117 temperature, as interpreted with the application of Bergmann's rule to warming (Gardner *et*
118 *al.*, 2011). Secondly, body size depends on food availability during ontogeny. For secondary
119 consumers, food availability depends on temperature-driven primary production (Yom-Tov &
120 Geffen, 2011). In temperate regions, precipitation is rarely limiting, and higher temperatures
121 would increase invertebrate abundance, i.e. the main resource for nestling and fledgling
122 songbirds (Bale *et al.*, 2002; but see Carroll *et al.* 2015 for an opposite response in hygrophilic
123 peatlands). In semi-arid systems, such as Mediterranean regions, invertebrate abundance is
124 more constrained by drought, resulting from limited rainfall combined with high temperatures
125 (Gardner *et al.*, 2014). An increase in spring temperature may therefore result in larger body
126 size in cool climates, whereas it could result in smaller body size in Mediterranean or dry
127 tropical climates, in the case of co-occurrence with limited precipitation. Hence, direct and
128 indirect effects of temporal variation in mean temperature on body size are expected to differ
129 between the hottest and the coldest parts of the species ranges (Fig. 1).

130 We assessed whether the effect of interannual variation in mean spring temperature on
131 juvenile body size varies along a thermal gradient (11.2°C between the coldest and the hottest
132 study sites; Fig. 1) in a temperate region (France) for nine songbird species. We predicted
133 that, during hot springs (relative to the local average temperature), juveniles should be larger
134 at the coldest sites, and smaller at the hottest sites (Fig. 1). In temperate climates, the tipping-
135 point of the effect of local temperature on body size sensitivity to temperature anomalies
136 should depend on the position of populations within the species thermal ranges: the colder the
137 location of a population, the more its growth should increase with temperature anomaly.

138

139 **METHODS**

140 **Bird survey**

141 We used individual records of songbirds caught during sessions of the French Constant bird
142 ringing Effort Sites (CES) scheme, from 2000 to 2014 (Robinson et al., 2009; more
143 information at <http://crbpo.mnhn.fr>, see 'STOC Capture'). Biometric data used in the present
144 study were collected at 204 sites by 132 volunteer bird ringers, each site being monitored
145 during 4.1 ± 3.3 SD years (Dehorter & CRBPO 2015). Each site was visited at least three
146 times during the breeding season (average 3.6 ± 1.6 SD), from 15 May until 19 July. For a
147 given site, number and location of mist-nets were kept constant throughout the years. Each
148 captured individual was individually marked, identified to species and aged (juvenile for birds
149 born during the ongoing breeding season; Svensson 1992). Most sites are located in
150 shrublands, woodlands with dense understorey, or reedbeds (Eglington *et al.*, 2015). Our
151 survey encompassed three major types of climate based on the Köppen Geiger classification
152 (Peel *et al.*, 2007): subalpine (corresponding to the subarctic climate, Dfc), temperate oceanic
153 (Cfb), and hot-summer Mediterranean climates (Csa), with a thermal range of 11.2°C between

154 the coldest (8.4°C on average) and the hottest sites (19.6°C on average; Fig. S1) during
155 spring.

156

157 **Biometric data**

158 Wing length measurements were used as a proxy for body size (Gosler *et al.*, 1998; data for
159 supposedly better proxies of body size, such as tarsus or longest feather lengths were not
160 available, and body mass data conveyed an information on precipitation-dependency of body
161 condition rather than on temperature-dependency of body size, see Dubos *et al.* 2018). We
162 worked on post-fledgling juveniles only, because individual body size is determined during a
163 short period of growth in small songbirds, taking place mainly during the nestling stage (c. 2-
164 3 weeks), and continuing for a few weeks after fledging (Salewski *et al.*, 2010; Yom-Tov &
165 Geffen 2011). When recaptures occurred (representing 10% of the data), we randomly
166 selected one measurement per individual. In May-July, when captures took place, juvenile
167 songbirds are still within a few kilometres from their birth site, and captured individuals can
168 be assumed to have grown under the documented local climatic conditions. Adults were not
169 considered as their wing length depends on multiple, confounding effects of climate
170 throughout the life cycle (ontogeny, yearly molt and size-dependent mortality; Yom-Tov &
171 Geffen 2011; Gardner *et al.*, 2014).

172 As small sample sizes and data sparseness can compromise the robustness of inferences
173 (Yom-Tov & Geffen, 2011), we decided to include data for only (i) species ≥ 1000 measured
174 individuals, and (ii) species.site.year sampling units with ≥ 10 measured individuals (Table
175 S1). Since the hypotheses to be tested required that population position within the species
176 thermal ranges varied across sampling sites (i.e., gradient of ‘northern’ / core / ‘southern’
177 populations), we measured the proportion of each species’ thermal range that was included in

178 our study area. To do this, we relied on the population thermal coordinate (Jiguet *et al.*, 2010),
179 an index of the relative position of a given site, for a given species, within its European
180 thermal range (Table S1; Fig S1). A population thermal coordinate is computed as the
181 difference between the species thermal maximum (mean spring temperature of the hottest 5%
182 of European Atlas grid cell; Jiguet *et al.*, 2010) and the average temperature of a given site,
183 divided by the species thermal range (°C). This index varies between 0 and 1. Values close to
184 0 represent populations near the species thermal minimum; values closer to 1 are populations
185 near the species thermal maximum. We discarded one species (*Acrocephalus schoenobaenus*),
186 because the thermal gradient represented by the study sites was very narrow (2.2°C between
187 the coldest and the hottest sites, representing less than 15% of the species thermal range). For
188 the remaining species, a wider proportion of their thermal ranged was represented (minimum
189 for *Sylvia communis* = 31%, representing a thermal gradient of 4.2°; respectively, mean =
190 58% ± 13 SD and 8.5°C ± 2.3 SD for all species in Table S1). For seven species, surveyed
191 sites fell well within the species thermal range (and edges were not documented), whereas for
192 two species (Long-tailed tit *Aegithalos caudatus*, Common chiffchaff *Phylloscopus collybita*),
193 some sites corresponded the hot edge of their respective thermal ranges. According to habitat
194 preference, one species is a reedbed specialist (Common reed-warbler *Acrocephalus*
195 *scirpaceus*), whereas the eight others are shrubland / woodland generalists (Great tit *Parus*
196 *major*, Eurasian Blue tit *Cyanistes caeruleus*, Eurasian blackcap *Sylvia atricapilla*, Common
197 whitethroat *Sylvia communis*, Common chiffchaff, Long-tailed tit, Eurasian blackbird *Turdus*
198 *merula*, and European robin *Erithacus rubecula*; cf. Table S1, Fig. S2). The final dataset
199 included nine species, all living in relatively similar thermal niches, resulting in a total of
200 34 101 juveniles measured (see details per species in Table S1).

201

202 **Climatic data**

203 We used daily mean temperature data, obtained from E-Obs (Haylock *et al.*, 2008), and for
204 each site we computed: (i) yearly ‘spring temperatures’ (noted $T_{S,Y}$), i.e. the mean temperature
205 of a given year, at the site, for spring (from 1 April to 31 July, documenting between-year
206 fluctuations of local thermal conditions), and (ii) ‘local average temperature’ (noted T_S), as the
207 mean of $T_{S,Y}$ over the 2000-2014 period (documenting average or ‘normal’ thermal conditions
208 at the geographical location of the capture site for the 1 April – 31 July period). Because
209 species are expected to be adapted to local thermal conditions (c.f., Bergmann’s rule; Ashton
210 2002), we analysed the interannual variation in body size in response to temperature
211 variations using annual local temperature anomalies (instead of raw temperatures). Local
212 temperature anomalies (noted TA_{st}) were computed for each site as the difference between T_S
213 and $T_{S,Y}$. Analysing the effects of temperature anomaly and local average temperature
214 simultaneously, enables the respective effects of temporal ($T_{S,Y}$) and spatial (T_S) variations in
215 thermal conditions on body size to be disentangled. Temperature anomaly and local average
216 temperature were largely uncorrelated (Pearson’s $r = 0.007$).

217

218 **Statistical analysis**

219 Using Linear Mixed Models (MCMCglmm; Hadfield, 2010), we assessed the effects of yearly
220 temperature anomalies TA_{st} on the juvenile body size of our study species, and its interaction
221 with the local average temperature T_S (to assess whether the effect of TA_{st} varied along the
222 species thermal range). We used uniform priors, with a burn-in of 20 000 iterations, followed
223 by an additional 100 000 iterations for which posteriors were sampled with an interval of 100.

224 We first built null models (Model 0 in Table 1) that included only adjustment variables, to
225 verify that the inclusion of temperature variables enhanced the explanatory power. The null
226 model, and all the following models (Table 1) accounted for the following sources of

227 variation in wing length: (i) differences in mean size between species (fixed, factorial *Species*
228 effect), (ii) species-specific post-fledgling growth throughout the season, using log-
229 transformed Julian date (noted $\log(Date)$) as a fixed, linear effect in interaction with species
230 (Dubos *et al.*, 2018), (iii) temperature-driven spatial differences between sites (*e.g.*
231 Bergmann's rule) using a fixed, linear effect of local average temperature T_s , and (iv) species-
232 specific dependence on local average temperature (fixed, factorial *Species* x T_s interaction).
233 This interaction term is justified by the fact that species may intrinsically respond differently
234 to temperature (Ashton 2002), or may respond differently because the thermal ranges of the
235 study species differ (*e.g.*, for some species, French populations are located at the core of the
236 thermal range, whereas for other species, French populations are closer to the species hot
237 limit; Jarema *et al.*, 2009). Consistent (v) between-observer, (vi) between-site and (vii)
238 residual between-year variations were accounted for by random terms. Finally, (viii)
239 comparative tests across species accounted for phylogenetic relatedness using pairwise
240 phylogenetic distances. We extracted a set of 100 generated phylogenetic trees from Jetz *et*
241 *al.*, (2014) and integrated these using the 'pedigree' argument of the MCMCglmm function,
242 that allows the portion of body size variation due to additive genetic variance to be
243 disentangled from other sources of variance.

244 Then we built a set of models to assess the statistical support for our prediction. We first
245 considered the dependence of wing length on temperature anomalies (linear, additive effect of
246 TA_{st} , Model 1). Then we accounted for the possibility that species respond differently (Jiguet
247 *et al.*, 2006) by adding the $TA_{st} \times Species$ interaction term (Model 2). The dependence on
248 temperature anomaly could differ along the observed thermal gradient; this was allowed for
249 by adding the $TA_{st} \times T_s$ interaction term to model 1 (Model 3). In addition, this hypothesis was
250 assessed with a model that also accounted for the possibility that species response to TA_{st}
251 differed between species (*i. e.* adding the $TA_{st} \times T_s$ interaction to Model 2, resulting in Model

252 4). Eventually, we allowed for species-specific relationships between temperature anomaly
253 TA_{st} and local average temperature T_s , by adding a 3rd-order interaction term between the
254 effects of TA_{st} , T_s and species (Model 5). This model allows for a different direction and/or
255 strength of both temperature effects between species. Model 5 results in the following
256 formula:

$$\begin{aligned} 257 \text{Wing Length}_{isot} &\sim \alpha_i + \beta_{i1} \cdot \log(\text{Date}) + \beta_{i2} \cdot T_s \\ 258 &+ \beta_3 \cdot TA_{st} + \beta_{i3} \cdot TA_{st} + \beta_4 \cdot (TA_{st} \times T_s) + \beta_{i4} \cdot (TA_{st} \times T_s) \\ 259 &+ \varepsilon_s + \varepsilon_o + \varepsilon_t + \varepsilon_{isot} \end{aligned}$$

260 where α_i is the average size of species i (intercept), β_{i1} is the slope for the effect of log-
261 transformed Date for species i , β_{i2} is the species-specific slope for the effect of local average
262 temperature T_s , β_3 is the slope for the additive effect of temperature anomaly TA_{st} , β_{i3} is the
263 species-specific deviation from β_3 (species interaction term), β_4 is the slope for the interaction
264 between the effects of temperature anomaly TA_{st} and local average temperature T_s , β_{i4} is the
265 species-specific deviation from β_4 (species interaction term), ε_s , ε_o and ε_t hold respectively for
266 the random terms for site, observer and year effects, and ε_{isot} is the residual variation.

267 The stepwise examination of predictions relied on the comparison of the six aforementioned
268 models (Table 1), ranked on the basis of the Deviance Information Criterion (DIC, a Bayesian
269 version of Akaike Information Criterion; Spiegelhalter *et al.*, 2002). The model with the
270 lowest value of DIC is considered to represent the best trade-off between parsimony and fit of
271 the model to the data. Each model was fitted using 100 different phylogenetic trees, so that
272 the average of all posteriors accounted for between-species phylogenetic dependence. All
273 statistical analyses were performed under R version 3.3.0 (R Core Team, 2016).

274

275 **RESULTS**

276 The body size response to temperature anomaly TA_{st} differed between species. The model
277 allowing for species-specific responses was better supported than the model assuming an
278 additive response, common to all species (Model 2, Table 1). In accordance with our
279 prediction, this response to TA_{st} varied along thermal gradients (Model 4 and 5 received the
280 highest statistical support; Table 1). The effect of temperature anomaly on body size depends
281 on the local average temperature.

282 On average across species, at an intermediate site (i.e., for a mean local average temperature
283 $T_s = 15.05^\circ\text{C}$) the higher the temperature anomaly, the longer the wing length (+0.9 mm per
284 $^\circ\text{C}$ anomaly; Model 3 in Table S2). But, the warmer the site (local average temperature, T_s),
285 the lower the effect of temperature anomaly on wing length (for a $+1^\circ\text{C}$ increase in local
286 average temperature, the effect decreases by 0.052 mm per $^\circ\text{C}$ anomaly; Model 4 in Table S2).
287 At the hottest sites, the effect of temperature anomaly was even reversed, with a potential
288 decrease in wing length in the warmest years (Fig. 2). The nature of this ‘temperature
289 anomaly - by - local average temperature’ interaction may differ between species, but these
290 differences seem to be of minor importance in our dataset (since ΔDIC is only 2 between
291 models 4 and 5; Tables 1, S2). When plotting estimates for the interactive effects of TA_{st} and
292 T_s per species (Fig. 3, S2), the response of body size is largely similar across species. Relying
293 on model 5, the three species showing a significantly positive effect of temperature anomaly
294 at the coolest sites showed a significant interactive effect with local average temperature (i.e.,
295 Eurasian blackcap, long-tailed tit and great tit; Table S2). At the coolest sites (between 8.37
296 and 13.9°C depending on the species), body size increased significantly in warmer years for
297 these species (respectively, by 0.86, 1.71 and 0.54 mm per $^\circ\text{C}$; Table 2). The temperature
298 anomaly effect decreased when the local average temperature increased: for a $+1^\circ\text{C}$ increase
299 in local average temperature, the wing length of Eurasian blackcaps decreased by -0.072 mm

300 per °C of anomaly, -0.324 mm per °C for long-tailed tits, and -0.072 mm per °C for great tits
301 (Table S2). This effect decreased enough to become negative for two species at the warmest
302 sites (i.e., long-tailed tit: -1.06 mm per °C of anomaly; European blackcap: -0.29 mm per °C
303 of anomaly at a site with an average temperature of 18.2°C; Table 2; Fig. S3, S4). For these
304 two species, the ‘tipping-point’ of local temperature, i.e. at which the sign of the effect of
305 temperature anomaly changes, was located between the core and the hot edge of their
306 respective thermal range (respectively for thermal coordinates of 0.77 and 0.70). For the great
307 tit, the effect of temperature anomaly became null towards the hot edge of its thermal range
308 (Table 2).

309

310 **DISCUSSION**

311 As expected in Figure 1, the response of body size to temperature anomaly depended on the
312 position of populations within the species’ thermal range. At the coldest sites, juveniles were
313 larger in warmer years, but the size of those born at the warmest sites did not depend on
314 spring temperature anomalies (or even declined in hot springs for some species).

315 The positive effect of temperature anomalies in cold regions may be related to both direct
316 effects, through changes in thermoregulatory mechanisms, and indirect effects, through
317 changes in food availability (Yom-Tov & Geffen, 2011). Warmer years induce a reduction of
318 the cost of body heat maintenance in cool areas, enabling a higher energetic allocation to body
319 growth (Gillooly *et al.*, 2001). An alternative, non-exclusive hypothesis is that warming may
320 also increase net primary production, thus improving invertebrate abundance (Yom-Tov &
321 Geffen 2011; Dubos *et al.*, 2018). In the present study, all study species are insectivorous
322 during spring. Higher invertebrate abundance in some years may have enhanced juvenile
323 protein intake, allowing them to reach larger fledgling sizes at the coolest sites (Lindström,
324 1999).

325 The opposite effect, found for two species (long-tailed tits and Eurasian blackcaps) at the
326 warmest sites, is consistent with the application of Bergmann's rule to climate warming
327 (Gardner *et al.*, 2011). The consequences of a local increase in temperature on individual
328 fitness have been shown to differ between species of different latitudes in a previous study
329 (Deutsch *et al.* 2008). At low latitudes, warming has more deleterious consequences on fitness
330 than at higher latitudes. This is due to the fact that, at low latitudes (e.g., tropical), species live
331 close to the upper boundary of their thermal tolerance, while high latitude species live farther
332 from that lethal limit (Deutsch *et al.* 2008; Tewksbury *et al.* 2008). This process seems to
333 apply at the intraspecific level, within species range. The negative effect of temperature
334 anomaly on juvenile body size may be explained by two mechanisms. This may be the result
335 of (1) a plastic response to environmental change on growth rates (Teplitsky & Millien,
336 2014). Hotter years in warm areas would bring growing juveniles into suboptimal thermal
337 conditions for juvenile growth (Mertens, 1977; Rodríguez & Barba, 2016), which would
338 result in smaller individuals. Size declines in hotter years could also be the result of (2) size-
339 dependent mortality: the largest individuals would suffer the most from hyperthermia, and be
340 more likely to die in warm years. However, lethal temperatures are rarely reached in
341 temperate regions (mean number of days $> 35^{\circ}\text{C} = 0.13 \pm 0.28$ SD days per spring at our
342 study sites). Hence, from the present dataset, even at the hottest sites, a higher mortality in
343 larger individuals in hot years would not be expected in France. Most studies attempting to
344 find a selection for smaller size failed, or found the opposite pattern (Gardner *et al.*, 2014;
345 Dunn *et al.*, 2016). The hypothesis of a cold constraint release for juvenile growth in hotter
346 years is therefore the most likely in temperate climates. Our results are consistent with Danner
347 and Greenberg (2005), suggesting that in temperate species, morphology is constrained by
348 cold towards the coldest edge of their distribution range – and potentially across most of their
349 temperate distribution range (i.e. not all individuals achieve optimal body size) – whereas at

350 the hottest edge, heat (or drought-driven food shortage) would be the predominating
351 constraint. An additional hypothesis is that very high temperatures could reduce parental
352 foraging efficiency, e.g. due to physiological stress (hyperthermia, water loss) enhanced by
353 reduced invertebrate activity (Geiser *et al.*, 2008; Cunningham *et al.*, 2013). Lower parental
354 feeding frequency could affect offspring growth rate, and result in smaller fledglings (Searcy
355 *et al.*, 2004).

356 The indirect effects of temperature anomaly on ecosystem production – and therefore food
357 availability – at the hottest sites may also differ from the coldest sites. In semi-arid
358 environments, net primary production depends on precipitation to a greater extent than
359 temperature (e.g., Gardner *et al.*, 2014; Holmgren *et al.*, 2016). This may apply to the French
360 Mediterranean region, as both climates are similar (see www.worldclimate.com). Hence, it is
361 unlikely that temperature response is driven by changes in net primary production at the
362 warmest study sites, which may explain the decreasing effect of temperature anomaly towards
363 the hottest sites. Another hypothesis is that, because temperature change can impact food web
364 structures (e.g., Edeline *et al.*, 2013), a differential effect can be the consequence of differing
365 changes in the biotic environment. The effect of temperature change on body size, through
366 changes in food availability in ecosystems, may therefore depend on the regional climate and
367 ecosystems, regardless of the population position within the species thermal range. These
368 antagonistic or synergistic effects of local temperature, precipitation and ecosystem structures
369 on individual body size deserve to be investigated in future research.

370 Body size response to warming may depend on the average climate under which the local
371 population evolved, as found for temporal trends in population size (Jiguet *et al.*, 2010). The
372 consequences of climate warming on populations are often more deleterious at the hot edge of
373 species distribution, while it can be favourable at the cold edge (Parmesan & Yohe, 2003;
374 Hickling *et al.*, 2006; Leroy *et al.*, 2014), with a linear graded response in between (Jiguet *et*

375 *al.*, 2010). Although the present analysis included a relatively wide range of thermal
376 conditions ($> 11^{\circ}\text{C}$), the number of sites represented in cold and hot regions was limited (Fig.
377 S1). We used species for which the distribution edges are not (or rarely) included in our study
378 area (Fig. S2). Despite species response to warming which may be stronger at the edges of
379 their distribution range (Jarema *et al.*, 2009), we still detected a differential response along a
380 fragment of their range. Moreover, while responses to warming are expected to be greater in
381 thermal specialists (i.e., species with a narrow thermal range compared to other Palearctic
382 species; Jiguet *et al.*, 2006), our results were obtained from species that are mostly thermal
383 generalists (i.e., with a wide thermal range; Table S1). This suggests that differential effects
384 of temperature change on body size may apply to a wide range of species (including thermal
385 generalists), which is consistent with results obtained for population trends (Jiguet *et al.*,
386 2010). In spite of geographic and taxonomic limits, the pattern revealed is the one expected
387 theoretically (cf. abundance, phenology patterns), and we provide the first evidence for a
388 structured effect of temperature on body size. Studies performed at large geographic scale,
389 aiming at testing the effect of temperature variation on body size – while assuming a uniform
390 effect – may therefore fail to detect an effect of temperature change because it may be blurred
391 by opposing effects between sites.

392 The estimated effect sizes for the influence of temperature anomaly on body size are small,
393 ranging from -0.8 to 1.0 % of species' mean wing length per Celsius degree of annual
394 anomaly. Compared to spatial effects of temperature (i.e., local average temperature; cf.
395 Bergmann's rule), these effects sizes were of similar magnitude (-0.23 to 0.16 % per Celsius
396 degree; Table S2). In other studies focussing on temporal variation in bird size, the effect of
397 mean temperature of the breeding period was about 1 % of the juvenile wing length in
398 Australia (Gardner *et al.* 2014), and the effect of summer temperature ranged between -0.63
399 and 0.15 % per Celsius degree in eastern North America (Collins *et al.*, 2017). Formerly,

400 Dubos et al. (2018) have even clarified that, when analysing additive effects of annual
401 weather on wing length across sites and species, they could explain 5% of the total variance in
402 juvenile wing length at best, i.e. the additive and specie-specific variation between years. All
403 the remaining variance actually corresponds to site-specific annual variations (7%) or site-
404 and species-specific annual variations (88%). Hence, we acknowledge that effect sizes are
405 indeed small, and that this questions the biological relevance of the corresponding size
406 changes. This concern about small size effects applies to most existing studies on short-term
407 body size changes, and is a recurrent issue in ecology (Møller & Jennions, 2002). Given the
408 multiple determinants of body size, it even appears obvious that body size cannot drastically
409 change between years and generations. Hence, whatever the influence of the environment on
410 juvenile body size, it will always be restricted to a narrow range of change of average size,
411 beyond which other compensatory mechanisms start to play (e.g. offspring mortality, early
412 termination of growth). We are not aware of a statistical framework, applicable to existing
413 data, which would allow to objectively qualifying the biological relevance of the observed,
414 statistically robust effects of temperature on wing length.

415 In the present study, we focussed on spring temperatures because this corresponds to the
416 period of body growth, as body size has been shown to be mainly driven by the conditions
417 during this period (Yom-Tov Geffen, 2011), and because in songbirds, body growth ends
418 soon after fledging (some weeks). However, high temperatures may drive size-dependent
419 mortality in juveniles, as they are more exposed to hypo- or hyperthermia than their parents
420 (Mertens, 1977). In addition, size-dependent mortality can also affect adults (Gardner et al.,
421 2014), and mortality can occur at later stages of individuals' life (i.e., carry-over effects; van
422 de Pol & Cockburn, 2011). Getting the full picture of body size responses to temperature will
423 require to investigate its effects during other parts of the year (e.g., winter, when bird
424 mortality is the highest in temperate climates; Van Balen, 1980), at different time-scales

425 (Kruuk *et al.*, 2015), and include assessments of size-dependent mortality (e.g., using mark-
426 recapture approaches).

427 To conclude, the differential effect of climate warming along species range already found in
428 species distributions (Hickling *et al.*, 2006), phenological shifts (Both & te Marvelde, 2007)
429 and population trends (Jiguet *et al.*, 2010) also applies to body size. We predict that climate
430 warming would induce body size increases (up to optimal body size) more frequently at the
431 cold edge of species distribution ranges, and body size declines would be more likely at the
432 hot edge. In France, the impact of warming on avian population dynamics may impact body
433 size negatively at the warmest sites, corresponding to the Mediterranean region, where species
434 (including our study species) live closer to the upper boundary of their thermal tolerance
435 (Jiguet *et al.*, 2010). As individual fitness is often size-dependant, with the largest surviving
436 and/or reproducing better (Lindström 1999; Ronget *et al.*, 2017), it is to be feared that size
437 decline may impact populations negatively. To assess the robustness and generality of our
438 conclusions, future studies should investigate the synergistic effects of local temperature
439 anomalies (weather fluctuations) and local average temperatures (climate) on body size across
440 a larger number of species (including a broader spectrum of life-history traits, and particularly
441 more thermal specialists), and across a broader climatic range, to include the entire thermal
442 ranges of the species studied. Another challenge for future studies on the link between body
443 size and temperature fluctuations will be to sort out the proximate mechanisms at play (e.g.
444 ontogeny versus mortality, and thermal versus trophic pressure).

445

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595

596 **DATA ACCESSIBILITY:** The dataset used in this analysis is available as an R object in
597 supporting information.

598 **Table 1** Set of models used to assess the relationship between juvenile wing length, local
599 temperature anomaly, local average temperature and species identity. The lowest Deviance
600 Information Criterion (DIC) indicates the ‘best’ model (in bold), and Δ DIC is the DIC
601 difference with the best model. TA_{st} holds for the local temperature anomalies for a site s in
602 year t , during the breeding season. T_s is the average temperature for a site s across the 2000-
603 2014 breeding seasons. All models included the same adjustment variables (see text). Based
604 on DIC, Models 4 and 5 received similar statistical support.

Model	Model description	DIC	Δ DIC
M0	Species + T_s + Species \times T_s + other adjustment var. (see text)	150879	28
M1	M0 + TA_{st}	150878	27
M2	M1 + $TA_{st} \times$ Species	150860	9
M3	M1 + $TA_{st} \times T_s$	150869	18
M4	M2 + $TA_{st} \times T_s$	150851	2
M5	M4 + $TA_{st} \times T_s \times$ Species	150849	0

605

606

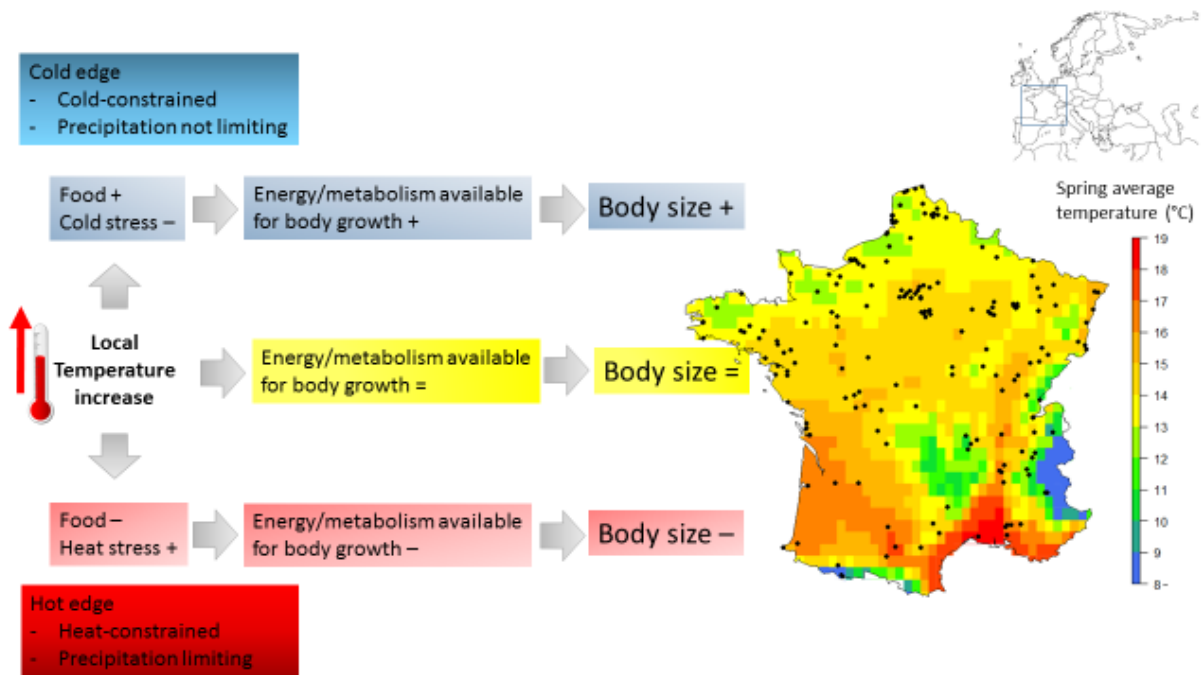
607 **Table 2** Estimates of Temperature anomaly (TA_{st}) at the observed coldest (T_s min) and hottest
608 (T_s max) species-specific study sites, and the local average temperature (T_s) where the
609 temperature anomaly effect is predicted to reverse (i.e., is null). Numbers in parentheses
610 indicate the corresponding thermal coordinate (a value of 0 represents the coldest sites where
611 the species can be present, and 1 represents the hottest sites; Table S1). Predicted values were
612 obtained from MCMCglmm posterior estimates (Model 5 in Table 1) and accounted for
613 phylogenetic relatedness (species are sorted accordingly).

Species	T_s min (°C)	TA_{st} effect at T_s min		T_s max (°C)	TA_{st} effect at T_s max		T_s (°C) at null TA effect
		Slope (mm.°C ⁻¹)	% of wing length		Slope (mm.°C ⁻¹)	% of wing length	
<i>Parus major</i>	13.2	0.54	1.0	19.6	-0.02	-0.3	20.9 (1.00)
<i>Parus caeruleus</i>	11.0	-0.25	-0.8	19.6	0.22	0.2	-
<i>Acrocephalus scirpaceus</i>	8.4	-0.13	-0.7	18.8	0.39	0.1	-
<i>Sylvia atricapilla</i>	8.5	0.86	0.5	18.2	-0.29	-0.3	15.1 (0.70)
<i>Sylvia communis</i>	12.0	0.28	0.7	19.6	-0.15	-0.3	15.1 (0.79)
<i>Phylloscopus collybita</i>	11.4	0.12	0.8	18.2	0.12	0.2	-
<i>Aegithalos caudatus</i>	8.4	1.71	0.9	18.2	-1.06	-0.1	16.4 (0.77)
<i>Turdus merula</i>	13.9	0.68	0.3	18.2	-0.39	-0.4	12.3 (0.60)
<i>Erithacus rubecula</i>	8.4	0.16	0.6	18.0	0.13	0.2	-

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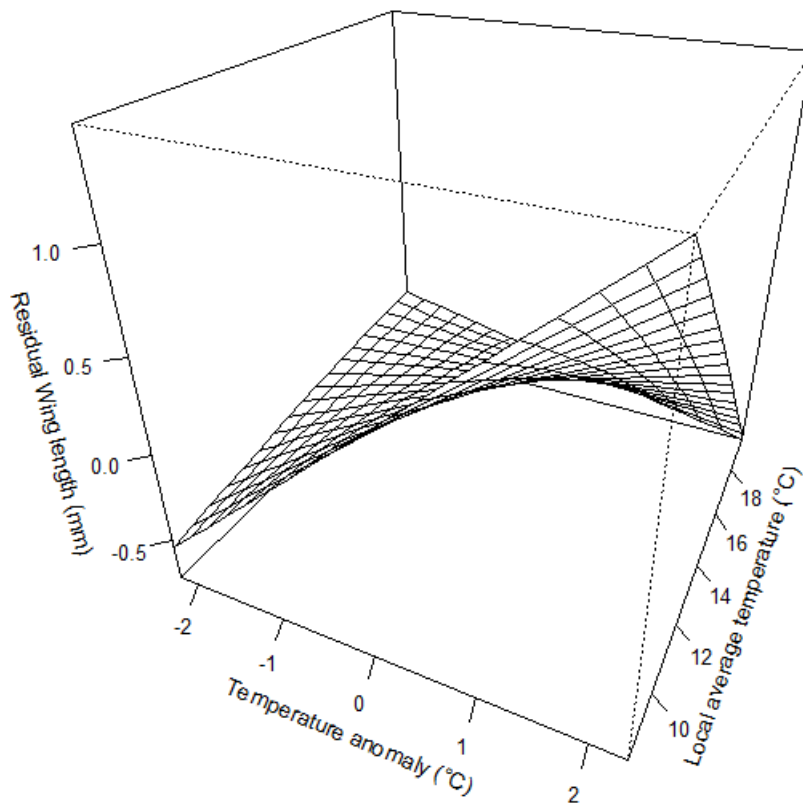
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617

618 **Fig. 1** Theoretical framework for a differential effect of climate warming on body size
619 depending on local climate (here, spring average temperatures). At hot sites (red, dark orange,
620 including the Mediterranean region), positive temperature anomalies are predicted to induce
621 body size reduction, whereas at cool sites (blue-green, including mountain regions), body size
622 enlargement is expected. The map shows the distribution of the 204 study sites in France.

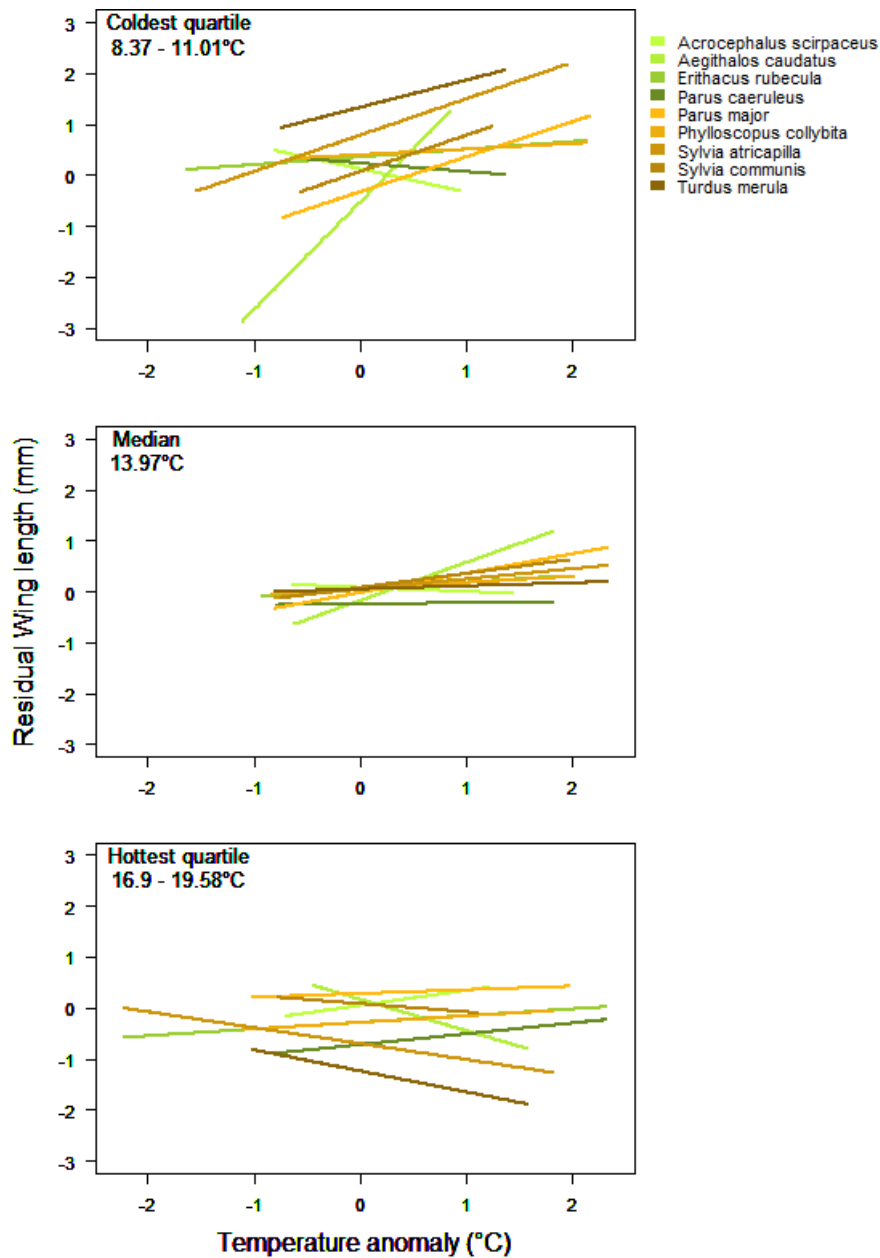
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624

625 **Fig. 2** Residual response of average juvenile wing length to temperature anomaly along a
 626 gradient in average local temperature, for nine breeding songbird species from France.
 627 Predicted values were obtained from MCMCglmm (Model 3, see text and Table 1). Local
 628 average temperature is the mean spring temperature of a given site for the period 2000-2014.
 629 Wing length was centred on the mean value per species. Species-specific predicted values are
 630 shown in supporting information (Fig. S3).

631



632

633 **Fig. 3** Species-specific response of juvenile wing length to spring temperature anomaly,
 634 separated into three quantiles of local average temperature, for nine breeding songbirds
 635 species from France. Predicted values were obtained from MCMCglmm (Model 5, Table 1).
 636 Wing length was centred on species means. Local average temperature is the mean spring
 637 temperature of a given site for the period 2000-2014. Coldest quartile: average response at the
 638 25%, coldest sites (n = 9); Median quartiles: average response at the 25-75% intermediate
 639 sites (n = 180); Hottest quartile: average response at the 75% hottest sites (n = 15).