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## **Disentangling the effects of spring anomalies in climate and net primary production on body size of temperate songbirds**

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1 **Disentangling the effects of spring anomalies in climate and net primary production on**  
2 **body size of temperate songbirds**

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23 **Abstract**

24 Body size is implicated in individual fitness and population dynamics. Mounting interest is  
25 being given to the effects of environmental change on body size, but the underlying  
26 mechanisms are poorly understood. We tested whether body size and body condition are  
27 related to ambient temperature (heat maintenance hypothesis), or/and explained by variations  
28 in primary production (food availability hypothesis) during the period of body growth in  
29 songbirds. We also explored whether annual population-level variations of mean body size are  
30 due to changes of juvenile growth and/or size-dependent mortality during the first year. For  
31 41 species, from 257 sites across France, we tested for relationships between wing length ( $n =$   
32 107,193) or body condition ( $n = 82,022$ ) and local anomalies in temperature, precipitation and  
33 net primary production (NDVI) during the breeding period, for juveniles and adults  
34 separately. Juvenile body size was best explained by primary production: wings were longer  
35 in years with locally high NDVI, but not shorter in years with low NDVI. Temperature  
36 showed a slightly positive effect. Body condition and adult wing length did not covary with  
37 any of the other tested variables. We found no evidence of climate-driven size-dependent  
38 mortality for the breeding season. In our temperate system, local climatic anomalies explained  
39 little of the body size variation. A large part of wing length variance was site-specific,  
40 suggesting that avian size was more dependent on local drivers than global ones. Net primary  
41 production influenced juvenile size the most through effects on body growth. We suggest that,  
42 during the breeding season in temperate systems, thermoregulatory mechanisms are less  
43 involved in juvenile growth than food assimilation.

## 44 INTRODUCTION

45

46 Body size is a key determinant of individual fitness and population dynamics, affecting  
47 reproductive performance and survival (Ozgul et al. 2010, Yom-Tov and Geffen 2011,  
48 Gardner et al. 2014b). With the increasing body of evidence of temporal changes in body size,  
49 there is an emerging interest in the impact of environmental factors, and in particular the  
50 influence of climate change (Gardner et al. 2011, Sheridan and Bickford 2011).

51 Rapid body size changes in a population can arise from changes in growth conditions  
52 (Gardner et al. 2014b). Body size is largely determined by environmental conditions during  
53 the period of growth (i.e., from egg laying to the post-fledging period in birds; Yom-Tov and  
54 Geffen 2011). In cool climates, warmer temperatures can increase body growth as a result of a  
55 change in the cost of heat maintenance (Kendeigh 1969). Thus, in warmer years, juveniles can  
56 allocate more energy towards body growth, resulting in larger individuals (Gillooly et al.  
57 2001).

58 In addition to external temperature, metabolic allocation to growth is also dependent on  
59 the amount of protein intake (Dawson et al. 2005). Between-year changes in body size may be  
60 driven by fluctuations in food availability (Yom-Tov and Geffen 2011). Food limitation is  
61 particularly expected when the temperature is high and precipitation is low (or when  
62 precipitation is low, independently of temperature in arid systems, e.g., Gardner et al. 2014b),  
63 i.e. conditions that reduce primary production, and ultimately result in low prey availability  
64 for secondary consumers (Aber and Federer 1992). Those climatic conditions are particularly  
65 constraining in arid ecosystems (Holmgren et al. 2006). For instance, in honeyeaters *Ptilotula*  
66 *penicillatus*, individuals are smaller in drier years, which are presumably the years with the  
67 lowest food availability (Gardner et al. 2014b). Hence, temperature can have both direct  
68 effects through thermoregulation, and indirect effects through its influence on food

69 availability. The relative dependence of temporal change in body size on climate and primary  
70 production has not been assessed for any taxa in temperate systems yet (but see Gardner et al.  
71 2014b for a case study in a semi-arid system).

72 In addition to body growth effects, body size composition in a given population can also  
73 be driven by size-dependent mortality (Gardner et al. 2014b). In temperate climates,  
74 temperatures rarely reach lethal or sub-lethal levels (Tewksbury et al. 2008; Khaliq et al.  
75 2014). Hence, selective pressure related to thermoregulatory mechanisms is unlikely to drive  
76 significant body size change in a temperate system. Size-dependent mortality may also be  
77 related to food availability. Small individuals suffer higher mortality when food becomes  
78 scarce (Ozgul et al. 2010). Studies that have investigated size-dependent mortality in  
79 terrestrial vertebrates were performed in arid, or semi-arid systems (McKechnie & Wolf 2010;  
80 du Plessis *et al.* 2012; Gardner *et al.* 2014b). In fact, little is known about the mechanisms  
81 underlying changes in body size induced by environmental changes in temperate climates.  
82 Specifically, there is a need to identify whether temperature and food availability operate  
83 through effects on juvenile growth or size-dependent mortality.

84 Differences in the relative importance of body growth effects and size-dependent  
85 mortality among species and populations could explain the lack of consensus about the  
86 direction of body size change. The few existing studies focusing on temporal change in body  
87 size showed contrasting trends between species (Gardner et al. 2014a, Salewski et al. 2014,  
88 but see Gardner et al. 2009; Van Buskirk et al. 2010) and/or between sites (Meiri et al. 2009,  
89 Collins et al. 2016). This disagreement is reinforced by a probable publication bias towards  
90 cases exhibiting significant changes (Meiri et al. 2009). Among these studies, only a few  
91 tested the effect of interannual variation in temperature on body size, and even fewer assessed  
92 the relative importance of temperature *versus* net primary production (but see Gardner et al.  
93 2014b). Moreover, some studies were based on Museum data (e.g., Salewski et al. 2014) and

94 may have been prone to temporal collection and curation biases. Some were based on one or  
95 two localities (Van Buskirk et al. 2010, Collins et al. 2016), which precludes drawing  
96 macroecological conclusions. For this reason, there is a need to assess the influence of  
97 temperature and food availability on body size at larger taxonomic and geographic scales.

98       When relying on wing length measurements, effects on growth or mortality apply to  
99 juveniles (through ontogeny), but also to adults as they undergo a moult of their flight feathers  
100 after breeding (Jenni and Winkler 1994). Therefore, the distribution of adult wing length in a  
101 population results from both the quality of feather growth during the period of moult and from  
102 size-dependent mortality. Here we assessed whether juvenile body growth and adult feather  
103 growth are influenced by interannual variation in local environmental conditions, which  
104 would account for the possibility that population-level body size variation is driven by  
105 changes in population composition through size-dependent mortality.

106       Body constitution is characterized by two independent dimensions: body size and body  
107 condition (Canale et al. 2016). Unfortunately, many studies infer temporal patterns of body  
108 size from body mass data, and typically confuse changes of these two dimensions. Body mass  
109 conveys information on both body size and individual body condition, i.e. the body fat and  
110 protein content (Labocha and Hayes 2012). We are rarely able to access independent  
111 measurements of both dimensions. For birds, the best data available at a large scale are wing  
112 length, used as an index of body size (Gosler et al. 1998), and wing length-adjusted body  
113 mass, used as an index of body condition (Labocha and Hayes 2012). Because the response of  
114 body size and body condition to climate variation can differ (e.g., Gardner et al. 2016), we  
115 assessed the relative importance of climatic conditions and primary production on both of  
116 these traits.

117       In the present study, for the 41 commonest songbird species of continental France, we  
118 explored between-year changes in body size and condition at the population-level by

119 analysing the interannual variation in wing length and wing length-adjusted body mass, and  
120 their dependence on interannual fluctuations in climate and primary production during the  
121 breeding period, over the past 15 years. We tested the effect of local, interannual  
122 environmental fluctuations only during the breeding season, which corresponds to the period  
123 of body growth, as body size has been shown to be mainly driven by the conditions during  
124 this period (e.g., Gardner et al. 2014b), and because we had no information on bird locations  
125 and conditions experienced during the rest of their annual cycle. We analysed first-year birds  
126 and adults separately, to distinguish potential effects due to changes in body growth from  
127 changes in body size distributions in the population. As the distribution ranges of our study  
128 species exceed the bounds of our study area, this study represents a case in a temperate  
129 climate, regardless of potential ‘edge effects’ (Jiguet et al. 2010). We addressed the following  
130 questions: (1) Are birds larger during or after warmer years, as expected under the heat  
131 maintenance hypothesis? (2) Are birds smaller or have lower body condition during or  
132 following poorly productive years? (3) Which driver (temperature or food availability) is the  
133 most important for body size, during the period of juvenile growth? (4) If they have any  
134 effect, do these drivers operate through effects on body growth or size-dependant mortality?

135

## 136 **MATERIALS AND METHODS**

### 137 **Bird survey**

138 We used individual records of juveniles for the 41 most captured songbird species  
139 extracted from the French Constant bird ringing Effort Sites (CES) scheme from 2000 to 2014  
140 (Robinson et al. 2009, more information at <http://crbpo.mnhn.fr>, see ‘STOC Capture’).  
141 Biometric data were collected by 382 volunteer bird ringers at 257 sites spread across France  
142 (Fig. S1 in Supporting Information), each site being monitored during  $5.1 (\pm 3.9 \text{ SD})$  years  
143 (Dehorter and CRBPO 2015). Overall, study sites were evenly distributed across the years

144 (Fig. S2), and there was no bias in site-specific average temperature or latitude (Table S1).  
145 Captures occurred  $2.5 \pm 1.3$  SD times per breeding season per site, from May/early June (3  
146 June  $\pm 12.7$  SD), until late June/early July (26 June  $\pm 11.8$  SD). For a given site, the number  
147 and date of capture sessions and the number and location of mist-nets were kept constant  
148 throughout the years. Each individual captured was individually marked, its species identified  
149 and aged (juvenile for birds born during the ongoing breeding season, or adult if born in  
150 previous years; Svensson 1992). Mist-netting of birds is most efficient in habitats with a low  
151 canopy (3-to-4 m high), so most CES sites are settled in shrublands, woodlands with dense  
152 understory, or reedbeds (Eglington et al. 2015).

153

#### 154 **Biometric data**

155 We used wing length as a proxy for body size (Gosler et al. 1998), and body mass adjusted to  
156 wing length as a proxy for body condition (hereafter ‘body condition index’, Labocha and  
157 Hayes 2012). Wing length was measured with a butt-ended ruler as the length of the flattened  
158 wing chord from the carpal joint to the tip of the longest primary, at an average precision of  
159 0.8 mm ( $\pm 0.1$  across observers; i.e. most observers rounded the value to the nearest integer).  
160 Body mass was measured with spring or electronic balances, to the nearest 0.5 g. We used  
161 fully grown juveniles measured during the breeding period (15 May – 15 July, i.e. some days  
162 to weeks after fledging) and adults measured during their species-specific breeding period  
163 (Appendix S1 in supporting information). Measurements were performed by 2.4 ( $\pm 2.3$  SD)  
164 trained measurers per site. Within-observer repeatability of wing length and of body mass  
165 measurements was 0.92 ( $\pm 0.11$  SD) and 0.91 ( $\pm 0.10$  SD), respectively (Appendix S2). For a  
166 given site, the observer is usually the same over the years. Differences in measurements  
167 between observers and sites were accounted for in our models (see statistical analysis below  
168 for model descriptions). For each species, we accounted for potential measurement errors by

169 removing measurements that were beyond the upper and lower 0.5% limits of a Gaussian  
170 distribution fitted to the data. Only one measurement per individual was used in the analyses  
171 (with random choice for the 9.1% of data that were repeated measurements on the same  
172 individual). Hereafter, wing length measurements were from 40,071 juveniles and 67,122  
173 adults, and body mass measurements from 30,783 juveniles and 51,239 adults.

174

### 175 **Environmental variables**

176 We used environmental variables that are already known to explain interannual  
177 fluctuations in avian body size, and that were relevant for the study period and area (Keller  
178 and Van Noordwijk 1994, Gardner et al. 2014b). For each site and each year between 2000  
179 and 2014, we computed average environmental conditions during the breeding period (1<sup>st</sup>  
180 April-1<sup>st</sup> July, i.e. the main period of reproduction, including parental allocation to egg laying,  
181 incubation, and nestling and post-fledging growth). These metrics were computed from daily  
182 records of mean temperature and total precipitation, and monthly records of NDVI images.  
183 Populations are supposedly adapted to local thermal and trophic conditions (Both et al. 2006).  
184 To reveal the influence of between-year fluctuations in the local environment at each study  
185 site, independently from average local conditions, each raw variable was transformed into  
186 site-specific yearly anomalies by subtracting the average value of the corresponding site for  
187 the 2000-2014 period. This allowed us to control for confounding spatial effects (e.g.,  
188 latitudinal size gradients). Site-specific yearly anomalies in mean temperature were expected  
189 to document fluctuations of the thermal constraint (Kendeigh 1969), whereas total  
190 precipitation (alone or in synergy with mean temperature) or net primary production  
191 anomalies would record fluctuations of trophic resources (Yom-Tov and Geffen 2011) during  
192 the breeding period (Appendix S3). We used these three complementary trophic-related  
193 surrogates as they may characterise resource availability differently (e.g., Gardner et al.

2014b). We extracted daily mean temperature and daily total precipitation from the E-OBS meteorological dataset (Haylock et al. 2008), with a 0.25° pixel resolution using climateExtract R package (<https://github.com/RetoSchmucki>). We used monthly averaged raster images of remotely sensed Normalized Different Vegetation Index (NDVI; Copernicus Service information 2016) as a proxy for net primary production (Pettoirelli et al. 2005). The spectral reflectance covered by these images were the red and near infrared wavebands (0.61 to 0.68 µm and 0.78 to 0.89 µm, respectively), generally used for vegetal characterisation (Kerr and Ostrovsky 2003). We computed mean NDVI inside a buffer zone with a 5 km radius around each site from the raster images. The 5 km radius was chosen because it coincides with the level of precision of CES site geolocations. All variables were included in the analyses since their variations were largely uncorrelated ( $r < 0.35$ ; Table S2). They were centred and scaled so that relative effect sizes could be compared between variables, regardless of their order of magnitude of mean and variance.

207

### 208 **Adjustment variables**

209 All statistical null models presented hereafter included the effects of (i) species (fixed term),  
210 and random variation between (ii) observers, (iii) sites and (iv) year. Wing length of juveniles  
211 increases slightly throughout the breeding season; this was accounted for by adding (v-a), a  
212 fixed effect of log-transformed date of the year, with a species interaction term. Body mass  
213 increases during the morning until it reaches a plateau at about noon; this was accounted for  
214 by adding (v-b) log-transformed time of the day (hour) as a fixed term, with a species  
215 interaction term (see justifications and model details in Appendix S4).

216

### 217 **Statistical analysis**

218 As population responses to environmental parameters can vary with their relative position in  
219 the species' thermal niche (Jiguet et al. 2010), we verified that the majority of the populations  
220 studied were not located at the edge of species distributions. Less than 4% of the data were  
221 located in the upper 10% of species' thermal ranges, and less than 0.4% were located in the  
222 lower 10% (See details in Appendix S5).

223

#### 224 *Interannual variation in environmental and biometric variables*

225 The first step was to identify whether environmental conditions and biometric variables varied  
226 between years, and whether those variations were consistent.

227 For environmental variables, we examined temporal fluctuations using a spline  
228 function to estimate parsimonious, smoothed patterns of interannual variation. This was  
229 implemented with generalised additive mixed models (GAMMs, `gamm4` R package; Wood  
230 and Scheipl 2014), with 'year' as a smoothed term and 'site' as a random effect.

231 For body constitution features, we assessed the proportion of interannual variation that  
232 was common to all sites (i.e. nation-wide variation) and/or common to all species (i.e.  
233 independent of species life history traits). This was assessed with a variance-partitioning  
234 method (Grosbois et al. 2009). For wing length and body condition index, we used Linear  
235 Mixed Models (LMM; `lme4` package version 1.1.7; Bates et al. 2014) to estimate between-  
236 year ( $b_{\text{year}}$ ), between-site ( $b_{\text{year}}$ ) and ( $b_i$ ) between-species  $i$  variances using random terms for the  
237 corresponding effects (Appendix S6). With these variance estimates, we identified the  
238 proportion of temporal variance in body size and condition ( $b_{\text{year}} + b_{\text{year},i} + b_{\text{year:site}} + b_{\text{year:site } i}$ ) that  
239 was common to all species and sites ( $b_{\text{year}}$ ), common to all sites but species-specific ( $b_{\text{year}} +$   
240  $b_{\text{year},i}$ ), or common to all species but site-specific ( $b_{\text{year}} + b_{\text{year:site}}$ ).

241

242 *Effect of environmental anomalies on wing length and body condition index*

243 We assessed the dependence of wing length and body condition index on local  
244 environmental anomalies during the breeding period for both adults and juveniles. For adults,  
245 we also assessed the dependence on environmental anomalies during the post-breeding moult  
246 period of the preceding year, of species for which a moult period could be identified at the  
247 capture site ( $n = 13$ ; Appendix S1; S7), and also during the breeding period of the year prior  
248 to capture (to account for potential lags between change in environmental conditions and the  
249 response of body size and condition; e.g., Gardner et al. 2014b). The post-breeding moult  
250 occurred at the breeding site for most of the study species (Morrison *et al.* 2015), so we tested  
251 the effect of environmental anomalies at the same location as during breeding periods. Models  
252 included mean temperature, total precipitation, the interaction between mean temperature and  
253 total precipitation, and mean NDVI for the breeding period (see equations in supporting  
254 information; Appendix S6).

255

256 *Attempting to infer climate-driven size-dependent mortality in first-year birds*

257 The risk of mortality before the first breeding attempt (as a yearling) may depend on the  
258 environmental conditions experienced throughout the year and varies among individuals,  
259 depending on their size: larger individuals would die more frequently in hotter years, and/or  
260 smaller individuals would die more often when born during poorly productive years. Ideally,  
261 the link between environmental conditions, size and survival should be investigated using  
262 mark-recapture models. However, the small sampling area (2-4 ha) of our study sites meant  
263 that our mark-recapture data were unsuitable for this analysis (high natal dispersal, transiency,  
264 and female breeding dispersal). Hence, size-dependent mortality was inferred from  
265 differences in average wing length (hereafter  $\Delta WL$ ) between juveniles in breeding season  $t$ ,

266 and yearling birds in breeding season  $t+1$ , after adjusting for feather abrasion and differences  
267 in capture probability between sexes (Appendix S9).  $\Delta$ WL was computed when at least 10  
268 measurements were available per site, year and species. This resulted in 138 data points for  
269 six species, from 46 sites (one data point representing one  $\Delta$ WL for one species, at one site  
270 for two consecutive years) obtained from 2020 individual measurements in total. We then  
271 assessed whether  $\Delta$ WL depended on local environmental anomalies of breeding season  $t$   
272 using LMMs accounting for random variation between sites and years.

273

#### 274 *Model selection process*

275 The dependence of wing length, body condition index and  $\Delta$ WL on environmental anomalies  
276 were inferred using a multi-model selection based on Akaike's Information Criteria (AIC;  
277 Burnham and Anderson 2002; adjusted for small sample size for  $\Delta$ WL, i.e. AICc). Models  
278 containing only effects with the highest statistical support have the lowest AIC values. The  
279 support for a model  $m$  relative to all other models considered was quantified by its AIC  
280 weight ( $w_m$ ). The relative importance of an explanatory variable  $i$  ( $\sum w_{m,i}$ ) was quantified as the  
281 sum of  $w_m$  of models containing this variable. To account for model selection uncertainty,  
282 model-averaged estimates of variable coefficients were computed using the 'best model set',  
283 defined as the set of models for which the cumulative sum of  $w_m \leq 95\%$ . We also showed  
284 averaged estimates, once uninformative models (Arnold 2010) had been removed. Model  
285 averaging was performed only if the best model set did not include the linear effect of a given  
286 variable together with its quadratic effect, or an interaction (Banner and Higgs 2017). Model  
287 selection and averaging were implemented using MuMIn R package version 1.9.13 (Barton  
288 2013). The MuMIn function builds all possible combinations of the aforementioned effects  
289 (with each combination corresponding to a single model). Full models corresponded to null  
290 models (i.e. with adjustment variables), to which were added the additive fixed effects of

291 environmental variables, an interaction between mean temperature and total precipitation  
292 anomalies (to allow for synergistic or antagonistic effects), and interactions between each  
293 environmental variable and species identity to allow species-specific responses. To  
294 accommodate for potential non-linear effects of environmental variables, a quadratic effect  
295 was also allowed for all environmental variables. Full model equations are described in  
296 Appendix S6. When a model included a quadratic term or an interaction term, the linear or  
297 additive effect, respectively, was systematically maintained in the model. For significant  
298 relationships, we verified the robustness of the linearity and quadratic assumptions using  
299 smoothed estimates obtained with a spline function of a GAMM version of the corresponding  
300 LMM.

301 Finally, we quantified the proportion of temporal variation in body size that was  
302 explained by each influential environmental variable (i.e. similar to a  $R^2$ ; Grosbois et al.  
303 2009). This proportion was computed as the ratio of interannual variances estimated  
304 respectively with the model including the environmental variable and the null model. All  
305 analyses were performed using R version 3.3.0 (R core team 2016).

306

## 307 **RESULTS**

### 308 **Temporal variations in environmental conditions and body constitution**

309 Between 2000 and 2014, during the breeding periods, climate variables showed significant  
310 temporal variations (degrees of freedom > 8 for all variables, all p values for smooth terms <  
311 0.001) but no temporal trends. NDVI showed a positive temporal trend over the study period  
312 (Fig. 1).

313 Interannual variations in wing length and body condition index were extremely heterogeneous  
314 across sites and species (Year:Site:Species interaction, Table 1). Juvenile wing length and

315 body condition index varied between years (17% and 51% of the total variance estimated by  
316 random effects, respectively). Most interannual variation occurred at the site level and was  
317 species-specific (88% and 96%; Table 1). These patterns were similar for juveniles and adults.

318

### 319 **Influence of local environmental anomalies on wing length and body condition index**

320 We found strong statistical support for a quadratic effect of NDVI on juvenile wing length.  
321 We did not find any effect of the tested environmental variable on adult wing length, nor on  
322 adult and juvenile body condition (Table 2; Appendices S7-S8).

#### 323 *Temperature*

324 The effect of temperature anomalies on juvenile wing length received weak statistical support,  
325 an absence of effect being the most likely ( $\Sigma w_m = 0.34$ ). In case of an effect, it would be linear  
326 and positive (GAMM: estimated degrees of freedom = 1,  $p < 0.0001$ ; Fig. 2). Temperature  
327 anomaly explained 10% of the interannual variance in wing length common to all species (i.e.  
328  $b_{\text{year}} + b_{\text{year:site}}$ ; Fig. 3). Coefficients were robust to model averaging pitfalls, as temperature  
329 was only included as an additive, linear effect. After rescaling, wing length would increase by  
330  $0.09 \text{ mm} \pm 0.03 \text{ SE}$  per degree Celsius ( $+0.31 \text{ mm} \pm 0.11 \text{ SE}$  in years with the highest  
331 anomalies compared to years with average conditions).

332 There was no support for an effect of temperature in any of the other analyses (i.e., juvenile  
333 body condition index, adult wing length and adult body condition index; Table 3).

334

#### 335 *Net primary production*

336 Juveniles were larger in years with positive NDVI anomalies ( $\Sigma w_i = 1$ , Table 3) with a  
337 quadratic relationship (see GAMM on Fig. 2;  $df = 2.34$ ,  $p$  (smooth term) = 0.02). This effect

338 of NDVI would be largely common to all species as models allowing for species-specific  
339 responses were not statistically supported ( $\Delta AIC > 100$ ). The squared-effect of NDVI  
340 explained 13% of the temporal variance in wing length common to all species (i.e.  $b_{\text{year}} +$   
341  $b_{\text{year:site}}$ ; Fig. 3). Coefficients were robust to model averaging pitfalls, as NDVI was  
342 systematically included with its squared-effect in the best model set. These were similar for  
343 the average model and the best model (Table 3). Wing length increased by  $1.1 \text{ mm} \pm 0.21 \text{ SE}$   
344 in years with the highest anomalies, compared to years with average conditions. Alternative  
345 variables related to primary production (precipitation, with interactive effects with  
346 temperature) did not receive any statistical support (Table 2). An interaction between  
347 temperature and precipitation was included in the best model set, but this effect was  
348 uninformative, as its statistical support was very weak ( $\Sigma w_m = 0.09$ ) and it only captured 2% of  
349 the interannual variance common to all species. When removing this interaction from the best  
350 model set, our results remained qualitatively unchanged: the coefficient for temperature  
351 decreased from 0.019 to 0.014 (NDVI coefficients remained unchanged).

352

### 353 **Climate-driven size-dependent mortality**

354 Differences in average wing length between juveniles in year  $t$  and yearling birds in year  $t+1$   
355 (i.e.  $\Delta WL$ ) were not related to any of the environmental variables (Appendix S9). Hence,  
356 there is no indication of climate-driven size-dependent mortality.

357

## 358 **DISCUSSION**

359 In our dataset, body size fluctuations of songbirds were best explained by interannual  
360 variations in food availability (NDVI), although much of the temporal variance remained  
361 unexplained. We showed that the effect of temperature anomaly is fairly positive as expected

362 under the heat maintenance hypothesis, but the effect is weak and relatively less important  
363 than net primary production in determining juvenile size. As we found no evidence for  
364 dependence of average adult body size, and yearling size-dependent mortality on NDVI or  
365 climatic anomalies, the relationship is probably driven by effects on body growth.

366

367 In contrast with former studies, we did not find a negative effect of temperature, a result  
368 most often found in species inhabiting arid regions (e.g., Yom-Tov 2001). In tropical and arid  
369 systems, species are more exposed to hyperthermia as they live closer to their upper thermal  
370 limit (Tewksbury et al. 2008). In a temperate climate such as that of France, the thermal  
371 envelope of species is much wider than at lower latitudes and climatic fluctuations rarely  
372 expose temperate animals to lethal or sub-lethal temperatures (Addo-Bediako et al. 2000,  
373 Deutsch et al. 2008, Khaliq et al. 2014). If temperature was to have an effect on body size  
374 (Table 3), it would be positive, which is contradictory to the expectations of Bergmann's rule  
375 over time. A similar effect was found for adults in Australia during the breeding period, and  
376 this effect was attributed to size-dependent mortality (Gardner et al. 2014b). This may not be  
377 the case in France, as the 2003 heatwave increased avian productivity (Julliard et al. 2004).  
378 Besides, avian mortality was not particularly high after the 2003 heatwave (Ghislain 2017).  
379 Moreover, preliminary analyses did not provide support for a potential effect of the number of  
380 days with maximum temperature  $> 35^{\circ}\text{C}$  (Gardner et al. 2014b) on juvenile body size  
381 (Appendix S10). These extremely hot conditions still remain rare in the French temperate  
382 climate. As temperatures rarely exceed near-lethal points in temperate systems, even at the hot  
383 edge of species distributions (Khaliq et al. 2014), a positive effect of temperature would  
384 probably be mediated through body growth. This is consistent with the conclusions of a recent  
385 review (Teplitsky and Millien 2014) which suggested that body size decline may be caused  
386 mainly by changes in body growth as a result of non-adaptive plasticity. Under temperate

387 climates, increasing temperature reduces the cost of juvenile heat maintenance (Kendeigh  
388 1969). This results in higher metabolic allocation for growth, which could explain the positive  
389 effect of high temperatures on juvenile size (Gillooly et al. 2001). The direction of the  
390 relationship is thus consistent with previous studies performed in cool or cold regions (e.g.,  
391 Collins et al. 2016, Pérez et al. 2016), or during a cool period of the year (e.g., Gardner et al.  
392 2014b), and supports the fact that warming can benefit juvenile growth through changes in  
393 metabolic allocation in temperate climates. In France, species are probably more cold-  
394 constrained than hot-constrained, and hot anomalies are probably less detrimental for  
395 reproduction and juvenile growth (Julliard et al. 2004) than at lower latitudes. It is also  
396 possible that species sensitivity to climatic anomaly depends on the location of a given  
397 population with reference to the cold edge of its geographic distribution (Jiguet et al. 2010).  
398 Warmer years would benefit species that are located near the cold edge, while it could harm  
399 those located at the hot edge. However, France is closer to the hot edge for most of our study  
400 species (i.e., typically Palearctic), and thus it is far from the cold edge of their distribution.  
401 Hence, a positive effect of temperature is expected in temperate climates, even in the core of  
402 species distribution ranges.

403         In cool regions, warming induces an increase in primary production, provided that  
404 precipitation is not limiting, which contributes to improved food supply and results in larger  
405 individuals (Searcy et al. 2004), so in contrast with arid systems where temperature and food  
406 availability are decoupled (Gardner et al. 2014b), it is hard to conclude whether the likely  
407 positive effect of temperature is related to reductions in the cost of body heat maintenance, or  
408 to increases in food availability in the system.

409         Higher NDVI values were associated with longer wings, presumably due to a positive  
410 relationship between vegetation production and invertebrate abundance (Wimp et al. 2010).  
411 During juvenile growth, most songbirds are insectivorous, so higher invertebrate abundance

412 improves juvenile protein intake, and may result in larger individuals (Lindström 1999). We  
413 did not detect any effect of NDVI on body condition, presumably because body mass is  
414 highly labile, varying over time-scales of hours, days and weeks (Canale et al. 2016), and  
415 therefore within-breeding period fluctuations may not be correctly documented when  
416 analysing a single value per individual. In accordance with Keller and Van Noordwijk (1994),  
417 we found no effect of NDVI in years with low or average primary production. In years with  
418 poor resource availability, species may adjust the number of offspring to maintain a fair body  
419 size (i.e., size-number trade-off; Lack 1968). The absence of effect of negative NDVI  
420 anomalies might be explained by the adjustment of brood size according to climatic  
421 conditions and expected food abundance (Parker and Begon 1986). In years with lower food  
422 availability, birds may produce less juveniles, thus enabling higher parental investment in  
423 individual offspring (Smith et al. 1989), resulting in unchanged body size in years with scarce  
424 resources.

425         As expected, given the complexity of biological and ecological processes, the predictive  
426 power of our variables was relatively low. Primary production and climatic anomalies do  
427 influence juvenile size. However, the true proportion of body size variation that can be  
428 formally attributed to fluctuations in primary production and climate remains unknown, and is  
429 probably under-estimated given the simple, averaged variables used in the present study.  
430 Body size is largely heritable, and most of the interannual variation should be captured by  
431 heritability (e.g., 75% in great tits; Garnett 1981). For this reason, only a small part of body  
432 size variance can be captured by environment. Yet, our variables were still able to capture  
433 some interannual variation in juvenile size, suggesting that their effect is not negligible. The  
434 influence of temperature fluctuations on wing length was weak, with a maximum increase  
435 estimated at 0.31 mm for the highest temperature anomaly (+3.6°C) compared to years with  
436 average conditions. High primary production had a stronger effect on wing length, resulting in

437 an increase estimated at +1.1 mm in the year with the highest NDVI value. As climate  
438 warming is expected to increase the frequency of positive anomalies in primary production  
439 (Melillo et al. 1993), we predict that climate change will induce a body size increase in  
440 temperate songbirds. Temperature and precipitation showed important fluctuations over the  
441 study period. The extent of interannual fluctuations in our variables was similar to other  
442 studies (e.g., Gardner et al. 2014b, Teplitsky and Millien 2014), treating each year as  
443 independent category, with cold and hot years, and dry and wet years. This suggests that the  
444 relatively low explanatory power of the tested variables does not result from a lack of  
445 temporal variance. Our statistical models were based on extensive long-term data obtained  
446 from a large-scale monitoring program and took into account most of the possible sources of  
447 bias and noise: such as observer effect, spatial and temporal variability. With the high  
448 statistical support attributed to NDVI anomalies, we can safely conclude that net primary  
449 production is a better predictor of juvenile growth than temperature in our system.

450       Interannual variation was largely heterogeneous between sites, suggesting that variation  
451 in body size was largely related to local, rather than global factors. This is consistent with  
452 other studies performed on multiple species at different sites (Meiri et al. 2009, Collins et al.  
453 2016). This emphasises the necessity of considering alternative environmental variables or  
454 variables at finer spatial resolution to understand the very local determinants of size. The  
455 sensitivity to climate change is known to vary within species range (Jiguet et al. 2010, Pearce-  
456 Higgins et al. 2015). In our study area, mean temperature of the breeding season ranged from  
457 6°C to 20°C, depending on the site. The effect of temperature anomaly may then differ  
458 between the hottest and the coldest sites. Yet, our results rely on the assumption of a uniform  
459 response to climatic variation across species ranges, thus ignoring possible spatial  
460 heterogeneity in the response to climatic anomalies. Variation in body size may also be driven  
461 by land use changes (e.g., Schmidt and Jensen 2005, Desrochers 2010). Human activities such

462 as agriculture, logging, garbage and gardening may affect food availability, and in turn could  
463 impact body size. However, volunteer bird ringers generally settle CES in places that are  
464 protected from deleterious anthropogenic activities. Food availability at the study sites should  
465 be closely related to primary production, with a limited confounding effect of human  
466 activities.

467 Another factor that may contribute to limitations of the explanatory power of NDVI is  
468 the temporal resolution (e.g., Kruuk et al. 2015). Bones and feathers are grown over a short  
469 period (*ca.* 1 month for juvenile growth, and *ca.* 2 weeks for primary moult), and the  
470 environmental conditions during this growing period are expected to be the most influential.  
471 This period varies between sites (latitude, altitude and habitat), species and individuals.  
472 Therefore, despite significant correlations with invertebrate abundance (Wimp et al. 2010),  
473 proxies such as NDVI, which are averaged for the whole breeding season, inevitably  
474 document only a limited fraction of the dependence of primary production on growth. The  
475 limited explanatory power of NDVI could also be explained by a temporal mismatch between  
476 species phenology and prey dynamics which are known to affect body size (Husby et al.  
477 2011). Nonetheless, we can hardly improve the temporal relevance of NDVI proxies, as this  
478 would require knowledge about each species, the sites and the yearly basis of the actual  
479 periods of growth.

480 As we did not perform a mark-recapture analysis, strictly speaking, we could not  
481 formally disentangle the contributions of tissue growth *versus* size-dependant mortality. Yet,  
482 only juvenile wing length depended on NDVI, and it did not explain differences in wing  
483 length between juvenile and 1<sup>st</sup>-year birds in the next year. We can thus reasonably presume  
484 that the proximate mechanism is mainly a direct influence of food availability on nestling and  
485 post-fledgling growth. This direct effect on growth may also have been reinforced by size-  
486 dependent mortality in the nest, but we could not document mortality before the first capture.

487 After the juvenile stage, we did not obtain evidence of climate-driven size-dependant  
488 mortality or impaired feather growth during moulting. To our knowledge, only one study  
489 revealed a contribution of both growth and size-dependent mortality on population body size  
490 variation (Gardner et al. 2014b). A key challenge for future studies documenting the influence  
491 of environmental variability on body size, is to convincingly disentangle the respective  
492 contributions of growth and mortality. We did not consider winter conditions here because  
493 individual bird locations were unknown during the winter. However further work to  
494 investigate winter conditions and mortality is needed, since mortality in temperate climates is  
495 the most prevalent during the winter (van Balen 1980), and winter conditions may drive size-  
496 dependent mortality (Van Buskirk et al. 2010, Brown et al. 2013, Björklund et al. 2015,  
497 Danner and Greenberg 2015).

498

## 499 **CONCLUSIONS**

500 This study shows that, in a temperate system, temporal variation in body size is better  
501 predicted by net primary production than climatic variables. Our results support the role of  
502 food availability during the breeding period on juvenile body size. In turn, body size variation  
503 was largely asynchronous between species and sites, and the predictive power of climate and  
504 net primary production was limited, emphasising the need to account for finer-grained local  
505 factors.

506

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519

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661 **Table 1** Interannual variance partitioning of wing length and body condition index, for  
662 juveniles and adults of 41 songbird species. Variances were estimated from random effects of  
663 Linear Mixed Models. Models were adjusted for feather growth/abrasion, within-day body  
664 mass variation and adult sexual dimorphism. Percentages (in parenthesis) correspond to the  
665 proportion of the total temporal variance (i.e. the sum of all temporal variances).

Random effect	Wing length		Body condition index	
	Juveniles	Adults	Juveniles	Adults
Year : Site : Species	1.045 (88%)	0.449 (89%)	4.279 (96%)	1.123 (93%)
Year : Site	0.079 (7%)	0.048 (9%)	0.068 (2%)	0.066 (5%)
Year : Species	0.050 (4%)	0.003 (1%)	0.088 (2%)	0.011 (1%)
Year	0.018 (1%)	0.005 (1%)	0.000 (0%)	0.009 (1%)
Observer	0.165	0.113	0.098	0.078
Site	0.170	0.208	0.177	0.128
Residual	5.595	4.603	3.846	8.920

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**Table 2** Best model sets for body constitution responses to climate and net primary production (NDVI) local anomalies. The models presented are included within a 95% interval of AIC weight ( $w_m$ ), and ranked by increasing values of  $\Delta AIC$  relative to the best model (i.e., with the lowest AIC value) and decreasing  $w_m$ . We assume body condition to be body mass adjusted to wing length. All models also included adjustment variables (see Methods).

Response variable	Best models	Rank	$\Delta AIC$	$w_m$	
<i>Juveniles</i> Wing length	<i>Current breeding period</i> NDVI + NDVI <sup>2</sup>	1	0.00	0.616	
	NDVI + NDVI <sup>2</sup> + Temperature	2	1.96	0.231	
	NDVI + NDVI <sup>2</sup> + Temperature * Precipitation	5	4.08	0.080	
Body condition	Adjustment variables only	1	0.00	0.724	
	Precipitation	2	0.33	0.229	
<i>Adults</i> Wing length	<i>Current breeding period (before moulting)</i> Adjustment variables only	1	0.00	0.581	
	Precipitation	2	0.95	0.361	
	<i>Previous breeding period</i> Adjustment variables only	1	0.00	0.759	
	Precipitation	2	3.48	0.133	
	<i>Previous moulting period</i> Adjustment variables only	1	0.00	0.817	
	NDVI	2	4.17	0.101	
	Body condition	<i>Current breeding period (before moulting)</i> Adjustment variables only	1	0.00	0.928
		NDVI	2	6.63	0.034
		<i>Previous breeding period</i> Adjustment variables only	1	0.00	0.901
		NDVI	2	5.72	0.052
		<i>Previous moult period</i> Adjustment variables only	1-	0.00	0.598
		NDVI	2	2.37	0.183

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677 **Table 3** Variables explaining juvenile wing length and body condition variations for 41  
678 songbird species in France between 2000 and 2014. Coefficients ( $\beta$ ), standard errors (SE) and  
679 z values were averaged from a ‘best model set’ (i.e., that included 95% of AIC weight) and  
680 weighted by Akaike weights. Within best model sets, some models could be uninformative  
681 (see Methods). Coefficients are shown when estimated from the ‘full’ best model set, and  
682 after removing potentially uninformative models (in parentheses, shown only if the latter  
683 differs). Cumulative AIC weights ( $\Sigma w_i$ ) indicate the relative importance of each variable. All  
684 environmental variables were centred and scaled. Detailed estimates for the effect of  
685 adjustment variables and species-specific effects are provided in Appendix S8. Statistically  
686 supported effects are in bold. <sup>1</sup> Variables included in a potentially uninformative model.

Response variables	Predictor variables (fixed effects)	$\beta$	SE	$\Sigma w_i$
<i>Wing length</i>	Temperature	0.019 (0.014)	0.025 (0.029)	0.34 (0.27)
	Precipitation <sup>1</sup>	-0.016	0.024	0.09
	Precipitation : Temperature <sup>1</sup>	0.029	0.019	0.09
	<b>NDVI</b>	<b>0.048</b>	<b>0.017 (0.018)</b>	<b>1</b>
	<b>NDVI<sup>2</sup></b>	<b>0.062</b>	<b>0.014 (0.010)</b>	<b>1</b>
	Species	See Appendix S8		1
	Species*log(Date)	See Appendix S8		1
<i>Body condition index</i>	Precipitation <sup>1</sup>	0.010	0.019	0.24
	Species	See Appendix S8		1
	Species*log(Hour)	See Appendix S8		1

687

688

689 **Figure legends**

690 **Fig. 1** Partial residual climate anomalies during the breeding season in France for the 2000-  
691 2014 period: (a) temperature, (b) precipitation and (c) NDVI. Solid lines represent the  
692 regression spline fit obtained from GAMMs, with year as smooth term and site as random  
693 effect. Dashed lines represent 95% confidence intervals. All variables varied significantly and  
694 non-linearly (Temperature: degrees of freedom (df) = 8.94.  $p < 0.001$ ; Temperature  
695 variability: df = 8.97.  $p < 0.001$ ; Precipitation: df = 8.85.  $p < 0.001$ ; NDVI: df = 8.79.  $p <$   
696 0.001).

697

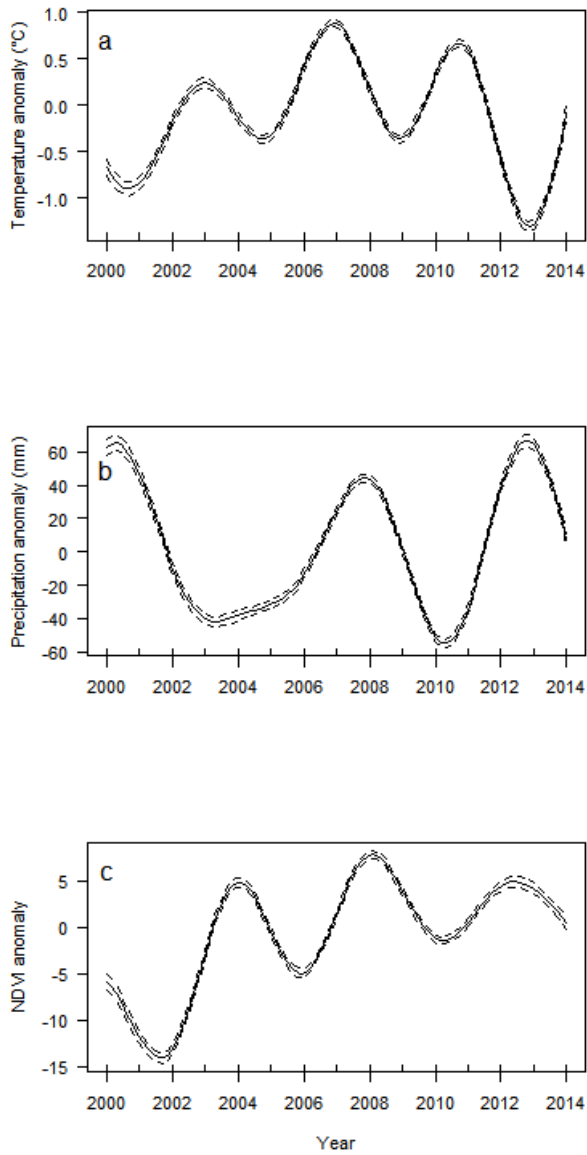
698 **Fig. 2** Relationship between partial residual wing length and local anomalies of (a) NDVI and  
699 (b) temperature for 41 songbird species. These relationships were common to all species.  
700 Solid lines represent regression spline fits from GAMMs. Dashed lines represent 95%  
701 confidence intervals. High values of NDVI anomaly are supposed to represent years with high  
702 food availability.

703

704 **Fig. 3** Variance partitioning Juvenile wing length for 41 songbird species in France between  
705 2000 and 2014, and environmental contribution (NDVI and Temperature anomalies). NDVI  
706 and temperature anomaly respectively captured 13% and 10%, of the interannual variation  
707 that is common to all species.

708

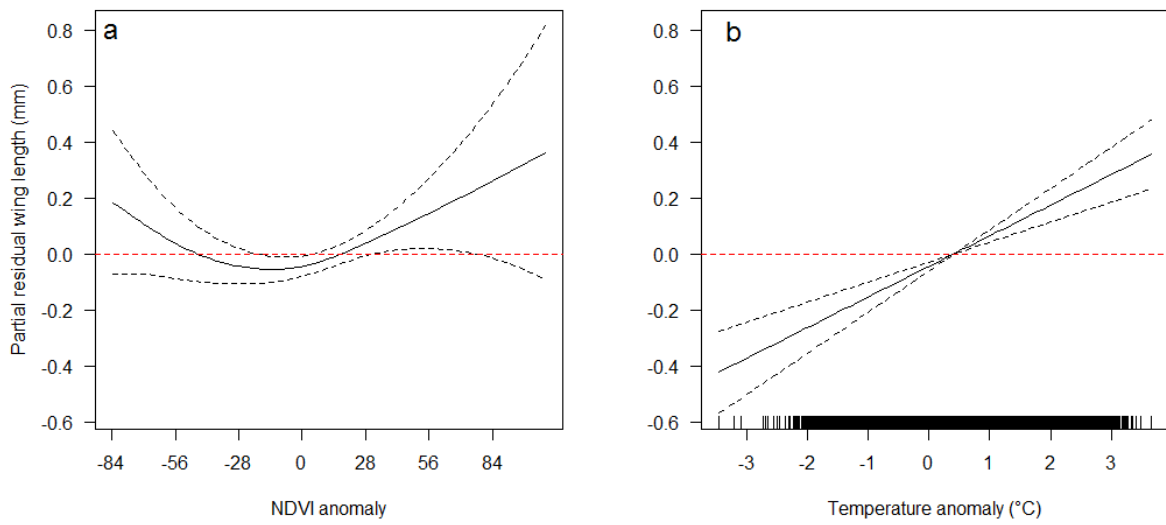
709 Figure 1.



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711

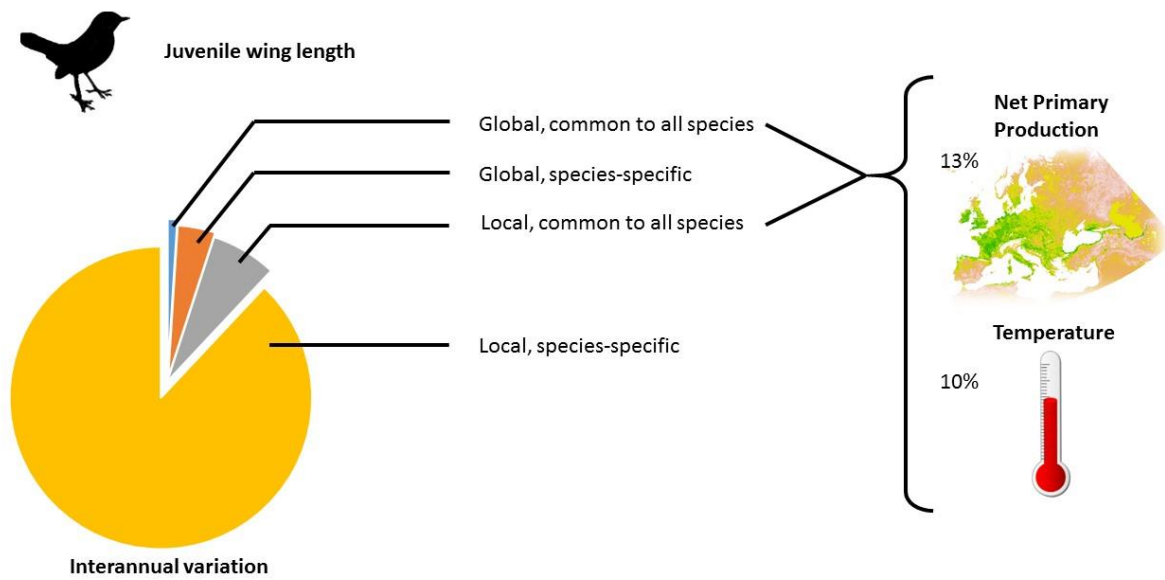
712 Figure 2.



713

714

715 Figure 3



716