

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

Nicolas Dubos, Isabelle Le Viol, Alexandre Robert, Céline Teplitsky, Manon Ghislain, Olivier Dehorter, Romain Julliard, Pierre Yves Henry

► **To cite this version:**

Nicolas Dubos, Isabelle Le Viol, Alexandre Robert, Céline Teplitsky, Manon Ghislain, et al.. Disentangling the effects of spring anomalies in climate and net primary production on body size of temperate songbirds. *Ecography*, Wiley, 2018, 41 (8), pp.1319-1330. 10.1111/ecog.03413 . hal-02308480

HAL Id: hal-02308480

<https://hal.sorbonne-universite.fr/hal-02308480>

Submitted on 8 Oct 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Running title: Climate and Body size of temperate songbirds

5

6 Nicolas Dubos^{1,2}, Isabelle Le Viol¹, Alexandre Robert¹, Céline Teplitsky^{1,3}, Manon
7 Ghislain^{1,2}, Olivier Dehorter¹, Romain Julliard¹ and Pierre Yves Henry^{1,2}

8

9 ¹Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Centre de
10 Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Sorbonne Universités,
11 MNHN, CNRS, UPMC, CP135, 43 rue Buffon, 75005 Paris, France, ²Mécanismes adaptatifs
12 et évolution (MECADEV UMR 7179), Sorbonne Universités, CNRS, MNHN, 1 avenue du
13 Petit Château, 91800 Brunoy, France, ³Centre d'Ecologie Fonctionnelle et Evolutive (CEFE
14 UMR 5175), 1919 route de Mende, 34000 Montpellier, France.

15

16 Correspondence: Nicolas Dubos (dubos.research@gmail.com; henry@mnhn.fr)

17

18

19 Type of Paper: Original Research Article

20 Abstract word count: 263

21 Word count: 5735

22 Number of references: 68

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 ± 1.3 SD times per breeding season per site, from May/early June (3
146 June ± 12.7 SD), until late June/early July (26 June ± 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 (± 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 (± 2.3 SD)
164 trained measurers per site. Within-observer repeatability of wing length and of body mass
165 measurements was 0.92 (± 0.11 SD) and 0.91 (± 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 (1st
180 April-1st 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.

194 2014b). We extracted daily mean temperature and daily total precipitation from the E-OBS
195 meteorological dataset (Haylock et al. 2008), with a 0.25° pixel resolution using
196 climateExtract R package (<https://github.com/RetoSchmucki>). We used monthly averaged
197 raster images of remotely sensed Normalized Different Vegetation Index (NDVI; Copernicus
198 Service information 2016) as a proxy for net primary production (Pettoirelli et al. 2005). The
199 spectral reflectance covered by these images were the red and near infrared wavebands (0.61
200 to 0.68 µm and 0.78 to 0.89 µm, respectively), generally used for vegetal characterisation
201 (Kerr and Ostrovsky 2003). We computed mean NDVI inside a buffer zone with a 5 km
202 radius around each site from the raster images. The 5 km radius was chosen because it
203 coincides with the level of precision of CES site geolocations. All variables were included in
204 the analyses since their variations were largely uncorrelated ($r < 0.35$; Table S2). They were
205 centred and scaled so that relative effect sizes could be compared between variables,
206 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_{year}), between-site (b_{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_{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 ΔWL) 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). Δ 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 Δ WL for one species, at one site
270 for two consecutive years) obtained from 2020 individual measurements in total. We then
271 assessed whether Δ 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 Δ 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 Δ 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. ΔWL) 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 1st-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

507 **ACKNOWLEDGEMENTS**

508 We thank the 382 bird ringers who voluntarily collected biometric data (Appendix S11) and
509 made the present study possible, along with the continuous support of MNHN and CNRS. We
510 are also grateful to Morgane Barbet-Massin, Léo Bacon, Eric Edeline, Vincent Devictor,

511 Pierre Fiquet, Aliénor Jéliaszkov, Frédéric Jiguet, Boris Leroy, Karine Princé and Victor Saito
512 for providing useful material and wise advice. N.D. was funded by LabEx BCDiv.; CT and
513 AR were funded by ANR Bioadapt ANR-12-ADAP-0006. We acknowledge Copernicus for
514 providing NDVI data, the E-OBS dataset from the EU-FP6 project ENSEMBLES
515 (<http://ensembles-eu.metoffice.com>) and data providers in the ECAandD project
516 (<http://www.ecad.eu>). We finally thank Liam Bailey, and six anonymous reviewers and Editors
517 for their useful comments on previous versions of the manuscript. The final dataset used in
518 this study is available online as supporting information.

519

520 **REFERENCES**

- 521 Aber, J.D. and Federer, C.A. 1992. A generalized, lumped-parameter model of
522 photosynthesis, evapotranspiration and net primary production in temperate and boreal
523 forest ecosystems. - *Oecologia*. 92: 463–474
- 524 Addo-Bediako, A. et al. 2000. Thermal tolerance, climatic variability and latitude. - *Proc.*
525 *Biol. Sci.* 267: 739–745.
- 526 Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's
527 Information Criterion. - *J. Wildl. Manage.* 74, 1175–1178
- 528 Balen JH van 1980. Population fluctuations of the great tit and feeding conditions in winter. -
529 *Ardea*. 68: 143–164.
- 530 Banner, K. M. and Higgs, M. D. 2017. Considerations for assessing model averaging of
531 regression coefficients. - *Ecol. Appl.* 27: 78–93.
- 532 Barton K 2013. MuMIn: Multi-model inference. R package version 1.9.13. [http://CRAN.R-](http://CRAN.R-project.org/package=MuMIn)
533 [project.org/package=MuMIn](http://CRAN.R-project.org/package=MuMIn).
- 534 Bates, D. et al. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package
535 version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- 536 Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.
537 *Gottinger studien*, 3: 595–708.
- 538 Björklund, M. et al. 2014. Increase in body size is correlated to warmer winters in a passerine
539 bird as inferred from time series data. - *Ecol. Evol.*: 59–72.
- 540 Brown, C. R. et al. 2013. Fluctuating viability selection on morphology of cliff swallows is
541 driven by climate. - *J. Evol. Biol.* 26: 1129–1142.
- 542 Both, C. et al. 2006. Climate change and population declines in a long-distance migratory
543 bird. - *Nature*. 441: 81–3.

544 Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: a
545 practical information-theoretic approach. Springer Science and Business Media.

546 Canale, C. I. et al. 2016. Differential plasticity of size and mass to environmental change in a
547 hibernating mammal. - *Glob. Chang. Biol.* 22: 3286–3303.

548 Collins, M. D. et al. 2017. Heterogeneous changes in avian body size across and within
549 species. - *J. Ornithol.* 158: 39–52.

550 Copernicus Service information 2016. Available at <http://land.copernicus.eu>.

551 Danner, R. M. and Greenberg, R. 2015. A critical season approach to Allen’s rule: bill size
552 declines with winter temperature in a cold temperate environment (L Manne, Ed.). - *J.*
553 *Biogeogr.* 42: 114–120.

554 Dawson, R. D. et al. 2005. The importance of microclimate variation in determining size,
555 growth and survival of avian offspring: experimental evidence from a cavity nesting
556 passerine. - *Oecologia* 144: 499–507.

557 Dehorter, O. and CRBPO 2015. Bird ringing and movement database for France. Centre de
558 Recherches sur la Biologie des Populations d’Oiseaux, Muséum National d’Histoire
559 Naturelle, Paris, France. <http://crbpo.mnhn.fr/>. Accessed on 24/12/2015.

560 Desrochers, A. 2010. Morphological response of songbirds to 100 years of landscape change
561 in North America. *Ecology.* - 91: 1577–1582.

562 Deutsch, C.A. et al. 2008. Impacts of climate warming on terrestrial ectotherms across
563 latitude. *Proc. Natl. Acad. Sci. U. S. A.* - 105: 6668–6672

564 Eglinton, S. M. et al. 2015. Latitudinal gradients in the productivity of European migrant
565 warblers have not shifted northwards during a period of climate change. - Glob. Ecol.
566 Biogeogr. 24: 427–436.

567 Gardner, J. L. et al. 2014a. Temporal patterns of avian body size reflect linear size responses
568 to broadscale environmental change over the last 50 years. - J. Avian Biol. 45: 001–007.

569 Gardner, J. L. et al. 2014b. Dynamic size responses to climate change: prevailing effects of
570 rising temperature drive long-term body size increases in a semi-arid passerine. - Glob.
571 Chang. Biol. 20: 2062–2075.

572 Gardner, J. L. et al. 2016. Individual and demographic consequences of reduced body
573 condition following repeated exposure to high temperatures. - Ecology 97: 786–795.

574 Gardner, J. L. et al. 2009. Shifting latitudinal clines in avian body size correlate with global
575 warming in Australian passerines. - Proc. Biol. Sci. 276: 3845–52.

576 Gardner, J. L. et al. 2011. Declining body size: a third universal response to warming? -
577 Trends Ecol. Evol. 26: 285–91.

578 Garnett, M. C. 1981. Body size, its heritability and influence on juvenile survival among great
579 tits, *Parus major*. - Ibis. 123: 31-41.

580 Ghislain, M. 2017. Réponses démographiques des oiseaux aux changements globaux dans
581 l'espace : des tendances nationales à la gestion locale. PhD thesis, Muséum National
582 d'Histoire Naturelle, Paris, France, 162 pages.

583 Gillooly, J.F. et al. 2001. Effects of size and temperature on metabolic rate. - Science. 293:
584 2248–2251.

585 Gosler, A. G. et al. 1998. The field determination of body size and condition in passerines: a
586 report to the British Ringing Committee. - *Bird Study* 45: 92–103.

587 Grosbois, V. et al. 2009. Modeling survival at multi-population scales using mark-recapture
588 data. - *Ecology* 90: 2922–32.

589 Haylock, M. R. et al. 2008. A European daily high-resolution gridded data set of surface
590 temperature and precipitation for 1950–2006. - *J. Geophys. Res.* 113: D20119.

591 Holmgren, M. et al. 2006. Extreme climatic events shape arid and semiarid ecosystems. -
592 *Front. Ecol. Environ.* 4: 87-95.

593 Husby, A. et al. 2011. Testing mechanisms of Bergmann's rule: phenotypic decline but no
594 genetic change in body size in three passerine bird populations. - *Am. Nat.* 178: 202–
595 213.

596 Jenni, L. and Winkler, R. 2011. *Moult and ageing of European passerines*. A. and C. Black.

597 Jiguet, F. et al. 2010. Bird population trends are linearly affected by climate change along
598 species thermal ranges. - *Proc. Biol. Sci.* 277: 3601–8.

599 Julliard, R. et al. 2004. Evidence for the impact of global warming on the long-term
600 population dynamics of common birds. - *Proc. Biol. Sci.* 271: S490–2.

601 Khaliq, I. et al. 2014. Global variation in thermal tolerances and vulnerability of endotherms
602 to climate change. - *Proc. Biol. Sci.* 281: 20141097-.

603 Keller, L.F. and Van Noordwijk, A.J. 1994. Effects of local environmental conditions on
604 nestling growth in the great tit *Parus major* L. - *Ardea*. 82: 349–362.

- 605 Kendeigh, C. 1969. Tolerance of Cold and Bergmann's Rule. - *Auk* 86: 13–25.
- 606 Kerr, J. T. and Ostrovsky, M. 2003. From space to species: Ecological applications for remote
607 sensing. - *Trends Ecol. Evol.* 18: 299–305.
- 608 Kruuk, L. E. B. et al. 2015. Contrasting effects of climate on juvenile body size in a Southern
609 Hemisphere passerine bird. - *Glob. Chang. Biol.*: 21: 2929-2941.
- 610 Labocha, M. K. and Hayes, J. P. 2012. Morphometric indices of body condition in birds: A
611 review. - *J. Ornithol.* 153: 1–22.
- 612 Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- 613 Lindström, J. 1999. Early development and fitness in birds and mammals. - *Trends Ecol.*
614 *Evol.* 14: 343–348.
- 615 Meiri, S. et al. 2009. Global change and carnivore body size: data are stasis. - *Glob. Ecol.*
616 *Biogeogr.* 18: 240–247.
- 617 Melillo, J.M. et al. 1993. Global climate change and terrestrial net primary production. -
618 *Nature.* 363: 234–240
- 619 Morrison, C. A. et al. 2015. Flexibility in the timing of post-breeding moult in passerines in
620 the UK. - *Ibis.* 157: 340–350.
- 621 Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R² from
622 generalized linear mixed-effects models. - *Methods Ecol. Evol.* 4: 133–142.
- 623 Ozgul, A. et al. 2010. Coupled dynamics of body mass and population growth in response to
624 environmental change. - *Nature* 466: 482–485.

- 625 Parker, G. A. and Begon, M. 1986. Optimal egg size and clutch size – effects of environment
626 and maternal phenotype. – Am. Nat. 128: 573–592.
- 627 Pearce-higgins, J. W. et al. 2015. Geographical variation in species’ population responses to
628 changes in temperature and precipitation. - Proc. Biol. Sci. 282: 20151561.
- 629 Pérez, J.H. et al. 2016. Nestling growth rates in relation to food abundance and weather in the
630 Arctic. - Auk. 133: 261–272.
- 631 Pettorelli, N. et al. 2005. Using the satellite-derived NDVI to assess ecological responses to
632 environmental change. - Trends Ecol. Evol. 20: 503–510.
- 633 R core team 2016. R: A language and environment for statistical computing. R Foundation for
634 Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- 635 Robinson, R. a. et al. 2009. Constant effort: Studying avian population processes using
636 standardised ringing. - Ringing Migr. 24: 199–204.
- 637 Salewski, V. et al. 2014. Morphological change to birds over 120 years is not explained by
638 thermal adaptation to climate change. - PLoS One 9: e101927.
- 639 Schmidt, N. M. and Jensen, P. M. 2005. Concomitant patterns in avian and mammalian body
640 length changes in Denmark. - Ecol. Soc. 10: (on line).
- 641 Searcy, W. A. et al. 2004. Effects of early nutrition on growth rate and adult size in song
642 sparrows *Melospiza melodia*. - J. Avian Biol. 35: 269–279.
- 643 Smith, H. G. et al. 1989. The trade-off between offspring number and quality in the great tit
644 *Parus major*. - J. Anim. Ecol. 58: 383–401.

645 Svensson, L. 1992. Identification Guide to European Passerines. Stockholm, Märstatryck.

646 Teplitsky, C. and Millien, V. 2014. Climate warming and Bergmann's rule through time: is
647 there any evidence? - *Evol. Appl.* 7: 156–68.

648 Tewksbury, J.J. et al. 2008. Putting the Heat on Tropical Animals The Scale of Prediction. -
649 *Science*. 320: 1296-1297.

650 Van Buskirk, J. et al. 2010. Declining body sizes in North American birds associated with
651 climate change. - *Oikos*. 119: 1047–1055.

652 Wimp, G.M. et al. 2010. Increased primary production shifts the structure and composition of
653 a terrestrial arthropod community. - *Ecology*. 91: 3303–3311.

654 Wood, S. and Scheipl, F. 2014. gamm4: Generalized additive mixed models using mgcv and
655 lme4. R package version 0.2-3. <http://CRAN.R-project.org/package=gamm4>.

656 Yom-Tov, Y. 2001. Global warming and body mass decline in Israeli passerine birds. - *Proc.*
657 *Biol. Sci.* 268: 947–52.

658 Yom-Tov, Y. and Geffen, E. 2011. Recent spatial and temporal changes in body size of
659 terrestrial vertebrates: probable causes and pitfalls. - *Biol. Rev.* 86: 531–41.

660

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

666

667

668

669 **Table 2** Best model sets for body constitution responses to climate and net primary production

670 (NDVI) local anomalies. The models presented are included within a 95% interval of AIC

671 weight (w_m), and ranked by increasing values of Δ AIC relative to the best model (i.e., with the672 lowest AIC value) and decreasing w_m . We assume body condition to be body mass adjusted to

673 wing length. All models also included adjustment variables (see Methods).

674

Response variable	Best models	Rank	Δ AIC	w_m	
<i>Juveniles</i> Wing length	<i>Current breeding period</i>				
	NDVI + NDVI ²	1	0.00	0.616	
	NDVI + NDVI ² + Temperature	2	1.96	0.231	
	NDVI + NDVI ² + 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		

675

676

677 **Table 3** Variables explaining juvenile wing length and body condition variations for 41
678 songbird species in France between 2000 and 2014. Coefficients (β), 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 (Σw_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. ¹ Variables included in a potentially uninformative model.

Response variables	Predictor variables (fixed effects)	β	SE	Σw_i
<i>Wing length</i>	Temperature	0.019 (0.014)	0.025 (0.029)	0.34 (0.27)
	Precipitation ¹	-0.016	0.024	0.09
	Precipitation : Temperature ¹	0.029	0.019	0.09
	NDVI	0.048	0.017 (0.018)	1
	NDVI²	0.062	0.014 (0.010)	1
	Species	See Appendix S8		1
	Species*log(Date)	See Appendix S8		1
<i>Body condition index</i>	Precipitation ¹	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

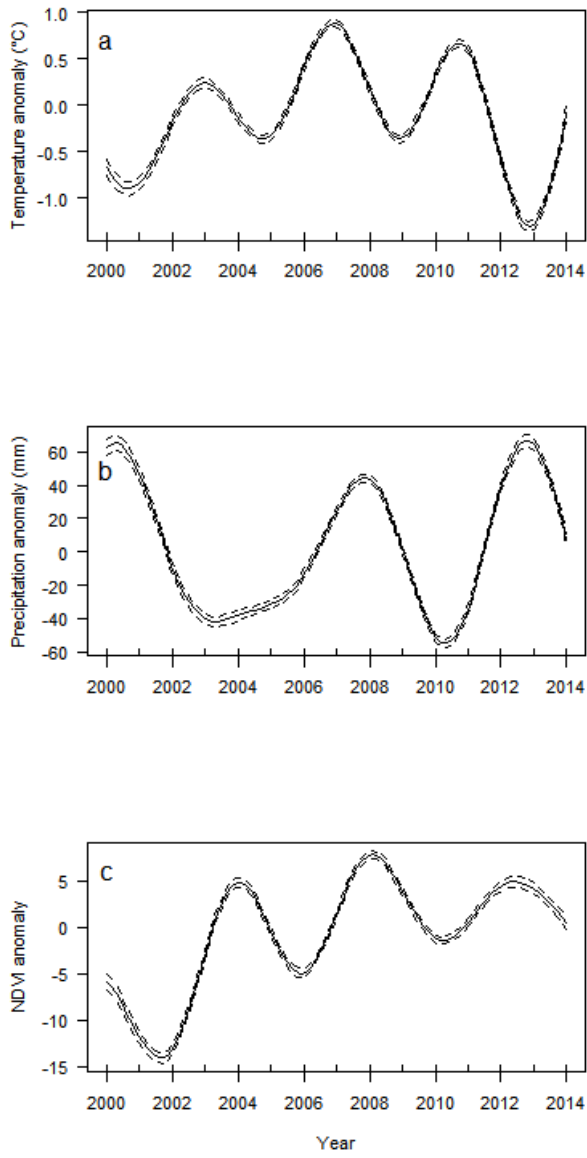
698 **Fig. 2** Relationship between partial residual wing length and local anomalies of (a) NDVI and
699 (b) temperature for 41 songbird species. These relationships were common to all species.
700 Solid lines represent regression spline fits from GAMMs. Dashed lines represent 95%
701 confidence intervals.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

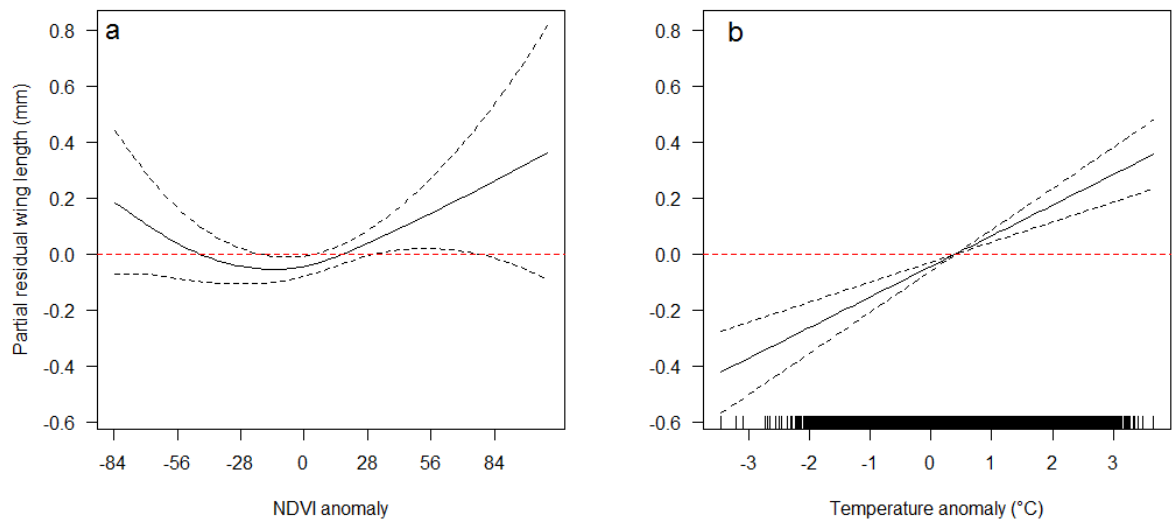
709 Figure 1.



710

711

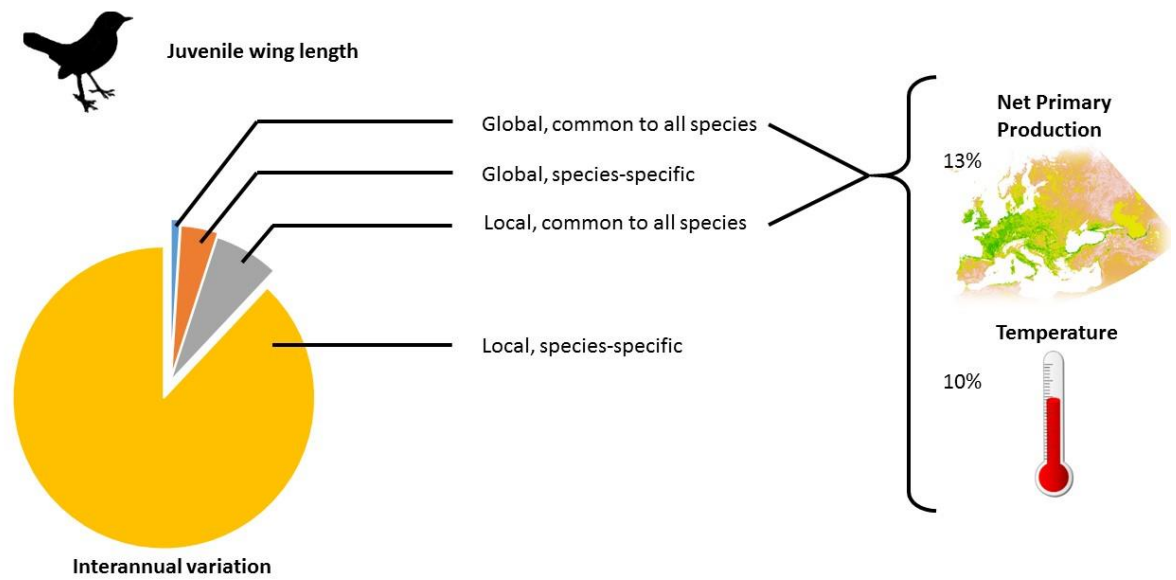
712 Figure 2.



713

714

715 Figure 3



716