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

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2 **body size of temperate songbirds**

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Abstract

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

INTRODUCTION

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

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

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

availability. The relative dependence of temporal change in body size on climate and primary

production has not been assessed for any taxa in temperate systems yet (but see Gardner et al.

2014b for a case study in a semi-arid system).

In addition to body growth effects, body size composition in a given population can also

be driven by size-dependent mortality (Gardner et al. 2014b). In temperate climates,

temperatures rarely reach lethal or sub-lethal levels (Tewksbury et al. 2008; Khaliq et al.

2014). Hence, selective pressure related to thermoregulatory mechanisms is unlikely to drive

significant body size change in a temperate system. Size-dependent mortality may also be

related to food availability. Small individuals suffer higher mortality when food becomes

scarce (Ozgul et al. 2010). Studies that have investigated size-dependent mortality in

terrestrial vertebrates were performed in arid, or semi-arid systems (McKechnie & Wolf 2010;

du Plessis *et al.* 2012; Gardner *et al.* 2014b). In fact, little is known about the mechanisms

underlying changes in body size induced by environmental changes in temperate climates.

Specifically, there is a need to identify whether temperature and food availability operate

through effects on juvenile growth or size-dependent mortality.

Differences in the relative importance of body growth effects and size-dependent

mortality among species and populations could explain the lack of consensus about the

direction of body size change. The few existing studies focusing on temporal change in body

size showed contrasting trends between species (Gardner et al. 2014a, Salewski et al. 2014,

but see Gardner et al. 2009; Van Buskirk et al. 2010) and/or between sites (Meiri et al. 2009,

Collins et al. 2016). This disagreement is reinforced by a probable publication bias towards

cases exhibiting significant changes (Meiri et al. 2009). Among these studies, only a few

tested the effect of interannual variation in temperature on body size, and even fewer assessed

the relative importance of temperature *versus* net primary production (but see Gardner et al.

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

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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

MATERIALS AND METHODS

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 (± 3.9 SD) years

143   (Dehorter and CRBPO 2015). Overall, study sites were evenly distributed across the years

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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.

8

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 (Pettorelli 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 ($b_{year} + b_{year,i} + b_{year:site} + b_{year:site\ i}$) that

239 was common to all species and sites (b_{year}), common to all sites but species-specific ($b_{year} +$

240 $b_{year,i}$), or common to all species but site-specific ($b_{year} + b_{year:site}$).

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*,

11

266 and yearling birds in breeding season *t+1*, after adjusting for feather abrasion and differences

267 in capture probability between sexes (Appendix S9). ΔWL 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 ΔWL for one species, at one site

270 for two consecutive years) obtained from 2020 individual measurements in total. We then

271 assessed whether ΔWL 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 ΔWL 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 ΔWL, 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* ($\Sigma w_{m,i}$) 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

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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

RESULTS

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

13

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    $b_{year} + b_{year:site}$; 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 mm ± 0.03 SE per degree Celsius (+0.31 mm ± 0.11 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 (ΔAIC > 100). The squared-effect of NDVI

340 explained 13% of the temporal variance in wing length common to all species (i.e. b_{year} +

341 $b_{year:site}$; 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 mm ± 0.21 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 (Σw_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

15

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

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

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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

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

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

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

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

As we did not perform a mark-recapture analysis, strictly speaking, we could not formally disentangle the contributions of tissue growth *versus* size-dependant mortality. Yet, only juvenile wing length depended on NDVI, and it did not explain differences in wing length between juvenile and 1st-year birds in the next year. We can thus reasonably presume that the proximate mechanism is mainly a direct influence of food availability on nestling and post-fledgling growth. This direct effect on growth may also have been reinforced by size-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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REFERENCES

Aber, J.D. and Federer, C.A. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. - Oecologia. 92: 463–474

Addo-Bediako, A. et al. 2000. Thermal tolerance, climatic variability and latitude. - Proc. Biol. Sci. 267: 739–745.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. - J. Wildl. Manage. 74, 1175–1178

Balen JH van 1980. Population fluctuations of the great tit and feeding conditions in winter. - Ardea. 68: 143–164.

Banner, K. M. and Higgs, M. D. 2017. Considerations for assessing model averaging of regression coefficients. - Ecol. Appl. 27: 78–93.

Barton K 2013. MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN. R-project.org/package=MuMIn.

Bates, D. et al. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4.

Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Gottinger studien, 3: 595–708.

Björklund, M. et al. 2014. Increase in body size is correlated to warmer winters in a passerine bird as inferred from time series data. - Ecol. Evol.: 59–72.

Brown, C. R. et al. 2013. Fluctuating viability selection on morphology of cliff swallows is driven by climate. - J. Evol. Biol. 26: 1129–1142.

Both, C. et al. 2006. Climate change and population declines in a long-distance migratory 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 Eglington, 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

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668

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 ΔAIC 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).

674

Response variable	Best models	Rank	ΔAIC	w_m
Juveniles	*Current breeding period*			
Wing length	NDVI + NDVI²	1	0.00	0.616
	NDVI + NDVI² + Temperature	2	1.96	0.231
	NDVI + NDVI² + Temperature * Precipitation	5	4.08	0.080
Body condition	Adjustment variables only	1	0.00	0.724
	Precipitation	2	0.33	0.229
Adults	*Current breeding period (before moulting)*			
Wing length	Adjustment variables only	1	0.00	0.581
	Precipitation	2	0.95	0.361
	Previous breeding period			
	Adjustment variables only	1	0.00	0.759
	Precipitation	2	3.48	0.133
	Previous moulting period			
	Adjustment variables only	1	0.00	0.817
	NDVI	2	4.17	0.101
Body condition	*Current breeding period (before moulting)*			
	Adjustment variables only	1	0.00	0.928
	NDVI	2	6.63	0.034
	Previous breeding period			
	Adjustment variables only	1	0.00	0.901
	NDVI	2	5.72	0.052
	Previous moult period			
	Adjustment variables only	1-	0.00	0.598
	NDVI	2	2.37	0.183

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31

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
Wing length	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
Body condition index	Precipitation[1]	0.010	0.019	0.24
	Species	See Appendix S8		1
	Species*log(Hour)	See Appendix S8		1

687

688

689

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.
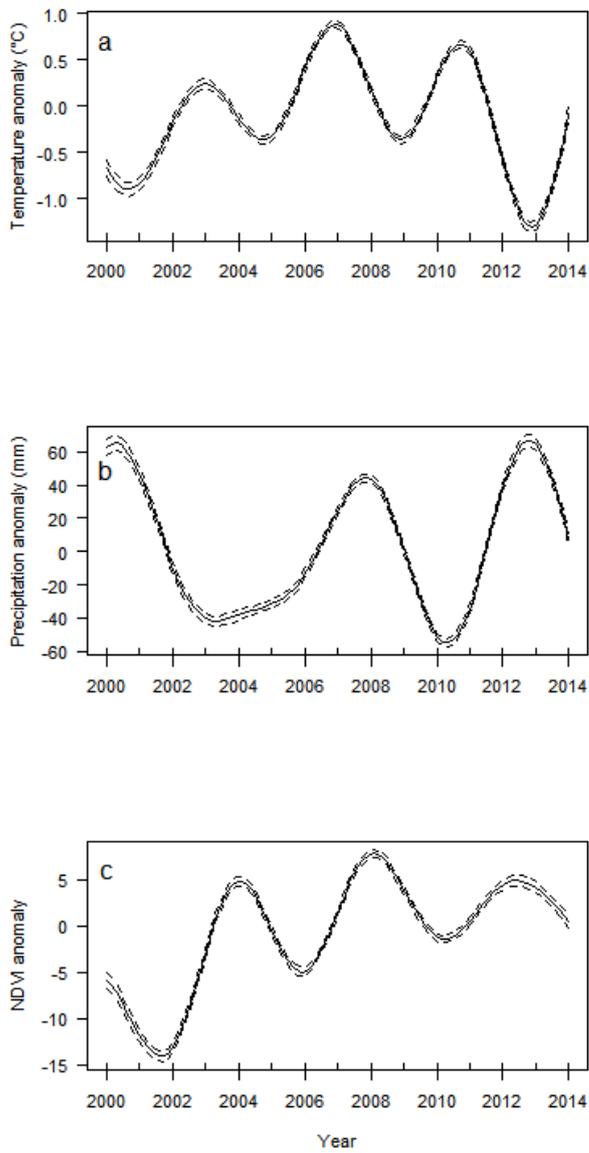
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712   Figure 2.

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715   Figure 3

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