ECOGRAPHY

Research

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 and Pierre Yves Henry

N. Dubos (http://orcid.org/0000-0002-1224-2598) (dubos.research@gmail.com), I. Le Viol, A. Robert, C. Teplitsky, M. Ghislain, O. Dehorter, R. Julliard and P. Y. Henry, Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Sorbonne Univ., MNHN, CNRS, UPMC, CP135, Paris, France. NB, MG and PYH also at: Mécanismes adaptatifs et évolution (MECADEV UMR 7179), Sorbonne Univ., CNRS, MNHN, Brunoy, France. CT also at: Centre d'Ecologie Fonctionnelle et Evolutive (CEFE UMR 5175), Montpellier, France.

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.

Keywords: body size, climate, birds

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).

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, 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 (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. 2017). 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 (Salewski et al. 2014) and may have been prone to temporal collection and curation biases. Some were based on one or two localities (Van Buskirk et al. 2010, Collins et al. 2017), which precludes drawing macroecological conclusions. For this reason, there is a need to assess the influence of temperature and food availability on body size at larger taxonomic and geographic scales.

When relying on wing length measurements, effects on growth or mortality apply to juveniles (through ontogeny), but also to adults as they undergo a moult of their flight feathers after breeding (Jenni and Winkler 2011). Therefore, the distribution of adult wing length in a population results from both the quality of feather growth during the period of moult and from size-dependent mortality. Here we assessed whether juvenile body growth and adult feather growth are influenced by interannual variation in local environmental conditions, which would account for the possibility that population-level body size variation is driven by changes in population composition through size-dependent mortality.

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

In the present study, for the 41 commonest songbird species of continental France, we explored between-year changes in body size and condition at the population-level by analysing the interannual variation in wing length and wing length-adjusted body mass, and their dependence on interannual fluctuations in climate and primary production during the breeding period, over the past 15 yr. We tested the effect of local, interannual environmental fluctuations only during the breeding season, which corresponds to the period of body growth, as body size has been shown to be mainly driven by the conditions during this period (Gardner et al. 2014b), and because we had no

information on bird locations and conditions experienced during the rest of their annual cycle. We analysed first-year birds and adults separately, to distinguish potential effects due to changes in body growth from changes in body size distributions in the population. As the distribution ranges of our study species exceed the bounds of our study area, this study represents a case in a temperate climate, regardless of potential 'edge effects' (Jiguet et al. 2010). We addressed the following questions: 1) are birds larger during or after warmer years, as expected under the heat maintenance hypothesis? 2) Are birds smaller or have lower body condition during or following poorly productive years? 3) Which driver (temperature or food availability) is the most important for body size, during the period of juvenile growth? 4) If they have any effect, do these drivers operate through effects on body growth or size-dependant mortality?

Material and methods

Bird survey

We used individual records of juveniles for the 41 most captured songbird species extracted from the French Constant bird ringing Effort Sites (CES) scheme from 2000 to 2014 (Robinson et al. 2009, more information at < http://crbpo. mnhn.fr >, see 'STOC Capture'). Biometric data were collected by 382 volunteer bird ringers at 257 sites spread across France (Supplementary material Fig. A1), each site being monitored during 5.1 (± 3.9 SD) years (Dehorter and CRBPO 2015). Overall, study sites were evenly distributed across the years (Supplementary material Fig. A2), and there was no bias in site-specific average temperature or latitude (Supplementary material Table A1). Captures occurred 2.5 ± 1.3 SD times per breeding season per site, from May/ early June (3 June ± 12.7 SD), until late June/early July (26 June ± 11.8 SD). For a given site, the number and date of capture sessions and the number and location of mist-nets were kept constant throughout the years. Each individual captured was individually marked, its species identified and aged (juvenile for birds born during the ongoing breeding season, or adult if born in previous years; Svensson 1992). Mist-netting of birds is most efficient in habitats with a low canopy (3-to-4 m high), so most CES sites are settled in shrublands, woodlands with dense understory, or reedbeds (Eglington et al. 2015).

Biometric data

We used wing length as a proxy for body size (Gosler et al. 1998), and body mass adjusted to wing length as a proxy for body condition (hereafter 'body condition index', Labocha and Hayes 2012). Wing length was measured with a butt-ended ruler as the length of the flattened wing chord from the carpal joint to the tip of the longest primary, at an average precision of 0.8 mm (± 0.1 across observers; i.e. most

observers rounded the value to the nearest integer). Body mass was measured with spring or electronic balances, to the nearest 0.5 g. We used fully grown juveniles measured during the breeding period (15 May–15 July, i.e. some days to weeks after fledging) and adults measured during their species-specific breeding period (Supplementary material Appendix A1). Measurements were performed by 2.4 (± 2.3 SD) trained measurers per site. Within-observer repeatability of wing length and of body mass measurements was 0.92 (± 0.11 SD) and 0.91 (± 0.10 SD), respectively (Supplementary material Appendix A2). For a given site, the observer is usually the same over the years. Differences in measurements between observers and sites were accounted for in our models (see statistical analysis below for model descriptions). For each species, we accounted for potential measurement errors by removing measurements that were beyond the upper and lower 0.5% limits of a Gaussian distribution fitted to the data. Only one measurement per individual was used in the analyses (with random choice for the 9.1% of data that were repeated measurements on the same individual). Hereafter, wing length measurements were from 40 071 juveniles and 67 122 adults, and body mass measurements from 30 783 juveniles and 51 239 adults.

Environmental variables

We used environmental variables that are already known to explain interannual fluctuations in avian body size, and that were relevant for the study period and area (Keller and Van Noordwijk 1994, Gardner et al. 2014b). For each site and each year between 2000 and 2014, we computed average environmental conditions during the breeding period (1 April–1 July, i.e. the main period of reproduction, including parental allocation to egg laying, incubation, and nestling and post-fledging growth). These metrics were computed from daily records of mean temperature and total precipitation, and monthly records of NDVI images. Populations are supposedly adapted to local thermal and trophic conditions (Both et al. 2006). To reveal the influence of between-year fluctuations in the local environment at each study site, independently from average local conditions, each raw variable was transformed into site-specific yearly anomalies by subtracting the average value of the corresponding site for the 2000–2014 period. This allowed us to control for confounding spatial effects (e.g. latitudinal size gradients). Site-specific yearly anomalies in mean temperature were expected to document fluctuations of the thermal constraint (Kendeigh 1969), whereas total precipitation (alone or in synergy with mean temperature) or net primary production anomalies would record fluctuations of trophic resources (Yom-Tov and Geffen 2011) during the breeding period (Supplementary material Appendix A3). We used these three complementary trophic-related surrogates as they may characterise resource availability differently (Gardner et al. 2014b). We extracted daily mean temperature and daily total precipitation from the E-OBS

meteorological dataset (Haylock et al. 2008), with a 0.25° pixel resolution using climateExtract R package (< https://github.com/RetoSchmucki >). We used monthly averaged raster images of remotely sensed normalized different vegetation index (NDVI; Copernicus Service information 2016) as a proxy for net primary production (Pettorelli et al. 2005). The spectral reflectance covered by these images were the red and near infrared wavebands (0.61 to 0.68 µm and 0.78 to 0.89 µm, respectively), generally used for vegetal characterisation (Kerr and Ostrovsky 2003). We computed mean NDVI inside a buffer zone with a 5 km radius around each site from the raster images. The 5 km radius was chosen because it coincides with the level of precision of CES site geolocations. All variables were included in the analyses since their variations were largely uncorrelated (r < 0.35; Supplementary material Table A2). They were centred and scaled so that relative effect sizes could be compared between variables, regardless of their order of magnitude of mean and variance.

Adjustment variables

All statistical null models presented hereafter included the effects of 1) species (fixed term), and random variation between 2) observers, 3) sites and 4) year. Wing length of juveniles increases slightly throughout the breeding season; this was accounted for by adding $(v - a)$, a fixed effect of log-transformed date of the year, with a species interaction term. Body mass increases during the morning until it reaches a plateau at about noon; this was accounted for by adding $(v - b)$ log-transformed time of the day (hour) as a fixed term, with a species interaction term (see justifications and model details in Supplementary material Appendix A4).

Statistical analysis

As population responses to environmental parameters can vary with their relative position in the species' thermal niche (Jiguet et al. 2010), we verified that the majority of the populations studied were not located at the edge of species distributions. Less than 4% of the data were located in the upper 10% of species' thermal ranges, and less than 0.4% were located in the lower 10% (see details in Supplementary material Appendix A5).

Interannual variation in environmental and biometric variables

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

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

For body constitution features, we assessed the proportion of interannual variation that was common to all sites (i.e. nation-wide variation) and/or common to all species (i.e. independent of species life history traits). This was assessed with a variance-partitioning method (Grosbois et al. 2009). For wing length and body condition index, we used linear mixed models (LMM; lme4 package ver. 1.1.7; Bates et al. 2014) to estimate between-year (b_{year}), between-site (b_{year}) and (b_i) between-species i variances using random terms for the corresponding effects (Supplementary material Appendix A6). With these variance estimates, we identified the proportion of temporal variance in body size and condition ($b_{year} + b_{year,i} + b_{year:site} + b_{year:site\ i}$) that was common to all species and sites (b_{year}), common to all sites but species-specific ($b_{year} + b_{year,i}$), or common to all species but site-specific ($b_{year} + b_{year:site}$).

Effect of environmental anomalies on wing length and body condition index

We assessed the dependence of wing length and body condition index on local environmental anomalies during the breeding period for both adults and juveniles. For adults, we also assessed the dependence on environmental anomalies during the post-breeding moult period of the preceding year, of species for which a moult period could be identified at the capture site (n = 13; Supplementary material Appendix A1; A7), and also during the breeding period of the year prior to capture (to account for potential lags between change in environmental conditions and the response of body size and condition; Gardner et al. 2014b). The post-breeding moult occurred at the breeding site for most of the study species (Morrison et al. 2015), so we tested the effect of environmental anomalies at the same location as during breeding periods. Models included mean temperature, total precipitation, the interaction between mean temperature and total precipitation, and mean NDVI for the breeding period (see equations in Supplementary material Appendix A6).

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

The risk of mortality before the first breeding attempt (as a yearling) may depend on the environmental conditions experienced throughout the year and varies among individuals, depending on their size: larger individuals would die more frequently in hotter years, and/or smaller individuals would die more often when born during poorly productive years. Ideally, the link between environmental conditions, size and survival should be investigated using mark–recapture models. However, the small sampling area (2–4 ha) of our study sites meant that our mark–recapture data were unsuitable for this analysis (high natal dispersal, transiency, and female breeding dispersal). Hence, size-dependent mortality was inferred from differences in average wing length (hereafter ΔWL) between juveniles in breeding season t, and yearling birds in breeding season $t + 1$, after adjusting for feather abrasion and differences in capture probability between sexes (Supplementary material Appendix A9). ΔWL was computed

when at least 10 measurements were available per site, year and species. This resulted in 138 data points for six species, from 46 sites (one data point representing one ΔWL for one species, at one site for two consecutive years) obtained from 2020 individual measurements in total. We then assessed whether ΔWL depended on local environmental anomalies of breeding season t using LMMs accounting for random variation between sites and years.

Model selection process

The dependence of wing length, body condition index and ΔWL on environmental anomalies were inferred using a multi-model selection based on Akaike's information criteria (AIC; Burnham and Anderson 2002; adjusted for small sample size for ΔWL, i.e. AICc). Models containing only effects with the highest statistical support have the lowest AIC values. The support for a model m relative to all other models considered was quantified by its AIC weight (w_m). The relative importance of an explanatory variable i ($\Sigma w_{m,i}$) was quantified as the sum of w_m of models containing this variable. To account for model selection uncertainty, model-averaged estimates of variable coefficients were computed using the 'best model set', defined as the set of models for which the cumulative sum of $w_m \leq 95\%$. We also showed averaged estimates, once uninformative models (Arnold 2010) had been removed. Model averaging was performed only if the best model set did not include the linear effect of a given variable together with its quadratic effect, or an interaction (Banner and Higgs 2017). Model selection and averaging were implemented using MuMIn R package ver. 1.9.13 (Barton 2013). The MuMIn function builds all possible combinations of the aforementioned effects (with each combination corresponding to a single model). Full models corresponded to null models (i.e. with adjustment variables), to which were added the additive fixed effects of environmental variables, an interaction between mean temperature and total precipitation anomalies (to allow for synergistic or antagonistic effects), and interactions between each environmental variable and species identity to allow species-specific responses. To accommodate for potential non-linear effects of environmental variables, a quadratic effect was also allowed for all environmental variables. Full model equations are described in Supplementary material Appendix A6. When a model included a quadratic term or an interaction term, the linear or additive effect, respectively, was systematically maintained in the model. For significant relationships, we verified the robustness of the linearity and quadratic assumptions using smoothed estimates obtained with a spline function of a GAMM version of the corresponding LMM.

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

Results

Temporal variations in environmental conditions and body constitution

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

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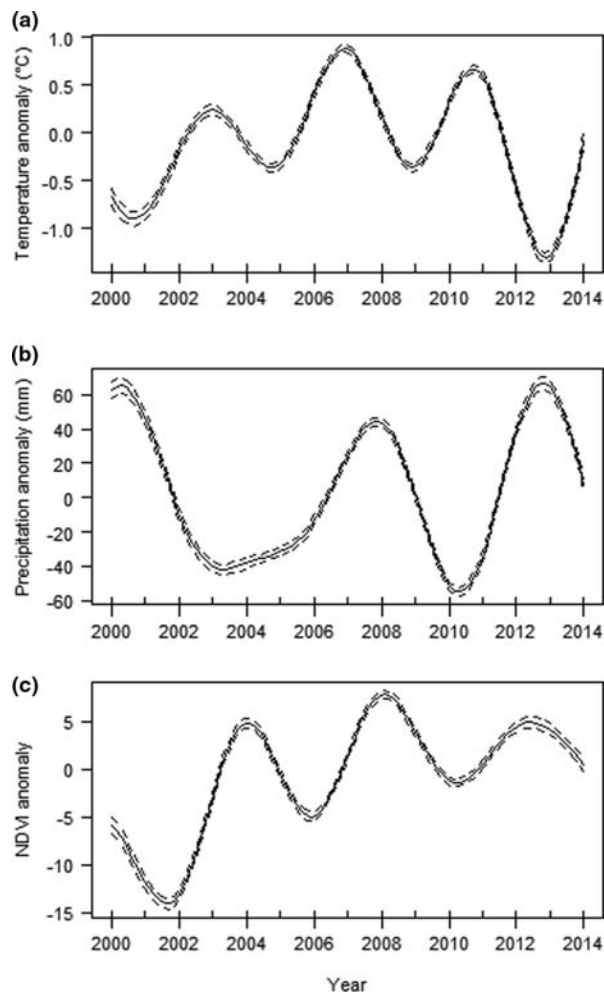

Figure 1. Partial residual climate anomalies during the breeding season in France for the 2000–2014 period: (a) temperature, (b) precipitation and (c) NDVI. Solid lines represent the regression spline fit obtained from GAMMs, with year as smooth term and site as random effect. Dashed lines represent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

Table 1. Interannual variance partitioning of wing length and body condition index, for juveniles and adults of 41 songbird species. Variances were estimated from random effects of linear mixed models. Models were adjusted for feather growth/abrasion, within-day body mass variation and adult sexual dimorphism. Percentages (in parenthesis) correspond to the 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

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

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

We found strong statistical support for a quadratic effect of NDVI on juvenile wing length. We did not find any effect of the tested environmental variable on adult wing length, nor on adult and juvenile body condition (Table 2; Supplementary material Appendix A7–A8).

Temperature
The effect of temperature anomalies on juvenile wing length received weak statistical support, an absence of effect being the most likely ($\Sigma w_m = 0.34$). In case of an effect, it would be linear and positive (GAMM: estimated degrees of freedom = 1, $p < 0.0001$; Fig. 2). Temperature anomaly explained 10%

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).

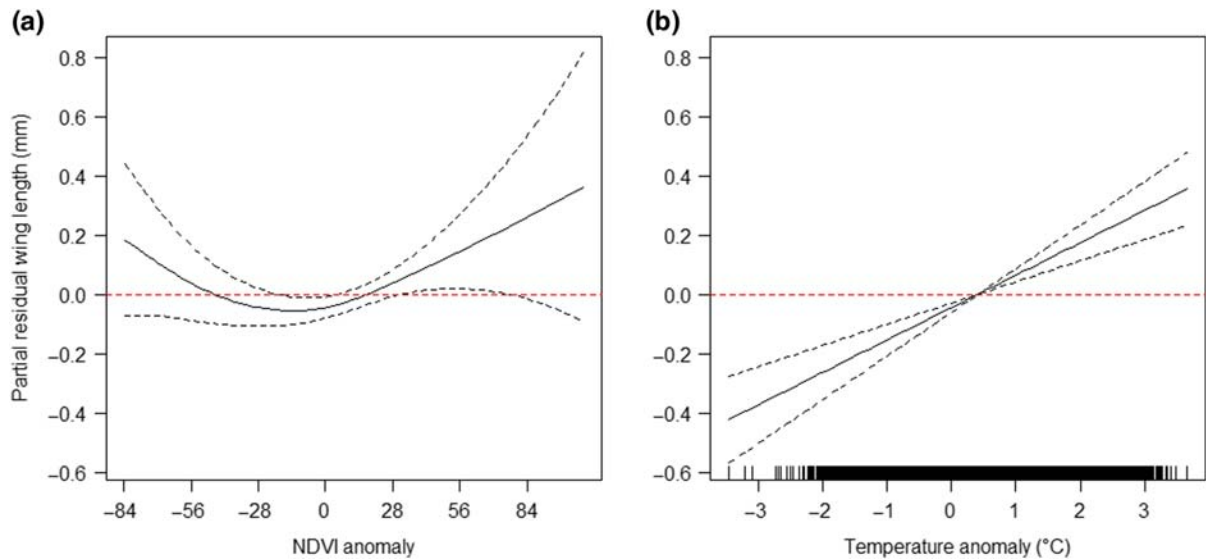| Response variable	Best models	Rank	ΔAIC	w_m
Juveniles	Current breeding period			
Wing length	NDVI+NDVI²	1	0.00	0.616
	NDVI+NDVI²+Temperature	2	1.96	0.231
	NDVI+NDVI²+Temperature × Precipitation	5	4.08	0.080
Body condition	Adjustment variables only	1	0.00	0.724
	Precipitation	2	0.33	0.229
Adults	Current 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

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

of the interannual variance in wing length common to all species (i.e. $b_{year} + b_{year:site}$; Fig. 3). Coefficients were robust to model averaging pitfalls, as temperature was only included as an additive, linear effect. After rescaling, wing length would increase by 0.09 mm ± 0.03 SE per degree Celsius (+0.31 mm ± 0.11 SE in years with the highest anomalies compared to years with average conditions).

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

Net primary production

Juveniles were larger in years with positive NDVI anomalies ($\Sigma w_i = 1$, Table 3) with a quadratic relationship (see GAMM on Fig. 2; df = 2.34, p (smooth term) = 0.02). This effect of NDVI would be largely common to all species as models allowing for species-specific responses were not statistically supported ($\Delta AIC > 100$). The squared-effect of NDVI explained 13% of the temporal variance in wing length common to all species (i.e. $b_{year} + b_{year:site}$; Fig. 3). Coefficients were robust to model averaging pitfalls, as NDVI was systematically included with its squared-effect in the best model
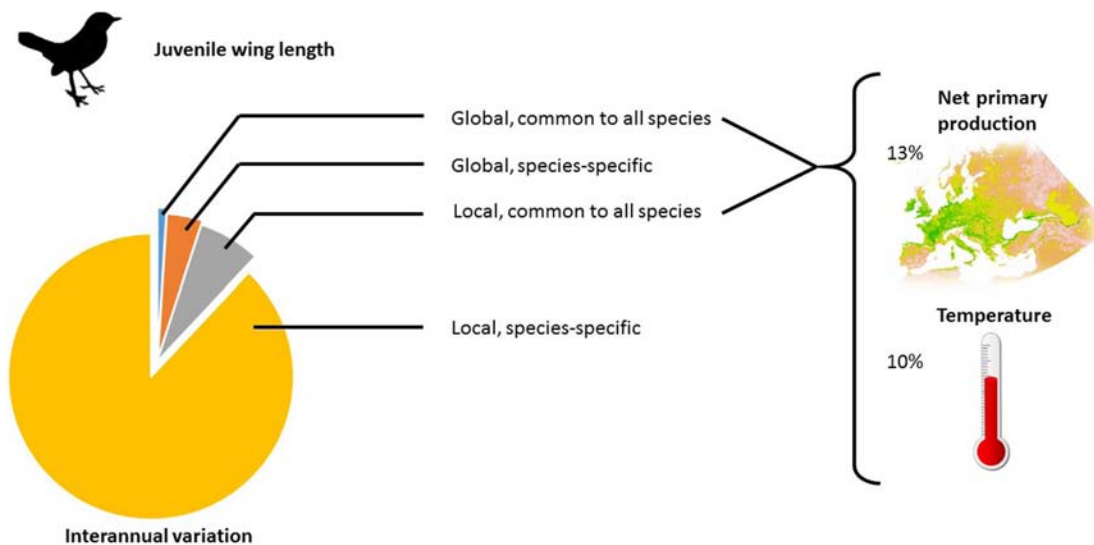

Figure 3. Variance partitioning juvenile wing length for 41 songbird species in France between 2000 and 2014, and environmental contribution (NDVI and temperature anomalies). NDVI and temperature anomaly respectively captured 13 and 10%, of the interannual variation that is common to all species.

Table 3. Variables explaining juvenile wing length and body condition variations for 41 songbird species in France between 2000 and 2014. Coefficients (β), standard errors (SE) and z values were averaged from a 'best model set' (i.e. that included 95% of AIC weight) and weighted by Akaike weights. Within best model sets, some models could be uninformative (see Methods). Coefficients are shown when estimated from the 'full' best model set, and after removing potentially uninformative models (in parentheses, shown only if the latter differs). Cumulative AIC weights (Σw_i) indicate the relative importance of each variable. All environmental variables were centred and scaled. Detailed estimates for the effect of adjustment variables and species-specific effects are provided in Supplementary material Appendix A8. Statistically 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	Supplementary material Appendix A8		1
	Species × log(Date)	Supplementary material Appendix A8		1
Body condition index	Precipitation[1]	0.010	0.019	0.24
	Species	Supplementary material Appendix A8		1
	Species × log(Hour)	Supplementary material Appendix A8		1

set. These were similar for the average model and the best model (Table 3). Wing length increased by 1.1 mm ± 0.21 SE in years with the highest anomalies, compared to years with average conditions. Alternative variables related to primary production (precipitation, with interactive effects with temperature) did not receive any statistical support (Table 2). An interaction between temperature and precipitation was included in the best model set, but this effect was uninformative, as its statistical support was very weak ($\Sigma w_m = 0.09$) and it only captured 2% of the interannual variance common to all species. When removing this interaction from the best model set, our results remained qualitatively unchanged: the coefficient for temperature decreased from 0.019 to 0.014 (NDVI coefficients remained unchanged).

Climate-driven size-dependent mortality

Differences in average wing length between juveniles in year t and yearling birds in year $t + 1$ (i.e. ΔWL) were not related to any of the environmental variables (Supplementary material Appendix A9). Hence, there is no indication of climate-driven size-dependent mortality.

Discussion

In our dataset, body size fluctuations of songbirds were best explained by interannual variations in food availability (NDVI), although much of the temporal variance remained unexplained. We showed that the effect of temperature anomaly is fairly positive as expected 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 (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 (Bergmann 1847). 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 (Supplementary material Appendix A10). 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 climates, increasing temperature reduces the cost of juvenile heat maintenance (Kendeigh 1969). This results in higher metabolic allocation for growth, which could explain the positive effect of high temperatures on juvenile size (Gillooly et al. 2001). The direction of the relationship is thus consistent with previous studies performed in cool or cold regions (Pérez et al. 2016, Collins et al. 2017), or during a cool period of the year (Gardner et al. 2014b), and supports the fact that warming can benefit juvenile growth through changes in metabolic allocation in temperate climates. In

France, species are probably more cold-constrained than hot-constrained, and hot anomalies are probably less detrimental for reproduction and juvenile growth (Julliard et al. 2004) than at lower latitudes. It is also possible that species sensitivity to climatic anomaly depends on the location of a given population with reference to the cold edge of its geographic distribution (Jiguet et al. 2010). Warmer years would benefit species that are located near the cold edge, while it could harm those located at the hot edge. However, France is closer to the hot edge for most of our study species (i.e. typically Palearctic), and thus it is far from the cold edge of their distribution. Hence, a positive effect of temperature is expected in temperate climates, even in the core of species distribution ranges.

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

Higher NDVI values were associated with longer wings, presumably due to a positive relationship between vegetation production and invertebrate abundance (Wimp et al. 2010). 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 an increase estimated at +1.1 mm in the year with the highest NDVI value. As climate warming is expected to increase the frequency of positive anomalies in primary production (Melillo et al. 1993), we predict that climate change will induce a body size increase in temperate songbirds. Temperature and precipitation showed important fluctuations over the study period. The extent of interannual fluctuations in our variables was similar to other studies (Gardner et al. 2014b, Teplitsky and Millien 2014), treating each year as independent category, with cold and hot years, and dry and wet years. This suggests that the relatively low explanatory power of the tested variables does not result from a lack of temporal variance. Our statistical models were based on extensive long-term data obtained from a large-scale monitoring program and took into account most of the possible sources of bias and noise: such as observer effect, spatial and temporal variability. With the high statistical support attributed to NDVI anomalies, we can safely conclude that net primary production is a better predictor of juvenile growth than temperature in our system.

Interannual variation was largely heterogeneous between sites, suggesting that variation in body size was largely related to local, rather than global factors. This is consistent with other studies performed on multiple species at different sites (Meiri et al. 2009, Collins et al. 2017). This emphasises the necessity of considering alternative environmental variables or variables at finer spatial resolution to understand the very local determinants of size. The sensitivity to climate change is known to vary within species range (Jiguet et al. 2010, Pearce-Higgins et al. 2015). In our study area, mean temperature of the breeding season ranged from 6°C to 20°C, depending on the site. The effect of temperature anomaly may then differ between the hottest and the coldest sites. Yet, our results rely on the assumption of a uniform response to climatic variation across species ranges, thus ignoring possible spatial heterogeneity in the response to climatic anomalies. Variation in body size may also be driven by land use changes (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

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

Conclusions

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

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. R. Soc. B 267: 739–745.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. – J. Wildl. Manage. 74: 1175–1178.

Balen, J. H. 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 ver. 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 ver. 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. 5: 59–72.

Both, C. et al. 2006. Climate change and population declines in a long-distance migratory bird. – Nature 441: 81–83.

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

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

Canale, C. I. et al. 2016. Differential plasticity of size and mass to environmental change in a hibernating mammal. – Global Change Biol. 22: 3286–3303.

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

Copernicus Service information 2016. – < http://land. copernicus.eu >.

Danner, R. M. and Greenberg, R. 2015. A critical season approach to Allen's rule: bill size declines with winter temperature in a cold temperate environment. – J. Biogeogr. 42: 114–120.

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

Dehorter, O. and CRBPO 2015. Bird ringing and movement database for France. – Centre de Recherches sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle, Paris, France, < http://crbpo.mnhn.fr/ > accessed 24 December 2015.

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

Deutsch, C. A. et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. – Proc. Natl Acad. Sci. USA 105: 6668–6672.

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

Gardner, J. L. et al. 2009. Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. – Proc. R. Soc. B 276: 3845–3852.

Gardner, J. L. et al. 2011. Declining body size: a third universal response to warming? – Trends Ecol. Evol. 26: 285–291.

Gardner, J. L. et al. 2014a. Temporal patterns of avian body size reflect linear size responses to broadscale environmental change over the last 50 years. – J. Avian Biol. 45: 1–7.

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

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

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

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

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

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

Grosbois, V. et al. 2009. Modeling survival at multi-population scales using mark–recapture data. – Ecology 90: 2922–2932.

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

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

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

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

Jiguet, F. et al. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. – Proc. R. Soc. B 277: 3601–3608.

Julliard, R. et al. 2004. Evidence for the impact of global warming on the long-term population dynamics of common birds. – Proc. R. Soc. B 271: S490–S492.

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

Kendeigh, C. 1969. Tolerance of cold and Bergmann's rule. – Auk 86: 13–25.

Kerr, J. T. and Ostrovsky, M. 2003. From space to species: ecological applications for remote sensing. – Trends Ecol. Evol. 18: 299–305.

Khaliq, I. et al. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. – Proc. R. Soc. B 281: 20141097.

Kruuk, L. E. B. et al. 2015. Contrasting effects of climate on juvenile body size in a Southern Hemisphere passerine bird. – Global Change Biol. 21: 2929–2941.

Labocha, M. K. and Hayes, J. P. 2012. Morphometric indices of body condition in birds: a review. – J. Ornithol. 153: 1–22.

Lack, D. 1968. Ecological adaptations for breeding in birds. – Methuen.

Lindström, J. 1999. Early development and fitness in birds and mammals. – Trends Ecol. Evol. 14: 343–348.

Meiri, S. et al. 2009. Global change and carnivore body size: data are stasis. – Global Ecol. Biogeogr. 18: 240–247.

Melillo, J. M. et al. 1993. Global climate change and terrestrial net primary production. – Nature 363: 234–240.

Morrison, C. A. et al. 2015. Flexibility in the timing of post-breeding moult in passerines in the UK. – Ibis 157: 340–350.

Ozgul, A. et al. 2010. Coupled dynamics of body mass and population growth in response to environmental change. – Nature 466: 482–485.

Parker, G. A. and Begon, M. 1986. Optimal egg size and clutch size – effects of environment and maternal phenotype. – Am. Nat. 128: 573–592.

Pearce-Higgins, J. W. et al. 2015. Geographical variation in species' population responses to changes in temperature and precipitation. – Proc. R. Soc. B 282: 20151561.

Pérez, J. H. et al. 2016. Nestling growth rates in relation to food abundance and weather in the Arctic. – Auk 133: 261–272.

Pettorelli, N. et al. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. – Trends Ecol. Evol. 20: 503–510.

Robinson, R. A. et al. 2009. Constant effort: studying avian population processes using standardised ringing. – Ring. Migr. 24: 199–204.

Salewski, V. et al. 2014. Morphological change to birds over 120 years is not explained by thermal adaptation to climate change. – PLoS One 9: e101927.

Schmidt, N. M. and Jensen, P. M. 2005. Concomitant patterns in avian and mammalian body length changes in Denmark. – Ecol. Soc. 10: 5.

Searcy, W. A. et al. 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. – J. Avian Biol. 35: 269–279.

Smith, H. G. et al. 1989. The trade-off between offspring number and quality in the great tit *Parus major*. – J. Anim. Ecol. 58: 383–401.

Svensson, L. 1992. Identification guide to European Passerines. – Märstatryck, Stockholm.

Teplitsky, C. and Millien, V. 2014. Climate warming and Bergmann's rule through time: is there any evidence? – Evol. Appl. 7: 156–168.

Tewksbury, J. J. et al. 2008. Putting the heat on tropical animals the scale of prediction. – Science 320: 1296–1297.

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

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

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

Yom-Tov, Y. 2001. Global warming and body mass decline in Israeli passerine birds. – Proc. R. Soc. B 268: 947–952.

Yom-Tov, Y. and Geffen, E. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. – Biol. Rev. 86: 531–541.

Supplementary material (Appendix ECOG-03413 at < www. ecography.org/appendix/ecog-03413 >). Appendix A1–A11.

Ecography

Supplementary material

Content

The final dataset used in this analysis is available as an R object online as a supporting information.

Figure A1a Distribution of the 257 study sites of the French Constant ringing Effort Site scheme.

Figure A1b Yearly distribution of study sites of the French Constant ringing Effort Site scheme.

Table A1 Temporal trends in site-specific average temperature, and latitude for the breeding period between 2000 and 2014 in France (n = 1290).

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	13.79223	5.140867	3.646	0.000267
Year	-0.02733	0.01886	-1.449	0.148
Intercept	47.42236	0.13336	355.602	<0.000001
Latitude	-0.01060	0.01507	-0.704	0.482

Appendix A1 Species-specific breeding periods and moult periods (for species for which a moult period could be identified, see Appendix A7). Numbers correspond to the number of days since 1st January.

Species	Between-moult		Moult period	
	Begining	Ending	Begining	Ending
Acrocephalus palustris	140	200		
Acrocephalus schoenobaenus	120	180		
Acrocephalus scirpaceus	130	180	190	220
Aegithalos caudatus	85	160		
Alcedo atthis	100	200		
Anthus trivialis	100	170		
Carduelis cannabina	75	160		
Carduelis carduelis	95	140		
Carduelis chloris	80	150	160	190
Certhia brachydactyla	100	175		
Cettia cetti	75	200		
Dendrocopos major	120	170		
Emberiza citrinella	100	150		
Emberiza schoeniclus	75	200		
Erithacus rubecula	125	175	175	220
Fringilla coelebs	75	175	175	220
Hippolais polyglotta	100	150	150	180
Luscinia megarhynchos	90	190	190	230
Luscinia svecica	80	210		
Parus caeruleus	75	160	160	300
Parus cristatus	100	150	150	180
Parus major	100	150	170	300
Parus montanus	100	150	150	180
Passer domesticus	100	180		
Phoenicurus phoenicurus	120	170		
Phylloscopus bonelli	150	180		
Phylloscopus collybita	90	170	175	205
Phylloscopus trochilus	105	185		
Prunella modularis	90	200		
Pyrrhula pyrrhula	100	190		
Saxicola torquata	75	220		
Sitta europaea	100	200		
Sturnus vulgaris	100	175		
Sylvia atricapilla	100	190	190	275
Sylvia borin	110	200		
Sylvia cantillans	120	170		
Sylvia communis	120	190		
Sylvia curruca	100	180		
Troglodytes troglodytes	100	200		
Turdus merula	120	180	190	300
Turdus philomelos	120	180		

Appendix A2 Method used to estimate measurers' repeatability.

To assess the quality of biometric measurements, we analysed the within-observer repeatability of measures (Nakagawa & Schielzeth, 2010) for the 128 measurers that collected at least 30 repeated measurements (36982 measures). Repeatability is computed as:

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

where σ_α^2 is the between-bird variance and σ_ε^2 is the residual variance (including between-measure variation). When a bird was measured more than once per day, we randomly selected one measure per day. To estimate repeatability with the maximum number of observers, we used measurements of adult birds. We used Markov Chain Monte Carlo generalized linear models with bird identity as random factor to obtain the between-bird variance component. Within-bird variance is included by σ_ε^2. Variation due to the following confounding effects was excluded from σ_ε^2. Body size measures were adjusted for the effects of sex (as three-level fixed factor: male, female and undetermined) and random between-year variation (as random effect of year). Wing length measures were adjusted for the effect of within-year wing wear (using a fixed effect of day of the year in log-transformed Julian date, see Fig. S2). Body mass measures were adjusted for sex-dependent within-year body condition variation (using a fixed effect of day number, in interaction with sex) and within-day increase in body mass (as fixed effect of time of the day, see appendix 2). Variance estimates were obtained using function MCMCglmm (version 2.21; Hadfield, 2010) for the R software. Eventually, mean and SD of repeatability across all observers were computed for wing length and body mass.

Appendix A3 Computing local environmental anomalies.

To account for potential local adaptation of birds to local environmental conditions (Jiguet et al., 2006), we assume that birds respond to deviations from usual conditions (i.e., anomalies) rather than to the actual value of environmental conditions (i.e., raw values). For a given year, environmental anomalies can largely differ between sites, some sites being for instance hotter than usual, whereas others are colder. Since breeding birds are exposed to local – and not to nation-wide – environmental anomalies, all environmental variables were computed at the local level, choosing the nearest data point according to the geographical coordinates of the site. Hence, yearly local anomalies were computed for each variable and each site as the difference between the local value of a given year and the mean value at the site for the whole study period (2000-2014). This results in the following formula: $Ca_{it} = C_{it} - \overline{C_\iota}$ where Ca_{it} is the environmental anomaly for site i in year t, C_{it} is the mean condition (daily temperature and precipitation, and monthly NDVI) for the breeding period for site i in year t, and $\overline{C_\iota}$ the mean condition for the breeding period for site i over the whole study period. Annual anomalies of temperature and precipitation variability per breeding period (April-July) were computed as the difference between the standard deviation (SD) of climatic condition of a given breeding period and the average SD of climatic condition across all breeding periods. It is defined as $SDCa_{it} = SDC_{it} - \overline{SDC_\iota}$ where, for site i in the breeding period of year t, $SDCa_{it}$ is the temperature variability anomaly, SDC_{it} is the SD of daily temperature for year t, and $\overline{SDC_\iota}$ the mean of SD of daily temperature across the whole study period.

Table A2 Pearson's r correlation matrix of the centred and scaled environmental anomaly variables that were included in the models (based on juvenile wing length data, n = 40,071).

	Temperature	Precipitation
Precipitation	-0.35	
NDVI	-0.02	0.17

Appendix A4 Adjustment variables.

Differences in body size between species were accounted for by a fixed effect of species identity. Observer, site and year identities were included as random effects to account for between-observer, between-site and between-year random variations. As juveniles captured late in the season have a longer wing (Fig. A2a), we also included the Julian date as a fixed, linear effect (hereafter *Date*, the number of days after May 15th) with a species interaction term to adjust for specie-specific linear changes in wing length within the breeding season. For body mass, we found no evidence of structured temporal variation throughout the breeding season, and therefore *Date* was not included in body mass analyses. However, birds get heavier throughout the morning as they accumulate food in their digestive tract, and their mass usually reaches a threshold after noon. To control for this within-day variation in body mass, we included the linear effect of the log-transformed time of day in body mass models, with a species interaction term (Fig. A2c). There may have been some spatial dependency in body size (Fig. A1), but models with spatially autocorrelated residuals rarely converged (or did not receive statistical support). Nevertheless, results remained unchanged when we included a Gaussian spatial autocorrelation structure in the best models. Hence, we only present models that do not account for spatial autocorrelation.

Protocol used to determine the adjustment methods in wing length and body mass modelling.

We used generalized additive mixed models (R package gamm4) to verify the shape of the relationship between (a) juvenile and adult wing length and day of the year, (b) juvenile body mass and day of the year and (c) juvenile body mass and time of day. Age classes (juvenile, adult) and species were treated separately. We controlled for observer, site and between-year random variation by including observer identity, site index and year as random effect. For adults, we included the effect of sex as a fixed term, and its interaction with species identity.

Within-year juvenile wing increased non-linearly throughout the breeding period (Fig A2a). The effect "day of the year" better fitted the data after being log-transformed (ΔAIC = 183). For adults, feather wear was linear (Fig A2b).

Within-year mass variation showed no variation during most of the breeding season (Fig A3c), and therefore was not included in models further.

Within-day body mass variation showed an increase before reaching a plateau (Fig A2d). The initial model (see main text) better fitted our data after "time of the day" was log-transformed (ΔAIC = 267). This enabled us to control for feather growth and daily mass variation by including Julian date and log-transformed time of day as linear effects, respectively.

As growth and daily mass variation may be uneven between species, we included a species interaction term.

Fig. A3a Relationship between juvenile wing length and (1) date of the year, and (2) log-transformed date of the year (all species pooled here). Regression lines were obtained from generalized additive mixed models. Species-specific coefficients were used for adjustment in the models.

Fig. A3b Relationship between adult wing length and date of the year (all species pooled). The regression line was obtained from generalized additive mixed models. Species-specific coefficients were used for adjustment in the models.

Fig. A3c Relationship between juvenile body mass and date of the year (all species pooled). The regression line was obtained from generalized additive mixed models.

Fig. S3d Relationship between juvenile body mass and (1) time of the day, and (2) log-transformed time of day (all species pooled). Regression lines were obtained from generalized additive mixed models. Species-specific coefficients were used for adjustment in the models.
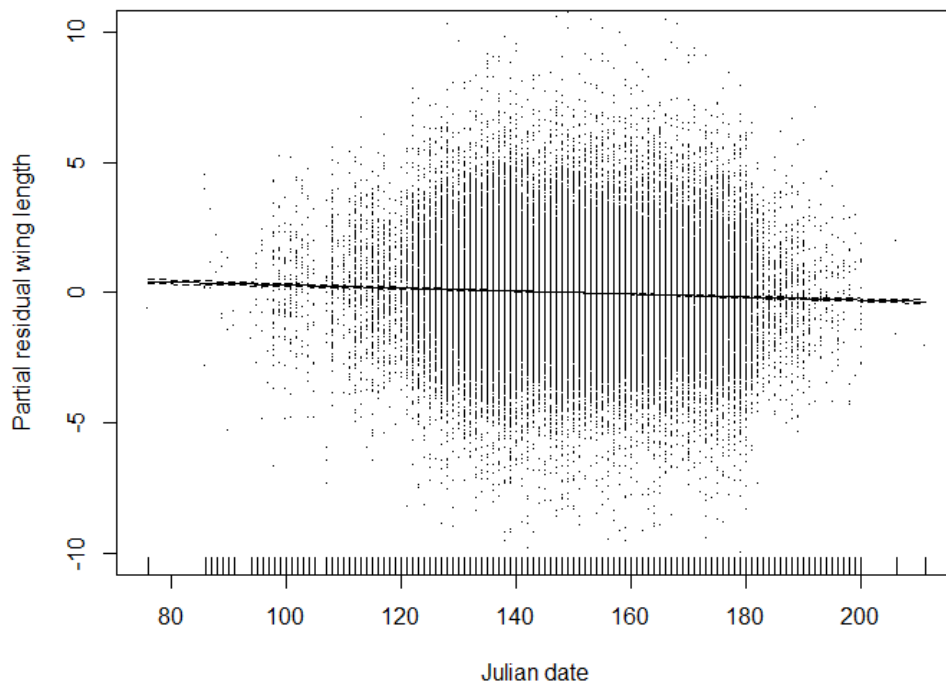
Appendix A5 Population locations, and distribution of their relative position in species thermal range.

Fig A4 Spatial distribution of study populations (left) and thermal coordinate distributions (right). The thermal coordinate of a given population is defined as the standardised difference between the average temperature of a given site and species thermal maximum (Jiguet et al., 2010). This indicates the relative position of a population in species thermal tolerance range. A value of 0 represents a population located at the cold edge, and a value of 1 represents a population located at the hot edge.

Aegithalos caudatus

Aegithalos caudatus

Alcedo atthis

Alcedo atthis

Anthus trivialis

Anthus trivialis

Fig. A4 *Continued.*

Carduelis cannabina

Carduelis cannabina

Carduelis carduelis

Carduelis carduelis

Carduelis chloris

Carduelis chloris

Fig. A4 *Continued.*

Certhia brachydactyla

Certhia brachydactyla

Cettia cetti

Cettia cetti

Dendrocopos major

Dendrocopos major

Fig. A4 *Continued.*

Emberiza cirlus

Emberiza cirlus

Emberiza citrinella

Emberiza citrinella

Emberiza schoeniclus

Emberiza schoeniclus

Fig. A4 *Continued.*

Erithacus rubecula

Fringilla coelebs

Hippolais polyglotta

Fig. A4 *Continued.*

Luscinia megarhynchos

Luscinia svecica

Parus caeruleus

Parus cristatus

Fig. A4 *Continued*.

Parus major

Parus montanus

Passer domesticus

Fig. A4 *Continued.*

Fig. A4 *Continued.*

Fig. A4 *Continued.*

Fig. A4 *Continued.*

Sylvia curruca

Troglodytes troglodytes

Turdus merula

Turdus philomelos

Fig. A4 *Continued.*

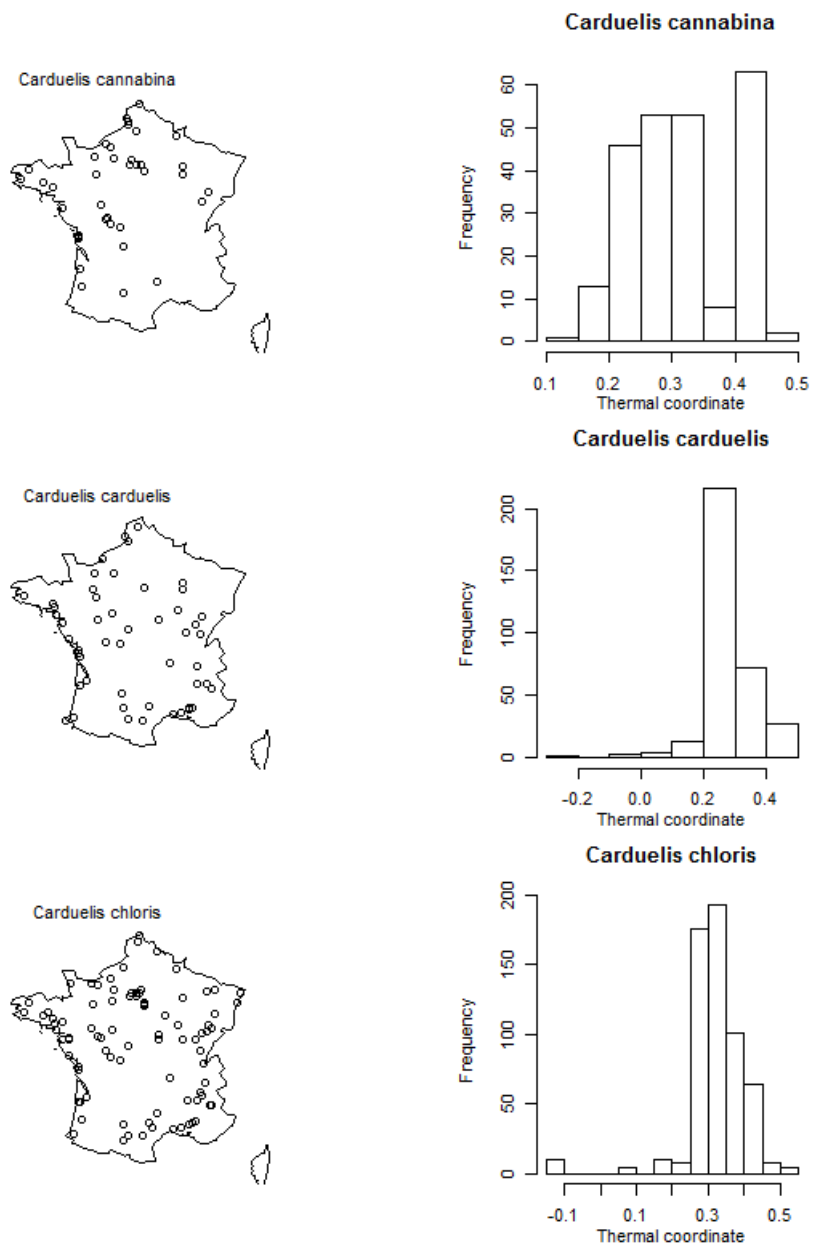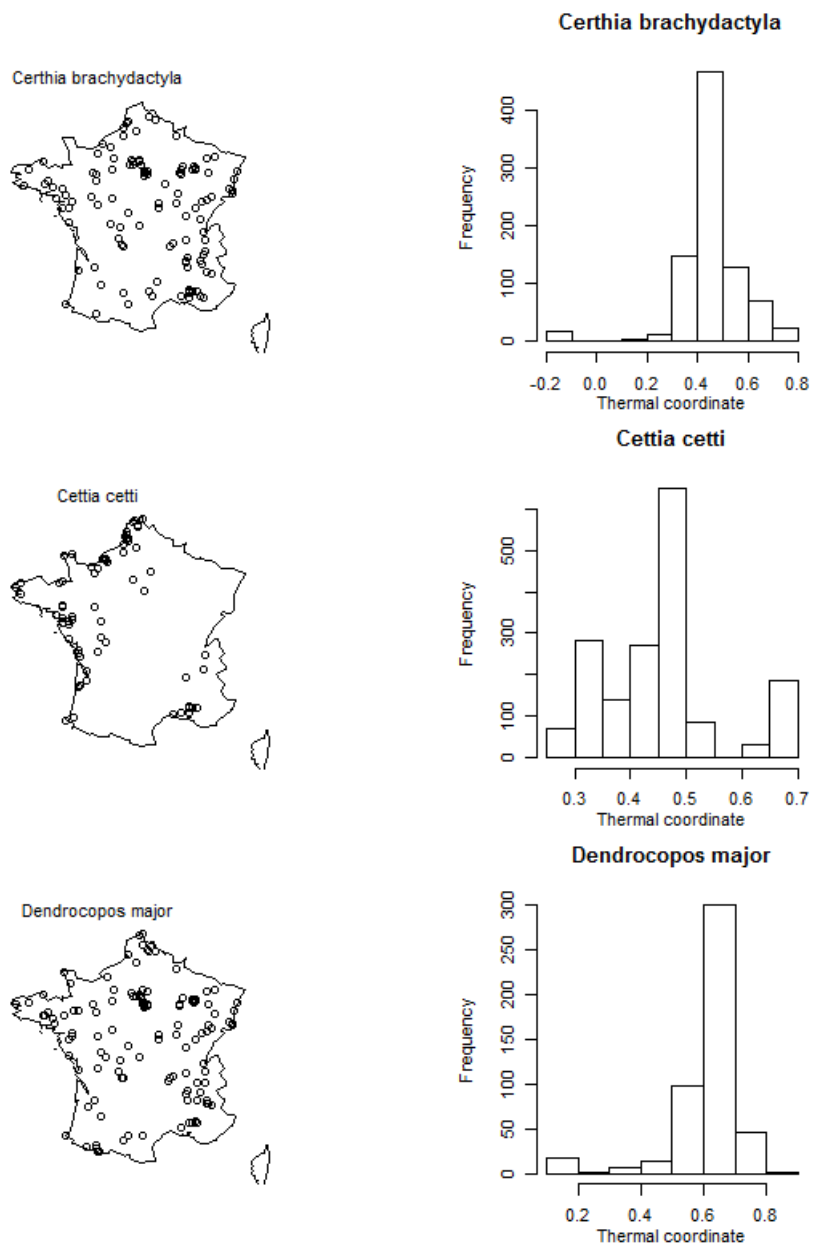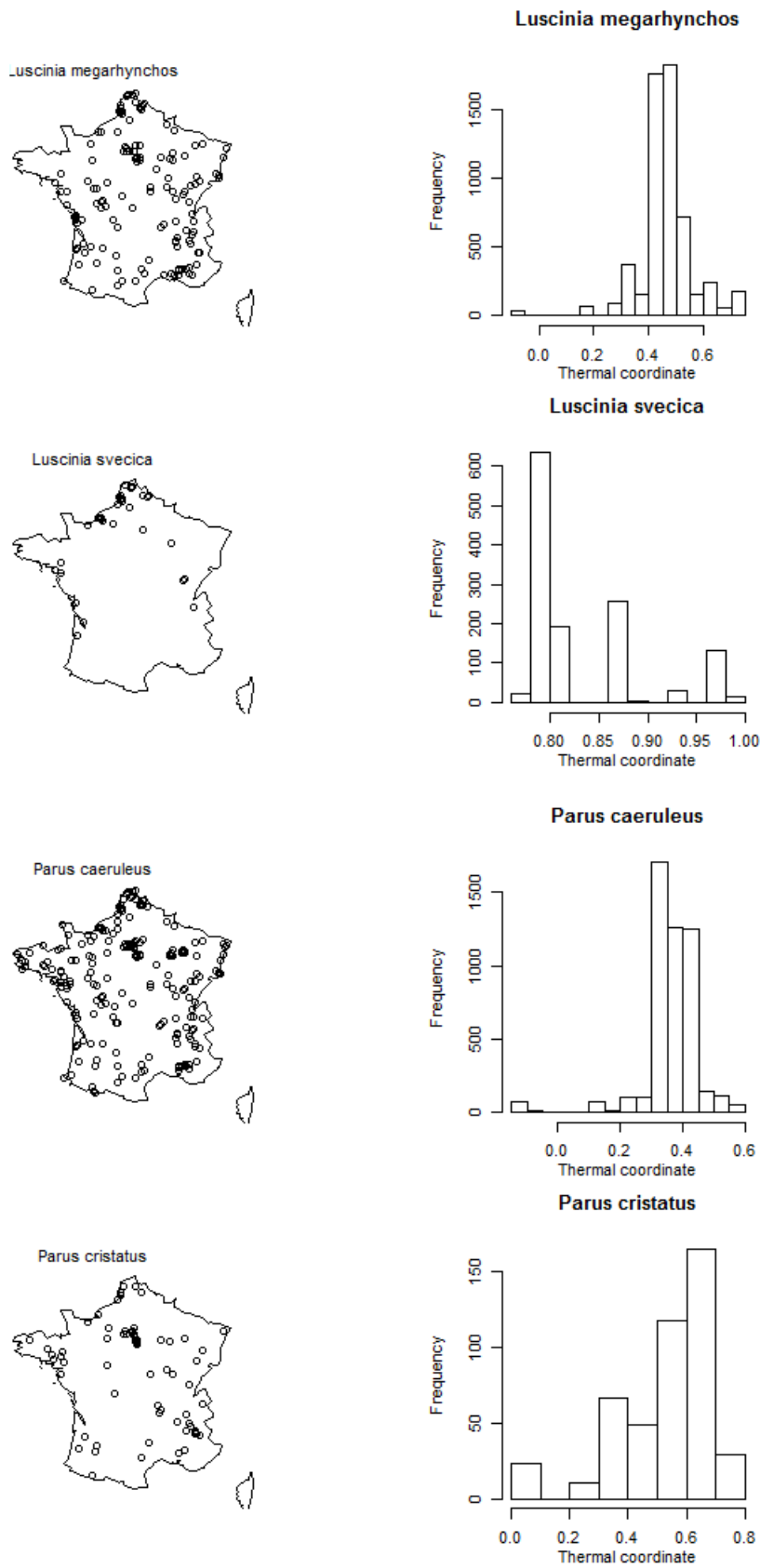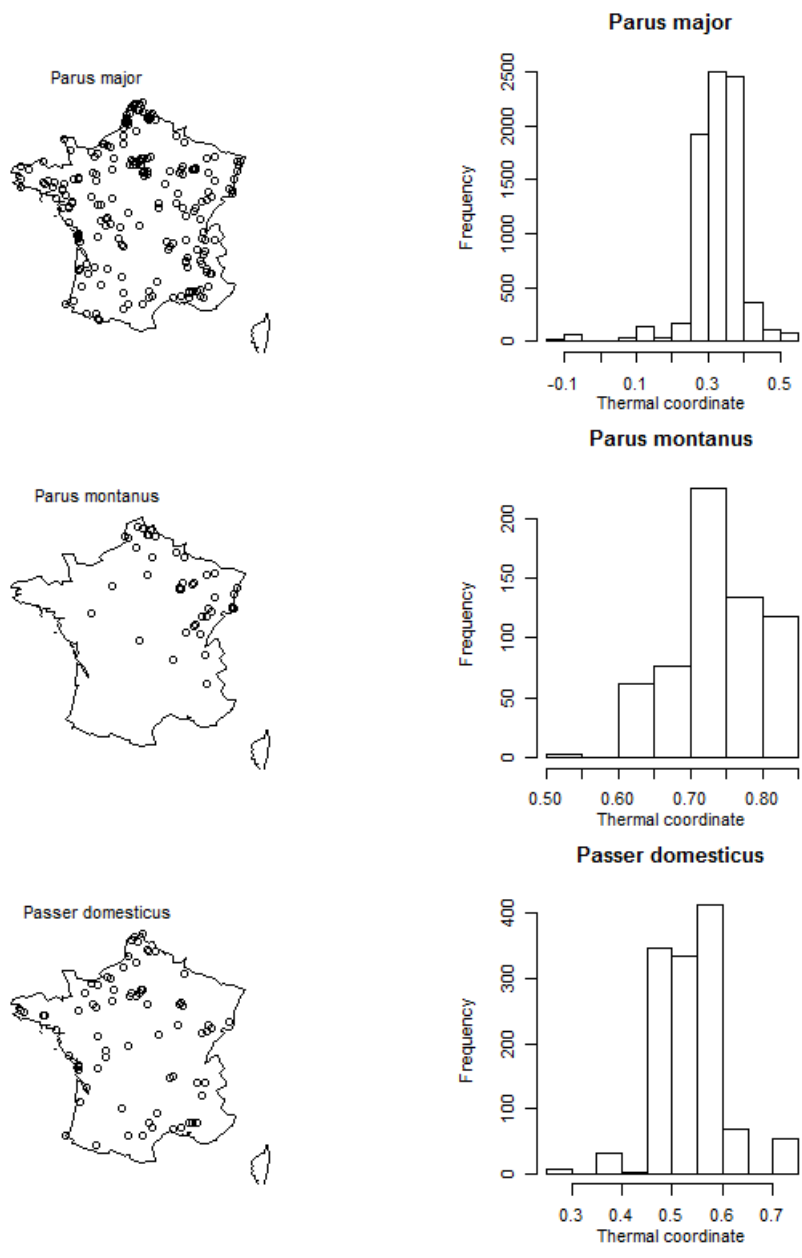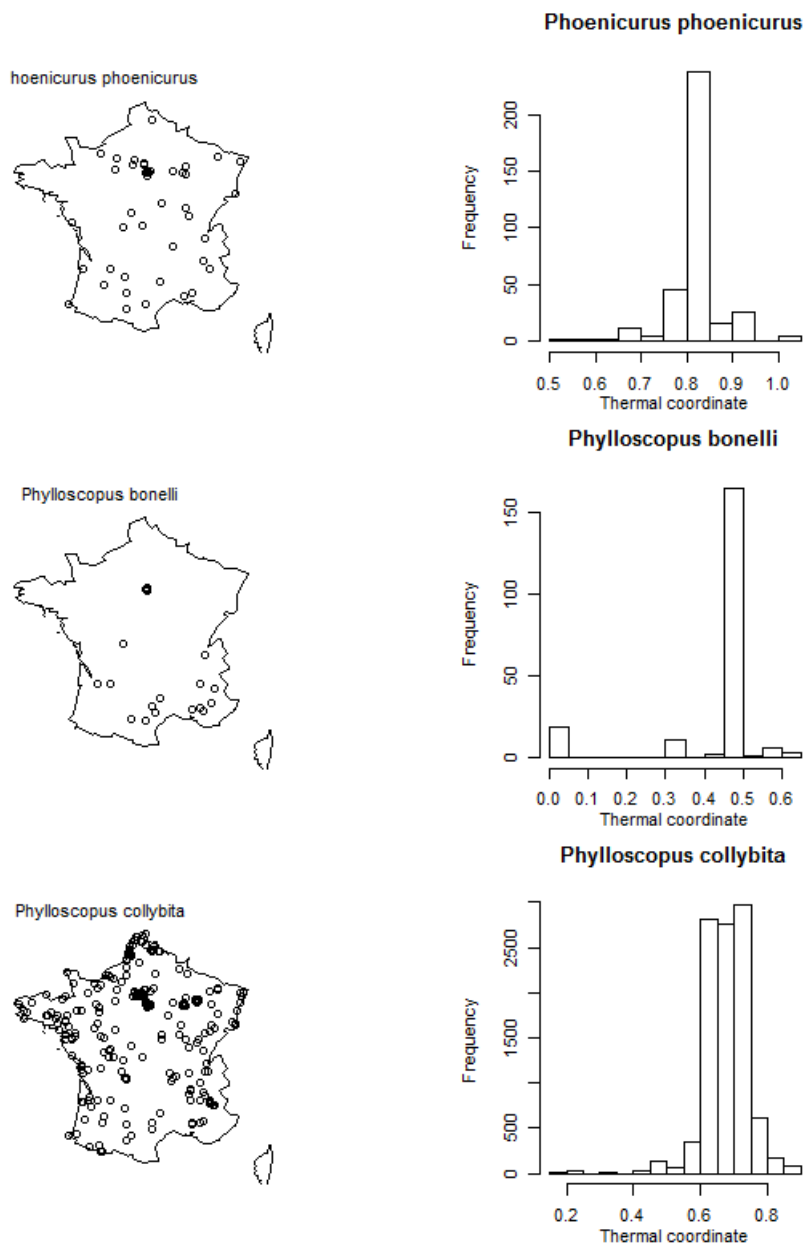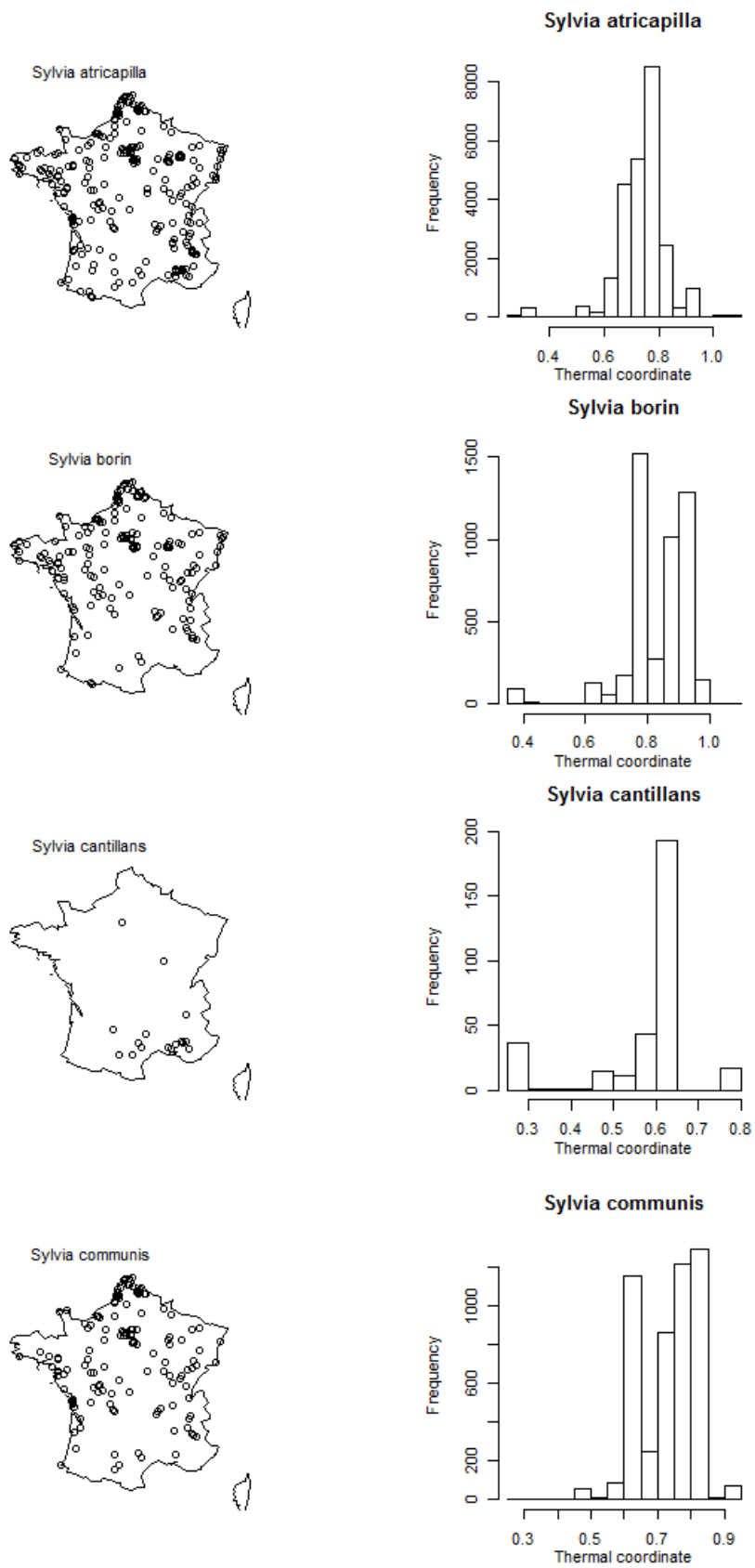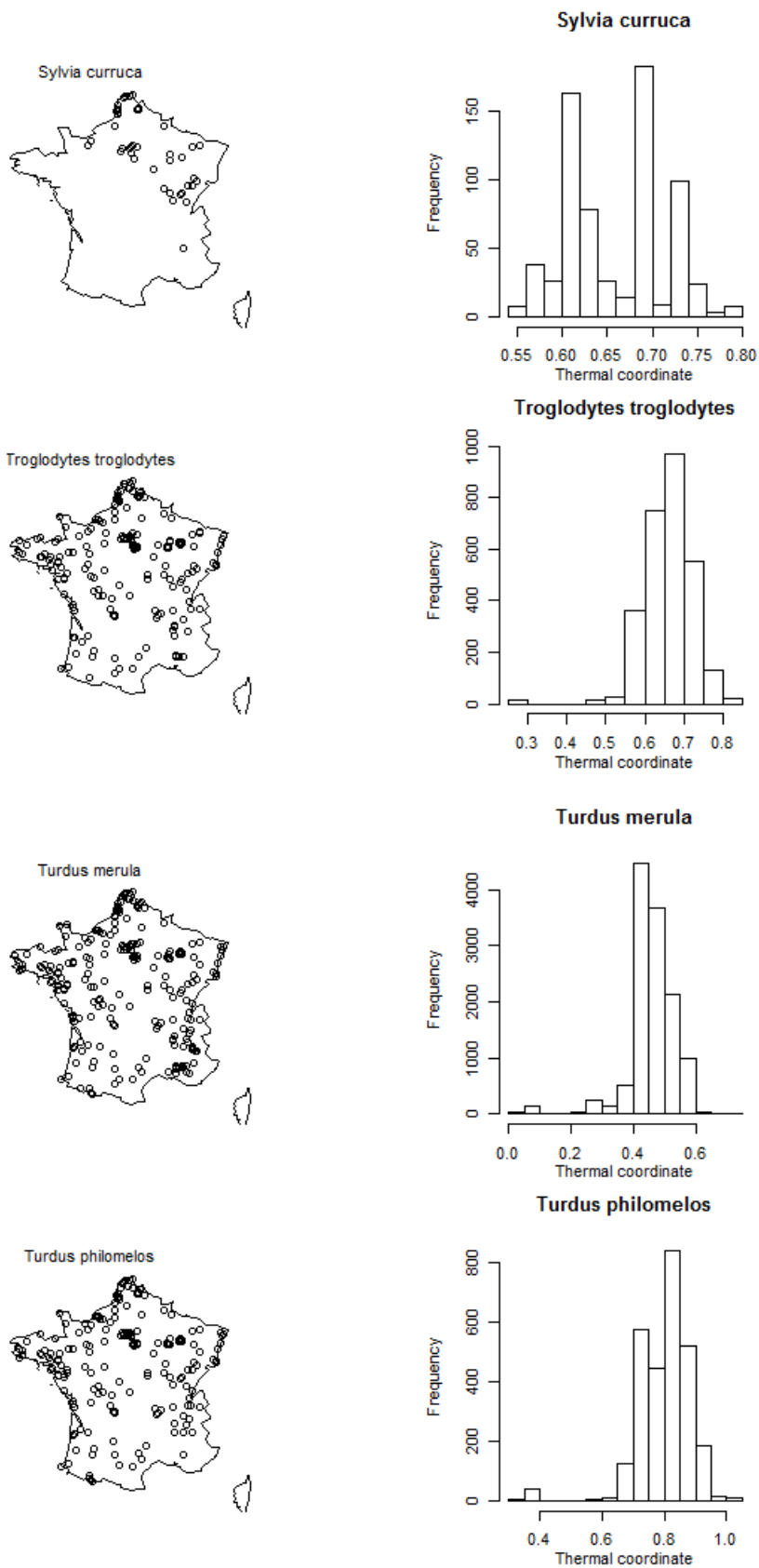**Appendix A6** Model equations for quantifying interannual variance in body size and condition, and assessing their relationship with environmental anomalies.

The model used to describe interannual variations in body size can be described by the following equations:

Juveniles:

Wing length = α_i + $\beta_{\text{Date},i}$. log(Date) + b_{obs} + b_{site} + b_{year} + $b_{\text{year},i}$ + $b_{\text{year:site}}$ + $b_{\text{year:site } i}$ + ε, (equation f_{WL})

Body mass = α_i + $\beta_{\text{log(Time)},i}$. log(Time) + b_{obs} + b_{site} + b_{year} + $b_{\text{year},i}$ + $b_{\text{year:site}}$ + $b_{\text{year:site } i}$ + ε, (equation f_{BM})

Adults:

Wing length = α_i + β_i . Sex + $\beta_{\text{Date},i}$. Date + b_{obs} + b_{site} + b_{year} + $b_{\text{year},i}$ + $b_{\text{year:site}}$ + $b_{\text{year:site } i}$ + ε, (equation $f_{\text{WL.ad}}$)

Body mass = α_i + β_i . Sex + $\beta_{\text{log(Time)},i}$. log(Time) + b_{obs} + b_{site} + b_{year} + $b_{\text{year},i}$ + $b_{\text{year:site}}$ + $b_{\text{year:site } i}$ + ε, (equation $f_{\text{MA.ad}}$)

where α_i is the average value for species i, $\beta_{\text{Date},i}$ is the slope for the effect of Date for species i, β_i . Sex is the species-specific sexual difference in size, $\beta_{\text{log(Time)},i}$ is the slope for the effect of the log-transformed time of the day for species i, b_{obs}, b_{site}, b_{year}, $b_{\text{year},i}$, $b_{\text{year:site}}$ and $b_{\text{year:site } i}$ hold respectively for the random terms for observer identity, site, year, species-specific interannual variations, site-specific interannual variations, species- and site-specific interannual variations and ε is the unexplained (residual) variation. We assessed the synchrony in temporal body constitution variations between species using the intra-class correlation (Grosbois et al., 2009) as the respective proportion of temporal variation in body size that was common (additive) to all species (i.e., b_{year}) versus species-specific temporal variations ($b_{\text{year},i}$).

Full models, used to characterise the relationship between body constitution and environmental variables, included the following terms:

Wing length or Body mass = $f_{\text{WL or BM or WL.ad}}$ + $\beta_1.T_{j,k}$ + $\beta_{2,i}$.$T_{j,k}$ + $\beta_3.T_{j,k}{}^2$ + $\beta_{4,i}$.$T_{j,k}{}^2$

$\quad$ + $\beta_5.P_{j,k}$ + $\beta_{6,i}$.$_{j,k}$ + $\beta_7.P_{j,k}{}^2$ + $\beta_{8,i}$ $P_{j,k}{}^2$

$\quad$ + $\beta_9.\text{NDVI}_{j,k}$ + $\beta_{10,i}$ $\text{NDVI}_{j,k}$ + $\beta_{11}.\text{NDVI}_{j,k}{}^2$ + $\beta_{12,i}$ $\text{NDVI}_{j,k}{}^2$

$\quad$ + $\beta_{13}.T_{j,k} \times P_{j,k}$ + $\beta_{14,i}$ $P_{j,k} \times T_{j,k}$

where β_1, β_5 and β_9 are the respective slopes for the additive effects of $T_{j,k}$ (temperature), $P_{j,k}$ (precipitation) and $\text{NDVI}_{j,k}$ anomalies in year j at site k, β_3, β_7 and β_{11} are the respective slopes for their quadratic effects, $\beta_{2,i}$, $\beta_{4,i}$, $\beta_{6,i}$, $\beta_{8,i}$, $\beta_{10,i}$, $\beta_{12,I}$ and $\beta_{14,i}$ are the slopes for the species-specific effects of $T_{j,k}$, $P_{j,k}$, $\text{NDVI}_{j,k}$ and their quadratic effects, β_{13} is the slope for the effect of the interaction between $T_{j,k}$ and $P_{j,k}$ across all species, and $\beta_{14,i}$ is the slope for the species-specific effect of the interaction between $T_{j,k}$ and $P_{j,k}$.

When the selected variables did not include a species interaction term, ICCs of the selected variables were estimated from the ratio between b_{year} of initial models and b_{year} of the best models.

Appendix A7 Analysis of adult wing length

Once or twice a year, bird species undergo a moult of their flight feathers during a short period. This period can occur at the end of the breeding period before migration or after migration. Average adult wing length in a population can be related to the quality of feather growth during the period of moult, and to size-dependent mortality. Hence, we used environmental variables that were recorded during species-specific moult and breeding periods (see Table A1 for species-specific periods). Breeding periods were chosen as they correspond to the between-moult period when individual location is certain (while most birds migrate or change their location during winter), and feathers are not in growth, enabling us to control for feather abrasion with linear effects (Appendix A4). We defined species breeding periods as the linear interval between two plateaus observed in wing length (the first peak corresponding to the prenuptial period; the second corresponding newly grown feathers, indicating the end of the postnuptial moulting period; see examples in Fig. A3). This was based on GAMMS (one GAMM per species), with a spline function applied to the date of the year, sex as fixed effect, and observer, year, and site as random effects.

We tested for the effect of environmental anomalies on adult body size and condition during the moult and between-moult periods. We matched all variables to each species-specific breeding and moult periods. Models included mean temperature, total precipitation, the interaction between mean temperature and total precipitation, and mean NDVI (see Appendix A5).

To consider potential lags between changes in environmental conditions and the response of body size, we tested for the response of adult wing length to environmental anomalies in the year preceding the year of hatching.

See results in Appendix A7.
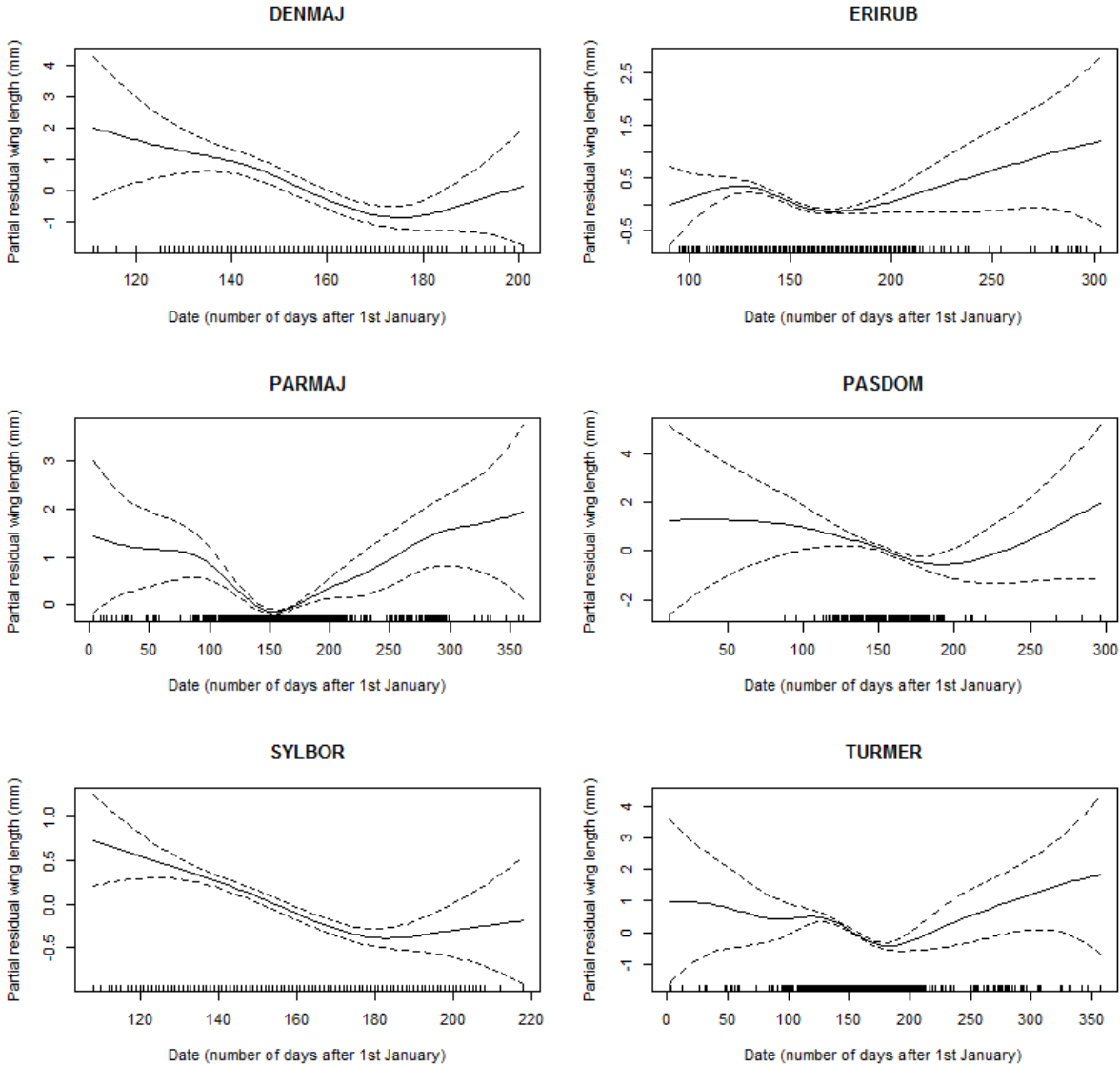

Fig. A5 Examples of within-year variations in wing length for six species (i.e., *Dendrocopos major*, *Erithacus rubecula*, *Parus major*, *Passer domesticus*, *Sylvia borin* and *Turdus merula*). Predicted curves were obtained with GAMMs.

Appendix A8 Detailed results in model selection and parameter estimates in wing length and body condition index.

Table A3 Detailed averaged coefficients of the factors influencing juvenile wing length. Estimates (β ± standard error, SE) and z values show species-specific averaged parameters of a best model set (95% of AIC weights) weighted by Akaike weight.

Variable	β	SE	z	p	
Temperature anomaly	1.900e-02	2.460e-02	0.675	0.519	
Temperature anomaly²	1.312e-03	1.312e-02	0.100	0.920324	
NDVI anomaly	4.481e-02	1.754e-02	2.534	0.006	**
NDVI anomaly²	6.198e-02	9.536e-03	6.985	3.26e-12	***
Precipitation anomaly	-2.378e-02	1.846e-02	-1.288	0.197927	
Temperature anomaly : Precipitation anomaly	3.176e-02	1.484e-02	.140	0.767	
Acrocephalus schoenobaenus	6.812e+01	7.034e+00	9.685	< 2e-16	***
Acrocephalus scirpaceus	5.678e+01	1.971e+00	28.811	< 2e-16	***
Aegithalos caudatus	6.882e+01	1.672e+00	41.168	< 2e-16	***
Alcedo atthis	5.761e+01	2.949e-01	195.321	< 2e-16	***
Anthus trivialis	7.613e+01	1.056e+00	72.060	< 2e-16	***
Carduelis cannabina	8.666e+01	4.722e+00	18.353	< 2e-16	***
Carduelis carduelis	8.337e+01	1.422e+00	58.644	< 2e-16	***
Carduelis chloris	7.273e+01	2.457e+00	29.604	< 2e-16	***
Certhia brachydactyla	8.913e+01	5.377e+00	16.577	< 2e-16	***
Cettia cetti	5.951e+01	1.413e+00	42.099	< 2e-16	***
Dendrocopos major	5.727e+01	1.742e+00	32.887	< 2e-16	***
Emberiza citrinella	1.208e+02	2.843e+00	42.495	< 2e-16	***
Emberiza schoeniclus	7.003e+01	5.819e+00	12.035	< 2e-16	***
Erithacus rubecula	7.680e+01	3.234e+00	23.747	< 2e-16	***
Fringilla coelebs	6.943e+01	1.882e+00	36.898	< 2e-16	***
Hippolais polyglotta	7.058e+01	3.011e-01	234.433	< 2e-16	***
Luscinia megarhynchos	7.940e+01	1.256e+00	63.238	< 2e-16	***
Luscinia svecica	7.368e+01	3.385e+00	21.770	< 2e-16	***
Parus caeruleus	6.872e+01	1.536e+00	44.733	< 2e-16	***
Parus cristatus	6.101e+01	1.932e+00	31.582	< 2e-16	***
Parus major	6.094e+01	4.045e-01	150.678	< 2e-16	***
Parus montanus	6.083e+01	9.752e-01	62.378	< 2e-16	***
Parus palustris	6.983e+01	2.495e-01	279.912	< 2e-16	***
Passer domesticus	5.708e+01	1.194e+00	47.799	< 2e-16	***
Phoenicurus phoenicurus	7.416e+01	9.715e-01	76.330	< 2e-16	***
Phylloscopus bonelli	6.622e+01	5.633e+00	11.756	< 2e-16	***
Phylloscopus collybita	5.216e+01	5.216e+00	9.999	< 2e-16	***
Phylloscopus trochilus	5.379e+01	4.991e-01	107.755	< 2e-16	***
Prunella modularis	5.582e+01	1.470e+00	37.985	< 2e-16	***
Pyrrhula pyrrhula	6.730e+01	4.783e-01	140.723	< 2e-16	***
Saxicola torquata	8.412e+01	2.290e+00	36.738	< 2e-16	***
Sitta europaea	6.453e+01	8.881e-01	72.664	< 2e-16	***
Sturnus vulgaris	7.931e+01	1.497e+00	52.981	< 2e-16	***
Sylvia atricapilla	1.153e+02	7.980e-01	144.479	< 2e-16	***
Sylvia borin	7.115e+01	3.818e-01	186.346	< 2e-16	***
Sylvia cantillans	7.629e+01	1.254e+00	60.857	< 2e-16	***
Sylvia communis	5.866e+01	3.537e+00	16.585	< 2e-16	***

Sylvia curruca	6.681e+01	1.207e+00	55.372	< 2e-16	***
Troglodytes troglodytes	5.299e+01	5.651e+00	9.378	< 2e-16	***
Turdus merula	4.665e+01	9.277e-01	50.284	< 2e-16	***
Turdus philomelos	1.231e+02	3.055e-01	403.035	< 2e-16	***
Log(Date):Acrocephalus schoenobaenus	1.138e+02	5.938e-01	191.589	< 2e-16	***
Log(Date):Acrocephalus scirpaceus	1.998e-01	1.763e+00	0.113	0.909740	
Log(Date):Aegithalos caudatus	1.696e+00	5.296e-01	3.203	0.001362	**
Log(Date):Alcedo atthis	-1.196e+00	4.368e-01	-2.739	0.006174	**
Log(Date):Anthus trivialis	8.759e-02	9.172e-02	0.955	0.339595	
Log(Date):Carduelis cannabina	5.325e-01	2.973e-01	1.791	0.073246	.
Log(Date):Carduelis carduelis	-5.125e-01	1.289e+00	-0.398	0.690910	
Log(Date):Carduelis chloris	7.929e-01	4.104e-01	1.932	0.053340	.
Log(Date):Certhia brachydactyla	1.447e+00	7.037e-01	2.056	0.039745	*
Log(Date):Cettia cetti	-3.672e+00	1.487e+00	-2.469	0.013540	*
Log(Date):Dendrocopos major	4.589e-01	3.946e-01	1.163	0.244946	
Log(Date):Emberiza citrinella	4.515e-01	4.762e-01	0.948	0.343075	
Log(Date):Emberiza schoeniclus	2.377e+00	7.835e-01	3.034	0.002416	**
Log(Date):Erithacus rubecula	2.593e+00	1.597e+00	1.624	0.104430	
Log(Date):Fringilla coelebs	2.433e+00	9.247e-01	2.631	0.008523	**
Log(Date):Hippolais polyglotta	1.506e+00	5.091e-01	2.958	0.003098	**
Log(Date):Luscinia megarhynchos	4.665e-01	8.383e-02	5.565	2.64e-08	***
Log(Date):Luscinia svecica	1.516e+00	3.592e-01	4.221	2.43e-05	***
Log(Date):Parus caeruleus	-2.503e+00	9.163e-01	-2.732	0.006292	**
Log(Date):Parus cristatus	3.234e+00	4.148e-01	7.798	6.44e-15	***
Log(Date):Parus major	2.739e+00	5.374e-01	5.098	3.45e-07	***
Log(Date):Parus montanus	1.081e+00	1.140e-01	9.483	< 2e-16	***
Log(Date):Parus palustris	5.472e-01	2.858e-01	1.914	0.055575	.
Log(Date):Passer domesticus	1.266e+00	6.992e-02	18.111	< 2e-16	***
Log(Date):Phoenicurus phoenicurus	5.839e-01	3.322e-01	1.758	0.078795	.
Log(Date):Phylloscopus bonelli	1.193e-01	2.864e-01	0.417	0.677038	
Log(Date):Phylloscopus collybita	2.763e+00	1.492e+00	1.851	0.064116	.
Log(Date):Phylloscopus trochilus	2.486e+00	1.417e+00	1.755	0.079317	.
Log(Date):Prunella modularis	1.066e+00	1.376e-01	7.748	9.55e-15	***
Log(Date):Pyrrhula pyrrhula	2.115e+00	4.021e-01	5.258	1.46e-07	***
Log(Date):Saxicola torquata	3.345e-01	1.374e-01	2.435	0.014880	*
Log(Date):Sitta europaea	-9.656e-01	6.324e-01	-1.527	0.126803	
Log(Date):Sturnus vulgaris	3.508e-01	2.594e-01	1.352	0.176373	
Log(Date):Sylvia atricapilla	1.676e+00	4.236e-01	3.956	7.64e-05	***
Log(Date):Sylvia borin	2.039e+00	2.489e-01	8.193	2.22e-16	***
Log(Date):Sylvia cantillans	5.368e-01	1.042e-01	5.154	2.57e-07	***
Log(Date):Sylvia communis	-7.054e-02	3.410e-01	-0.207	0.836091	
Log(Date):Sylvia curruca	-2.685e-02	1.010e+00	-0.027	0.978794	
Log(Date):Troglodytes troglodytes	1.054e+00	3.289e-01	3.203	0.001360	**
Log(Date):Turdus merula	3.073e+00	1.528e+00	2.011	0.044311	*
Log(Date):Turdus philomelos	3.426e-01	2.559e-01	1.339	0.180628	

Appendix A9 Size-dependent mortality between first-year and second-year birds: detailed methods and results

Controlling for feather abrasion between first and second year

Between their growth period and their first reproduction in the following breeding season, birds considered in this analysis do not moult. Hence, potential differences in individual wing length between first- and second-year individuals are related to feather abrasion only. Therefore, at the population level, potential differences in average wing length between first- and second-year birds would be related to (i) feather abrasion and/or (2) size-dependent mortality.

We estimated feather abrasion (Ab) as the difference between first-year and second-year wing length using repeated measures on the same individuals. Using LMM, we controlled for differences in wing length related to (i) species and (ii) the date of capture (feather growth for juveniles, feather abrasion for adults) with fixed effects, and an interaction term between species and date. Models also accounted for observer, site, and year random variations.

Controlling for sexual dimorphism

In a population, despite balanced sex ratio (Amrhein et al., 2012), adult males are more captured than adult females, as females spend more time at the nest, whereas males engage more in territorial defence. Hence, average wing length in the sample of captured second-year birds in year t+1 should be biased by the higher representation of males. We therefore accounted for sex dimorphism weighted by the proportion of captured males at t+1.

The estimation of average second-year wing length at t+1 corrected for feather abrasion, sex dimorphism and differential capture probability between sexes ($WL_{t+1corr}$) was computed with the following formula:

$$WL_{t+1corr} = WL_{t+1} + (0.5 - PC_m) * (WL_m - WL_f) - Ab$$

where WL_{t+1} is the observed species average wing length of second-year birds at year t+1, PC_m is the proportion of males in the sample of captured individuals; WL_m is the species average wing length of males; WL_f is the species average wing length of females; Ab is the estimated species-specific feather abrasion between year t and year t+1. These parameters were estimated for species/site/year that included at least 10 individual measurements (n = 138 species/site/year).

The estimation of the difference in average wing length between first-year birds at year t and second-year birds at year t+1 results in the following formula:

$$\Delta WL = WL_{t+1corr} - WL_t$$

where WL_t is average wing length of first-year birds at year t.

Table A4 Averaged model estimates for the response of ΔWL to environmental anomalies

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	2.942e-01	2.859e-01	2.879e-01	1.022	0.307
Temperature	-7.511e-02	3.053e-01	3.073e-01	0.244	0.807
NDVI	-5.989e-02	1.852e-01	1.866e-01	0.321	0.748
NDVI²	1.027e-01	1.790e-01	1.795e-01	0.572	0.567
Temperature :SPLUSMEG	-1.253e-01	4.896e-01	4.934e-01	0.254	0.800
Temperature :SPSYLATR	-5.045e-02	2.906e-01	2.933e-01	0.172	0.863
Temperature :SPTURMER	-2.972e-01	5.060e-01	5.075e-01	0.586	0.558
Precipitation	-5.586e-02	1.685e-01	1.695e-01	0.330	0.742
Precipitation : Temperature	-3.030e-02	1.055e-01	1.057e-01	0.287	0.774
NDVI :SPLUSMEG	7.848e-03	1.873e-01	1.891e-01	0.041	0.967
NDVI :SPSYLATR	5.757e-03	1.504e-01	1.519e-01	0.038	0.970
NDVI :SPTURMER	-2.495e-02	1.844e-01	1.857e-01	0.134	0.893
Precipitation :SPLUSMEG	6.337e-02	3.840e-01	3.861e-01	0.164	0.870
Precipitation :SPSYLATR	2.726e-02	1.595e-01	1.603e-01	0.170	0.865
Precipitation :SPTURMER	1.595e-02	1.406e-01	1.416e-01	0.113	0.910
Precipitation²	-5.442e-03	4.362e-02	4.385e-02	0.124	0.901
Temperature :SPLUSMEG	-6.548e-04	4.152e-02	4.194e-02	0.016	0.988
Temperature :SPSYLATR	-1.238e-03	3.748e-02	3.780e-02	0.033	0.974
Temperature :SPTURMER	1.825e-03	4.294e-02	4.325e-02	0.042	0.966
Precipitation : Temperature :SPLUSMEG	-1.286e-05	1.001e-02	1.011e-02	0.001	0.999
Precipitation : Temperature :SPSYLATR	-1.215e-05	8.308e-03	8.397e-03	0.001	0.999
Precipitation : Temperature :SPTURMER	-6.884e-05	9.650e-03	9.736e-03	0.007	0.994

Appendix A10 Preliminary analysis of the effect of extreme heat

Methods: Following the model selection method described in the main text, we re-performed the analysis while including the effect of local anomalies in the number of days with a maximum temperature > 35°C, and its interactive effect with species in the model selection process.

Results: The effect of extreme heat did not receive statistical support, as the inclusion of anomalies in the number of days > 35°C increased AICs of the best models by 4.5 and by 8.8, respectively for juveniles and adults (Table A5; A6).

Table A5. Model comparison for the relationship between environmental anomalies on juvenile wing length. We present the set of models that received the highest statistical support (i.e., models for which ΔAIC < 10).

(Intercept)	NDVI	NDVI²	Precipitation	Temperature	Temperature²	Date	N days > 35°	Species	Precipitation* Temperature	Date:Species	N days > 35°:Species	df	logLik	AIC	delta	weight
57.82	0.05064	0.06106				0.2751		+		+		90	-95245.15	190670.3	0.00	0.499
57.99	0.05170	0.06046		0.05627		0.2274		+		+		91	-95244.57	190671.1	0.84	0.327
58.47	0.05193	0.06183				0.1983	**1.719000**	+		+	+	132	-95205.39	190674.8	4.49	0.053
58.04	0.04757	0.06107	-0.0251200	0.06956		0.2224		+	0.04503	+		93	-95244.88	190675.8	5.47	0.032
58.62	0.05287	0.06132		0.05283		0.1565	**1.678000**	+		+	+	133	-95205.34	190676.7	6.38	0.021
58.02	0.04937	0.05997		0.08039	-0.0200300	0.2243		+		+		92	-95246.55	190677.1	6.80	0.017
57.90	0.05333	0.06083	-0.0183000			0.2539		+		+		91	-95247.76	190677.5	7.22	0.014
57.83	0.05138	0.06085				0.2734	**0.007628**	+		+		91	-95248.24	190678.5	8.19	0.008
58.00	0.04829	0.06019	-0.0436600	0.07138		0.2236		+	0.06637	+		94	-95245.30	190678.6	8.31	0.008
58.02	0.05275	0.06041	-0.0075620	0.05398		0.2206		+		+		92	-95247.59	190679.2	8.89	0.006
57.99	0.05218	0.06034		0.05572		0.2269	**0.004973**	+		+		92	-95247.74	190679.5	9.17	0.005

Table A6 Model comparison for the relationship between environmental anomalies on adult wing length for the breeding period. We present the set of models that received the highest statistical support (i.e., models for which ΔAIC < 10).

(Intercept)	NDVI	NDVI²	Precipitation	Temperature	Date	N days > 35°	Sex	Species	Precipitation* Temperature	Sex:Species	df	logLik	AIC	delta	weight
69.93					-0.004388		+	+	+	+	130	-144721.2	289702.4	0.00	0.581
69.90	0.0104000	0.02779			-0.004410		+	+	+	+	132	-144719.7	289703.4	0.95	0.361
69.93			0.014310		-0.004414		+	+	+	+	131	-144723.9	289709.9	7.48	0.014
69.90	0.0073370	0.02813	0.016280		-0.004435		+	+	+	+	133	-144722.2	289710.4	7.95	0.011
69.93				-0.0057120	-0.004379		+	+	+	+	131	-144724.5	289711.0	8.55	0.008
69.93					-0.004407	**-0.007237**	+	+	+	+	131	-144724.6	289711.2	8.83	0.007
69.93	0.0017710				-0.004392		+	+	+	+	131	-144724.8	289711.6	9.16	0.006
69.90	0.0101000	0.02783		-0.0063050	-0.004399		+	+	+	+	133	-144722.9	289711.9	9.46	0.005
69.90	0.0096660	0.02788			-0.004429	**-0.007975**	+	+	+	+	133	-144723.0	289712.1	9.67	0.005

Appendix A11 List of the 382 volunteer ringers for which records were used in this study.

ADRIEN SIMON, ALICE HEMERYCK, ALLAIN ANTOINE, ALLANIOUX STÉPHANIE, ALLARD RENAUD, AMANDINE L, ANDRE MATHIEU, ANDRE RÉGIS, ARCHAUX FRÉDÉRIC, ARLAUD CINDIE, AUBRY PHILIPPE, AURELIE DARDILLAC, BALLAGNY CEDRIC, BAQUART SAVINA, BARBIER LUC, BARBOIRON AURELIE, BAROTEAUX FRÉDÉRIC, BARTH FRANZ, BAUDET JEAN PIERRE, BAUDOIN CHRISTOPHE, BAUMANN MARC, BAUWIN JÉRÉMY, BEAUVAIS DOMINIQUE, BEAUVALLET YVES, BELIGNE LEA, BELLENOUE STÉPHANE, BELTRAMO MASSIMILIANO, BENOÎT GONIN OLIVIER, BESNAULT JACQUES, BIORET LAURENT, BIRARD JULIEN, BLACHE SEBASTIEN, BLAIZE CHRISTINE, JUSTINE MOUGNOT, BLANCHON YOANN, BLONDEL LUCIE DESAILLY PERNELLE CHATTON THOMAS LABIDOIRE GUY, VIRONDEAU ANTHONY DE RESSEIGUIER FRANÇOIS XAVIER TONNELIER MARIE LAURE, BOERE GERARD, BOILEAU NICOLAS, BORIE MICHEL, BOSQUET MARIE, BOULESTEIX PASCAL, BOULIGAND DELPHINE, BOULIGAND SANDRINE, BOULOGNE ANTOINE, BOUSQUET JEAN FRANÇOIS, BOUTROUILLE CHRISTIAN, BOUZENDORF EMELINE, BOUZENDORF FRANÇOIS, BRILLAND YAN, BROUTIN AURELIE, BRUCY LAURENT, BULENS PIERRE, CALLARD BENJAMIN, CALOIN FRÉDÉRIC, CANNESSON PHILIPPE, CANTERA JEAN PIERRE, CAPARROS OLIVIER, CARDONNEL SYLVAIN, CARON NICOLAS PIERRE, CARRIER LAURENT, CARRUETTE PHILIPPE, CATROUX HUBERT, CAVALIER FRANÇOIS, CAVALLIN PASCAL, CEBE NICOLAS, CECILE HIGNARD, CHABLE PATRICK, CHAMARD JOANIE, CHANCHUS BERNARD, CHARBONNIER YOHAN, CHARLOT ANDRE, CHATTON THOMAS BOTTE GUILLAUME, CHAUBY XAVIER, CHAUSSI GERARD, CHEMINEL JEAN MARIE, CHENY GILDAS, CHEVALIER MARIE, CHIL JEAN LUC, CHIRON FRANÇOIS, CLAESSENS OLIVIER, CLAVIER JEAN LOUIS, COCHARD GUILLAUME, COCHARD NICOLAS, COHEZ VINCENT, COLIN LAMBERT, COMMECY XAVIER, CORBEAU ALEXANDRE, COUILLENS BERTRAND, COULÉE THIERRY, COURANT SYLVAIN, COUZI LAURENT, DAURAT VINCENT, DAVID YVES, DE BOUET DU PORTAL PIERRE, DE FRANCESCHI CHRISTOPHE, DEBENESTE ÉTIENNE, DEBRABANT CHARLOTTE, DECET JEAN LOUIS, DECORY PATRICK, DEDRIE MAUD, DEFIVES PAULINE, DEHORTER OLIVIER, DELAMAÎRE MARIE, DELAPORTE PHILIPPE, DELECOUR VINCENT, DEMONGIN LAURENT, DENISE CYRIL, DEROLEZ BRUNO, DEROO SERGE, DESAILLY PERNELLE VAN INGEN LAURA GERBAA KARIM CHATTON THOMAS, DICHAMP MICHEL, DOMINIQUE BAUVAIS REGNIER MARIE CLAIRE, DORFIAC MATTHIEU, DOUMERET ALAIN, DUFOUR SEBASTIEN, DUFRESNE LAURENT, DUGUE HUBERT, DUHAYER JEANNE, DUMEIGE BRUNO, DUPONCHEEL CAMILLE, DUPOUX ÉTIENNE, DUPRIEZ QUENTIN, DUPUY FREDÉRIC, DUPUY JEREMY, DURIEZ OLIVIER, DURLET PIERRE, DUTHION GUILLAUME, DUTILLEUL SIMON, ELISE DELAGRÉE, ENRIQUE SANS, FAUCON LAURENT, FAURE BAPTISTE, FENART BEGHIN ÉRIC, FIQUET PIERRE, FLAMANT NICOLAS, FLITTI AMINE, FONTAINE BENOIT, FONTANILLES PHILIPPE, FOUCHER JULIEN, FOUGERE BERTRANE, FOURCADE JEAN MARC, FOURCY ÉRIC, FOURNIER JERÔME, FRANÇOIS BOUZENDORF, FRANÇOIS GABILLARD, FRANÇOIS JEANNE, FRANC EMMANUEL, FRANÇOIS HEMERY, FRANZ BARTH, FREBOURG PATRICK, FRODELLO JEAN PIERRE, GABET LUDIVINE, GABILLARD FRANÇOIS, GALLIEN FABRICE, GARCIN ROGER, GASPARD BERNARD, GAUTIER PHILIPPE, GAUTIER SEBASTIEN, GENTRIC ALAIN, GERNIGON JULIEN, GIRAUD GEST MARINE, GIRAUDOT ÉTIENNE, GIZART LUC, GOUELLO THOMAS, GOUJON GERARD, GOULEVANT CYRIL, GRABIERE GANIX, GRAFEUILLE DIDIER, GRAND BRIGITTE, GROLLEAU GERARD, GRUWIER XAVIER, GUERBAA KARIM DIDIER RÉGIS TONNELIER MARIE LAURE GIZARDIN CAMILLE SEBASTIEN, GUERBAA KARIM LAGARDE NICOLAS, GUILLO JEAN CLAUDE, GUITTON SANDRINE, GUYONNET BENJAMIN, GUYOT MATTHIEU, GYS MICHEL, HAMEAU OLIVIER, HARDY ALAIN, HAVET SAMUEL, HEMERY DAVID, HEMERY FRANÇOIS, HENRY PIERRE YVES, HENRY RÉMI, HERAULT THOMAS, HEROGUEL CLEMENT, HEROGUEL CLEMENT, HERRMANN VALENTINE, HERVE GAUCHE, HILDEBRAND CHRISTOPHE, HIRTZMANN THIERRY, HUCHIN FRANÇOIS, HUMBERT FRANÇOIS, IBANEZ FRANCK, ILIOU BERNARD, INGOUF

CLAUDE, ITTY CHRISTIAN, JERÔME PAOLI, JACOB HERVE, JACOB STAFFAN, JACOB YANNICK, JEAN BAPTISTE JAMES, JEAN PHILIPPE ORTS, JEANCLAUDE, JEANNEAU BENJAMIN, JENN HENRI, JEROME HANOL, JIGUET FREDÉRIC, JOACHIM JEAN, JOLIN CECILE, JOMAT LOIC, JOUAIRE STÉPHANE, JOUVEL MARIE, JOYEUX EMMANUEL, JUILLARD BORIS, JULLIARD ROMAIN, KERBIRIOU CHRISTIAN, KLEIN ANNE CATHERINE, KOENIG PAUL, KREDER MARINE, LABIDOIRE GUY, LACORRE BENOIT, LAGARDE MARIE, LAGARDE NICOLAS DIDIER RÉGIS CHATTON THOMAS, LAMBERT PEIO, LAMBOTTIN DAVID, LANDEAU RÉMI, LAPIOS JEAN MICHEL, LATRAUBE FRANCK, LAUBIN ALEXANDRE, LAURENSIC CHRISTOPHER, LAVAL BENOIT, LAVOGIEZ DAVID, LE BIHAN CYRILLE, LE GUILLOU GILLES, LE MAO PATRICK PANIZZA ANDREA, LE NEVE ARNAUD, LEBAS JEAN FRANÇOIS, LECHAT DAVID, LECONTE MICHEL, LEDUNOIS ROMAIN, LELONG VINCENT, LEMAITRE PIER LUIGI, LENGAGNE ROMAIN, LEPRETRE ADRIEN, LERAY GILLES, LERY JEAN PIERRE, LESCLAUX PAUL, LESLIE BOKOR, LEUCHTMANN MAXIME, LIEURY NICOLAS, LOÏS GREGOIRE, LOOSE DAVID, LORRILLIERE ROMAIN, LORTHIOIS MATTHIEU, MAGNE JEAN FRANÇOIS, MAHEU BERENGERE, MAINGUENEAU JEREMY, MANDON DALGER ISABELLE, MANIGOLD CHRISTIAN, MARIE CHEVALIER, MARION JULIE, MARTAYAN FABIEN, MARTIN LEO, MASQUELIER JULIEN, MASSEZ GREGOIRE, MASSUIR PHILIPPE, MAURICE CLAUDE, MAX RICHER, MAXIME GAUTIER, MAXIME JOUVE HERVE GAUCHE OLIVIER BARDET, MEGUIN JEAN, MELIN MARIE, MENUS OLIVIER, MERCIER FABIEN, MIGOT PIERRE, MIGUET PASCAL, MILLOT ALBERT, MOAL GAEL, MONCHAUX GEOFFREY, MONNIER GILDAS, MOREAU GASTON, MORGAN JOHN, MORTREUX STÉPHANE, MOULIN NICOLAS, MOUSSEAU AYMÉRIC, MOUSSUS JEAN PIERRE, MOYON CLAUDE, MUSSEAU RAPHAEL, MW/JJ, NABAIS SYLVIE, NADE PHILIPPE, NARCISSE GIANI, NEBOUT THIBAUT, NEWTON ANDREW, NICOLAU GUILLAUMET PIERRE, NORE THERESE, OLLIVIER PHILIPPE, PALLIER GILBERT, PAQUIN FREDERIQUE, PARMENTIER EMMANUEL, PAUCOT CHRISTIAN, PELE JEAN, PERIGNON LAURENT, PERROI PIERRE YVES, PICHARD ADELINE, PIEL PIERRICK, PIERRE THELLIER, PIGEON JOEL, PINCON SYLVAIN, PIOTTE PIERRE, PITOIS JOHANN, PLAT ROMUALD, PONCET SOPHIE, POURREAU JO, PREVOST MICHEL, PRINTEMPS THIERRY, PROVOST PASCAL, PROVOST ROMAIN, RÉMI HANOTEL, RAITIERE WILLY, RANVIER GERAUD, RÉEBER SEBASTIEN, REGNIER MARIE CLAIRE, REMOND ÉLODIE, ÉLODIERINGART CATHERINE, ROBBE ÉRIC, ROBIN JEAN GUY, ROGER THIERRY, ROLLAND SIMON, ROMAIN LENGAGNE, RONDEL STÉPHANIE, ROUSSEAU PIERRE, SALMON FRANCK, SARRAZIN CHRISTELLE, SAUVAGE ALAIN, SAVIN FRANÇOIS, SCAAR BERTRAND, SCHWARTZ TIMOTHÉE, SECHET EMMANUEL, SELIQUER PIERRE, SENECAL DIDIER, SIBILLE JEAN LUC, SIBLER FRANÇOIS, SOURDRILLE KÉVIN, STEIMER FRANÇOIS, STURM BRUNO, SYLVAIN VINCENT, TARDIVO GERARD, TERNOIS VINCENT, TEULIERE JEAN MICHEL, TEURQUETY FABRICE, THEILLOUT AMANDINE, THOUY PEIRE, TILLO STÉPHAN, TINE, TINE RÉMI, TOULOTTE FABIEN, TOUZE HUGO, TRON FRANÇOIS, URBINA PATRICE, URIOT SYLVAIN, VAN ACKER BERNARD, VAN HECKE BENOIT, VEILLE FRANTZ, VENTROUX JULIEN, VIALLET MELCHIOR, VIGOUR DAVID, VIRGINIE CULICCHI, VRIGNAUD NICOLAS, WILLIAMSON THOMAS, WROBEL SOPHIE, YVES DAVID, YVES DUBOIS, ZEDDAM PASCAL, ZUCCA MAXIME, ZUCCHET OLIVIER

References

Amrhein, V., Scaar, B., Baumann, M., Minéry, N., Binnert, J.-P. & Korner-Nievergelt, F. (2012). Estimating adult sex ratios from bird mist netting data. Methods Ecol. Evol., 3, 713–720

Grosbois V, Harris MP, Anker-Nilssen T, McCleery RH, Shaw DN, Morgan BJT, Gimenez O (2009) Modeling survival at multi-population scales using mark-recapture data. *Ecology*, **90**, 2922–32.

Hadfield, JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1-22.

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

Jiguet F, Julliard R, Thomas CD, Dehorter O, Newson SE, Couvet D (2006) Thermal range predicts bird population resilience to extreme high temperatures. *Ecology letters*, **9**, 1321–1330.

Nakagawa, S. & Schielzeth, H. (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biological reviews of the Cambridge Philosophical Society, **85**, 935–56.