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Increasing winter temperatures explain body size decrease in wintering bird populations of Northern Europe—But response patterns vary along the spatioclimatic gradient

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Abstract

Aim: Recent evidence has shown changes in body size and shape of individuals, which are suggested to be a result of global warming caused by climate change. Here, we explored the spatiotemporal changes in wing length and body mass of 24 wintering bird species in Northern Europe and how these relate to temperature anomaly.

Location: Finland and Sweden, Europe.

Time Period: 50 years, 1970 to 2020.

Major Taxa Studied: Birds, 24 species.

Methods: We used site-specific, long-term winter ringing data containing wing length and body mass measurements from across Sweden and Finland for 24 bird species. We modelled wing length and body mass change over time, in relation to the spatioclimatic gradient and as response to temperature anomalies (of [i] the same winter as the ringing took place, [ii] the previous winter and [iii] the previous spring) by accounting for phylogenetic relatedness between species and their species-specific responses to each predictor of interest.

Results: We show that across all species, body size has decreased since the 1970s, with a negative relationship between wing length and temperature anomalies of previous winters, suggesting carry-over effects likely linked to body size-related survival or dispersal. Body mass was negatively related to the temperature anomaly of the same winter, indicating more immediate effects related to reduced fat reserves during mild winters.

Main Conclusions: Our results highlight a climate-driven decrease in body size across several species and its association with positive anomalies in winter temperature in the high latitudes. However, the responses are not spatially uniform and there is considerable species-specific variation, emphasizing the importance of conducting multi-species studies when investigating responses to climate change. The mechanisms of decreasing wing length and body mass seem to differ and underline the immediate and carry-over effects of temperature warming during the nonbreeding season.

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KEYWORDS

birds, body mass, climate change, Fennoscandia, morphological changes, wing length

1 | INTRODUCTION

A continuously growing body of research is showing past, present and predicted future responses of species to anthropogenic climate change (Bellard et al., 2012; Chen et al., 2011; Thomas & Williamson, 2012), where most studies have been focussing on shifts in species distributions (Devictor et al., 2008; Lehikoinen & Virkkala, 2016; Platts et al., 2019) and phenology (Hällfors et al., 2020; Saino et al., 2011; Socolar et al., 2017). In addition to these spatiotemporal changes in species abundances, climate change may also affect the morphology of species, including colour, shape and overall body size (Ryding et al., 2021). Evidence from the last decades shows that many species are becoming smaller in body size globally (e.g. Gardner et al., 2011; Husby et al., 2011; McLean et al., 2022; Shipley et al., 2022; Weeks et al., 2020; Yom-Tov et al., 2006), which has been suggested to be a response to increasing temperatures (Baldwin et al., 2022; Dubiner & Meiri, 2022; Gardner et al., 2011; McLean et al., 2022; Romano et al., 2021; Weeks et al., 2020). One hypothesis supporting this evidence is Bergmann's rule, which proposes an association of warmer climate with smaller body size in endotherms, given a more beneficial surface-to-volume ratio (Bergmann, 1847; Gardner et al., 2009; Romano et al., 2021; Torres-Romero et al., 2016). Despite this overall trend in body size reduction, inter- and intraspecific variation in body size change over time is often considerably high and has been suggested to be mostly explained by nontemperature drivers in a recent study (McLean et al., 2022).

A variety of different traits are used as proxy for body size, including body mass (e.g. Furness & Robinson, 2019; Weeks et al., 2020), wing length (e.g. Remacha et al., 2020; Salewski et al., 2010), tarsus length (e.g. Weeks et al., 2020), head and body length (Dubiner & Meiri, 2022) or a combination of several traits (e.g. Weeks et al., 2020). For instance, a recent study on migratory birds showed that avian body mass has declined over the last four decades, while in contrast, wing length has increased (Weeks et al., 2020). This suggests that species may compensate for body size reduction with increased wing lengths to maintain—or in fact—improve efficient flight morphology enabling long-distance migration (Arizaga et al., 2006; Rayner, 1990). The decrease in body mass may also be linked to a decreased need for fat reserves during cold periods (i.e. winter) and not necessarily directly to body size of species as such (Furness & Robinson, 2019). Because of these varying responses, and complex interaction patterns with other factors than climate change alone (McLean et al., 2022), it is important to consider multiple morphological measures from species during both the breeding and nonbreeding season, to better understand the observed changes. In addition, precise site-specific data, more nuanced individual characteristics

such as age and sex, and long-term measurement data can aid practitioners in uncovering novel spatial and temporal changes in body size.

Especially at higher latitudes, winter temperatures have been increasing faster than spring temperatures (Masson Delmotte et al., 2018), and accordingly, species' abundance responses to changing climatic conditions have been much faster during the winter season than during the summer season (Lehikoinen et al., 2021). Furthermore, species overwintering in the same or similar area as they breed are not experiencing such strong pressure on optimal migratory flight morphology, due to shorter, fewer or lacking migration pathways, and might thus show fewer complex responses to climate change with regards to different morphometric changes. Thus, wing length change responses to climate warming in overwintering birds are likely species-specific and less influenced by species migration ecology (Weeks et al., 2020). Overall, the morphological changes of species have rarely been studied during the nonbreeding season (but see, e.g. Furness & Robinson, 2019; Gardner et al., 2018), although weather-dependent winter survival could be one of the mechanisms underlying the rapid changes in morphology of overwintering species during global warming. For instance, while strong selection may earlier have favoured larger body size, for increasing survival during the coldest periods, this pressure may have been gradually released over time. This could lead to a decrease in overall body size of the population due to improved survival of smaller sized individuals—although opposite patterns have been observed for two Australian bird species showing decreasing body size in relation to colder temperature (Gardner et al., 2018).

Given the existing evidence of decreasing body size in breeding birds as response to temperature warming, we here aimed to understand body size change in overwintering birds in relation to latitudinal gradient, increasing temperatures and age. We used a bird ringing and recovery data set spanning over 50 years, from across Sweden and Finland (Northern Europe), and tested whether the wing lengths and body mass of 24 overwintering bird species have decreased over time and whether those changes are driven by anomalies in annual spring or winter temperatures. We hypothesize that (i) birds are larger at higher (colder) than lower (warmer) latitudes within our study area following Bergmann's rule; (ii) overall species' body size (wing length and body mass) has become smaller during the past half-century but will show species-specific patterns; and (iii) body size declined with atypically warmer temperatures, where we predict winter temperatures to be more influential than spring temperatures (Figure 1; Table S3 in Supplementary Material). Additionally, we expect spatioclimatic patterns in body size trends over time and responses to annual temperature anomalies. We also expect temperature responses in body size to differ between age groups, because we hypothesize

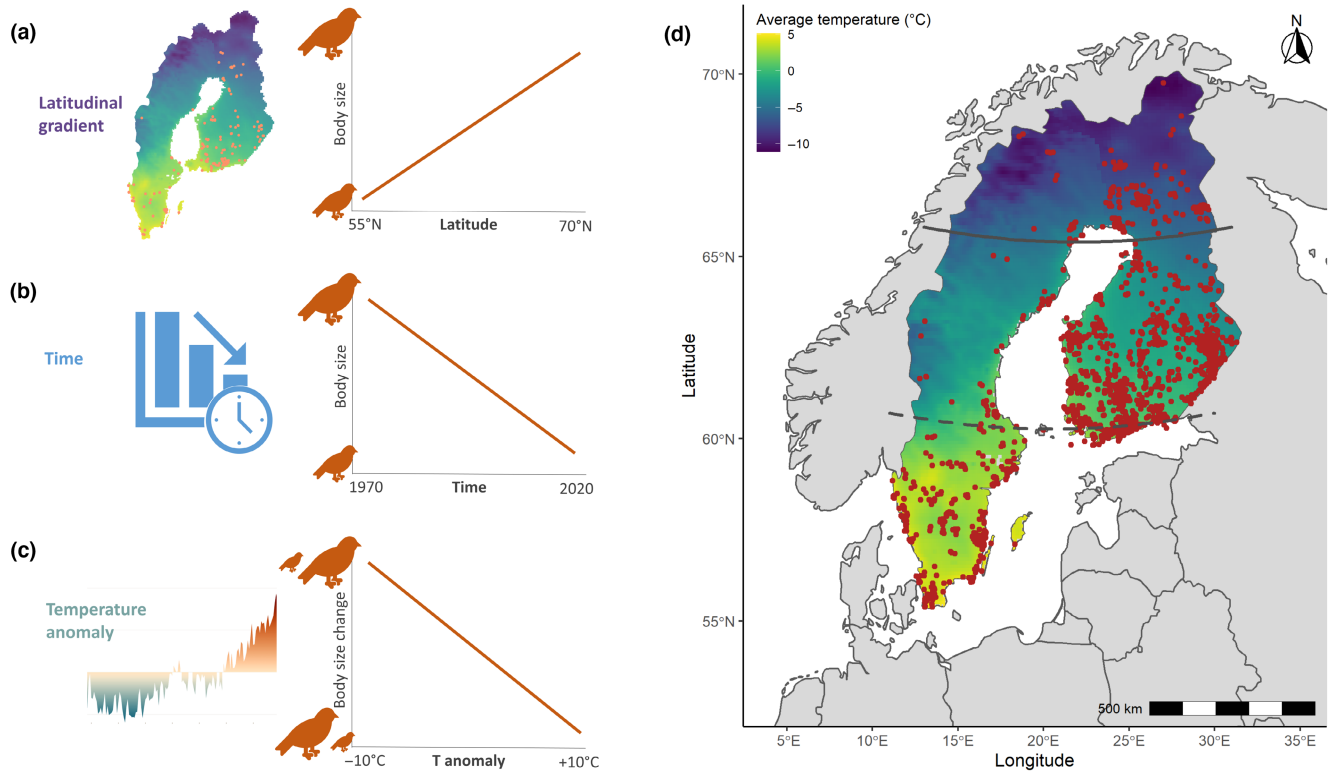


FIGURE 1 Schematic illustration of our three main hypotheses with the expected relationships with body size. Panel (a) shows the latitudinal gradient in the average winter temperature (map) as a proxy for the spatioclimatic gradient along the latitude and the expected positive relationship with body size (i.e. following Bergmann's rule). Panel (b) illustrates the decrease in body size over time and (c) the expected relationship with temperature (T) anomaly, so that with positive anomalies (warmer temperatures than usual), birds have become smaller. Panel (d) shows the gridded average winter temperatures in °C (10km resolution) over the entire study period for Sweden and Finland based on monthly mean temperatures for December, January and February. Neighbouring countries are depicted in grey. Red points show the ringing locations for all 24 species over the entire sampling period of 50 years. The dashed grey line divides the hemiboreal from the southern and middle boreal zone and the solid line the southern and middle boreal from the northern boreal zone (simplified representation of bioclimatic zones in Fennoscandia). Note that average spring temperatures (April–June) were analysed as well but not illustrated here.

that inexperienced 1st winter birds are more sensitive to climatic changes than more experienced adults (e.g. Dybala et al., 2013). Our study findings highlight spatioclimatic patterns in the climate-driven decrease of body size across several species and its association with positive anomalies in winter temperature in the high latitudes.

2 | MATERIALS AND METHODS

2.1 | Morphological data

Since the 1970s, volunteer bird ringers have captured and ringed overwintering birds in Finland and Sweden, usually at feeding stations. The ringers have measured the wing length (in mm) using the maximum chord method (Svensson, 1992, 100% data coverage) and body mass in grams using a mechanical or digital scale (77% data coverage). Since tarsus length measures were not or only very rarely taken ($N=65$ measurements in Finland for winter), we did not include this metric in this study, although it is known to be

a valuable metric for body size in birds (e.g. Rising & Somers, 1989; Senar & Pascual, 1997). Other relevant noted data are the ring ID number, identified age (1st winter, hereafter young; older than 1st winter, hereafter adult; or unknown), sex (male, female or unknown), date and time, precise coordinates of the ringing location, ringer name and ID. We filtered the data sets to include measurements from the months December, January and February, that is to include true overwintering individuals only. We selected 24 bird species (see full species list in Supplementary Material Table S4), representing the most common winter birds for both countries, spanning 11 families and 20 genera based on the following criteria: we included all common wintering land birds between the size of jay (*Garrulus glandarius*) and goldcrest (*Regulus regulus*), which are trapped regularly in North Europe with mist nets and which have had more than 200 birds trapped in total. Some species, Bohemian waxwing (*Bombycilla garrulus*) or pine grosbeak (*Pinicola enucleator*), were removed from the analyses, because the trapping intensity has been much higher during the past 20 years due to new trapping methods. For the nuthatch (*Sitta europaea*) and marsh tit (*Poecile palustris*), we had data from Sweden only ($N=925$ and

$N=2554$ observations, respectively), while for the willow tit (*Parus montanus*) we had data from Finland only ($N=11,165$).

We scanned and cleaned the 173,039 (Finland; Finnish Museum of Natural History, 2022) and 140,052 (Sweden; data available upon request from Swedish Museum of Natural History) observations for erroneous measurement outliers, so that wing length and body mass measurements were excluded if they were outside of three standard deviations from the mean and based on visual inspection of the raw data. Since some bird individuals were caught and measured multiple times by the same ringer during the same winter, we calculated average wing lengths and body mass per ring ID, ringer and winter. From this data set, we selected only unique values per ring ID, ringer, and winter, resulting in 290,412 ($N_{\text{Finland}}: 154,110$ and $N_{\text{Sweden}}: 136,302$) observations in the final data sets. For multiple observations per ring ID (i.e. recaptures), we selected the first observation made in the data set while dropping subsequent observations ($N_{\text{Recaptures}}=8669$). We further limited the body mass data to the main ringing hours between 7 AM and 5 PM (resulting in 214,890 observations; $N_{\text{Finland}}: 115,848$ and $N_{\text{Sweden}}: 99,042$) and added ringing hour as a continuous fixed effect to all body mass models since daytime is known to influence daily mass variation, especially so during winter (e.g. Lehikoinen, 1987).

2.2 | Climatic data

To test the hypotheses on the spatioclimatic and climate warming effects on changes in wing length and body mass, we generated site-specific data on winter temperatures matching the study period of the ringing data. Temperature is just one climatic aspect among others used as a proxy for climate change but has repeatedly been shown to be the most influential factor driving species responses to changing climatic conditions in the high latitudes (Tayleur et al., 2015), also specifically regarding body size anomalies (Furness & Robinson, 2019; Weeks et al., 2020). We extracted gridded monthly average winter temperature data from December, January, and February 1970–2020 and spring temperature from April, May and June 1970–2020 from the Finnish Meteorological Institute available at 10km spatial resolution for Finland and from Copernicus at ~10km resolution (0.1°) for Sweden. We computed two temperature variables representing (1) the spatioclimatic gradient of the ringing locations across the two countries and (2) the site- and year-specific climate fluctuation during the 50-year data series. For (1), we calculated average winter temperature per ringing site over the entire study period, where one winter equals the monthly mean temperatures from December, January and February (Figure 1d). For (2), we calculated three versions of temperature anomalies as a function of average temperature per site (i) of the same winter, (ii) of the previous winter and (iii) of the previous spring, minus the average temperature of the entire study period:

$$\text{temperature anomaly} = (\text{Temperature}_{\text{year } t \text{ or year } t-1} - \text{Temperature}_{\text{mean}}) \quad (1)$$

Including temperature anomaly from the previous winter or previous spring would account for carry-over effects on wing length and body mass anomaly with a time lag of 1 year, while same winter temperature anomalies account for synchrony in body size and temperature anomaly without a lag effect. For the spring temperature, we used the temperature anomaly calculated as described above, from the previous year (i.e. the year corresponding to the December morphology data but year $t-1$ for the January and February morphology data).

2.3 | Statistical analyses

We ran two different sets of models for each response variable, that is wing length and body mass (hereafter body size variables), to address our research questions. The two body size variables were transformed to a measure of change relative to the 24 species' average sizes. Percentages of change in body size variables were calculated as follows:

$$\text{body size}_{\text{change}} = \frac{(\text{body size}_{\text{year } t} - \text{body size}_{\text{mean}})}{\text{body size}_{\text{mean}}} * 100 \quad (2)$$

While these perceptual changes allow straightforward comparison of changes in species of different sizes, also the assumptions of normally distributed residuals were met, allowing us to fit linear mixed models with a Gaussian error distribution. We included sex and age as fixed effects in all models, to control for possible differential responses of body size change among groups. First, to test whether body size of species decreased over time and followed a spatioclimatic pattern in their body size, we ran a simple additive model, including the predictors year (continuous, scaled to a mean of zero and a standard deviation of one), average winter temperature (continuous, scaled to mean zero and standard deviation one), age (continuous, -0.5 =juveniles to 0.5 =adults, 0 =unknown) and sex (continuous, -0.5 =females to 0.5 =males, 0 =unknown) as fixed effects. The second model included year, average winter temperature and their interaction, temperature anomaly (continuous, scaled to mean zero and standard deviation one), the interaction between temperature anomaly and age, the interaction between temperature anomaly and average temperature, sex and age. We explored the interaction between year and average temperature to understand potential different rates of body size change along the spatioclimatic gradient. Similarly, the interaction between temperature anomaly and average temperature allowed us to explore varying responses to temperature anomalies along the spatioclimatic gradient. And finally, the interaction between temperature anomaly and age allowed to test for differences among age group responses to warming temperatures. Because we had three different temperature anomaly variables (previous winter, same winter and spring), we ran three competitive models, that is one per anomaly variable to select the best one based on the lowest DIC to be included in the second model (Table S2 in Supplementary Material).

We ran phylogenetic generalized linear models (pGLMM), which included a phylogenetic correlation structure, ringer ID as random effect and species-specific random slopes for all predictors present in each model. We used the R function 'pGLMM' from the package 'phyr' Li et al., 2020) and ran the models in a Bayesian framework (based on INLA, Rue et al., 2009; see Bosco et al., 2023 for modelling data and code). For the phylogenetic covariance matrix, we used a phylogenetic consensus tree, which was based on averages of 1000 trees downloaded from VertLife (Rubolini et al., 2015) for our 24 species (R package 'ape', Paradis & Schliep, 2019). To illustrate some of the observed changes in body size over time and in response to the spatioclimatic gradient and temperature anomalies, we plotted linear regressions for four example species (best demonstrating the observed relationships between body size change and the explored explanatory variables) among the 24 bird species based on single species linear mixed effect models, including the same terms and ringer as random effect as in the pGLMM models (R package lme4, Bates et al., 2015; see Bosco et al., 2023 for modelling data and code). All analyses were performed using R (version 4.2.0, R Core Team, 2022).

3 | RESULTS

The most abundantly ringed and measured species was the great tit *Parus major* (56,179 in total; 37,390 Finland and 18,789 Sweden), followed by blue tit *Cyanistes caeruleus* with 56,174 observations (35,854 in Finland and 20,320 in Sweden) and bullfinch *Pyrrhula pyrrhula* (24,549 in total; 16,380 Finland and 8,169 Sweden; detailed summary table in Supplementary Material section 2 based on body mass data set). Looking into average body size per species from the first decade (1970–1980) compared with the last decade (2010–2020), across all species, the mean wing length decreased by almost 0.34% from 86.7 mm in the 1970s to 86.3 mm in 2010s. The average change in body mass was stronger with a decrease of almost 2.44% from 34.2 to 33.4 g across all species.

Median average winter temperature (months December–February) rose from -6°C in the 1970s to -3.3°C in the 2010s across all sampled grid cells of Sweden and Finland together (see also Supplementary Material Figures S2 and S3), while the increase in median spring temperature (months April–June) was not as pronounced (8.4°C in 1970s to 9.8 in 2010s).

3.1 | Temporal and spatioclimatic trends of body size across species

Over all 24 species, we found a significant average decline in wing length over time, while for body mass the decline was negative but nonsignificant (Table 1, Model 1; Figures 2a,b and 3a). Along the spatioclimatic gradient, measured as average winter temperature, however, only body mass had an overall positive, significant response, such that birds are lighter at higher (colder) latitudes, while

there was no clear pattern for wing length across species (Table 1, Model 1; Figure 2a,b). The species phylogeny covariance explained the most variance among all random effects in both wing length and especially the body mass model, followed by a nonphylogenetic species effect (Table 1, Model 1). There was some variation in species-specific slopes for the random effects of year and average winter temperature for body mass (Year SD: 1.293, Average temperature SD: 1.265), while it was near-zero for wing length (Year SD: 0.032, Average temperature SD: 0.019; Table S1a in Supplementary Material). The interaction between year and average winter temperature in Model 2 was significantly positive for wing length and body mass, such that birds at colder average winter temperatures (more northern) showed a more negative response in body size over time (slope of year at average winter temperature of -9.53°C corresponding to the northern boreal zone for wing length = -0.17 mm/year and for body mass = -2.02 g/year), while birds at warmer average winter temperatures (more southern) showed a less negative response (slope of year at average winter temperature of -1.31°C corresponding to the hemiboreal zone for wing length = -0.04 mm/year and for body mass = -0.28 g/year; Table 1, Model 2; Figures 2c,d and 3b).

3.2 | Body size change in relation to climate warming across species

For wing length, temperature anomaly of the previous winter performed best compared with temperature anomaly of the same winter and of the previous spring and was thus included in Model 2 (Table S2 in Supplementary Material). For body mass, temperature anomaly of the same winter performed best and was included in Model 2, while neither temperature anomaly of the previous winter nor of spring showed significant effects (Table S2 in Supplementary Material).

Model 2 revealed a negative correlation between body size and winter temperature anomalies, such that wing lengths were significantly (i.e. the 95% credible intervals did not cross zero, see Table 1, Model 2) shorter with higher temperatures of the previous winter, while body mass declined with temperature anomalies of the same winter (Figures 2c,d and 3c). This pattern varied among age groups for wing lengths but not for body mass, such that young birds declined more strongly compared with adult birds in relation to more positive temperature anomalies of the previous winter (positive interaction; Table 1, Model 2; Figure 2c,d). On the contrary, the decline in body mass (but not wing length) with positive temperature anomalies of the same winter was more pronounced in warmer (more southern) areas based on the negative interaction with average winter temperature (Table 1, Model 2; Figures 2c,d and 3d). As in Model 1, the species phylogeny covariance explained the most variance in both wing length and body mass models, followed by a nonphylogenetic species effect (Table 1, Model 2). There was some variation in species-specific slopes for the effect of temperature anomaly for wing length and especially for body mass (wing length SD: 0.042 and body mass SD: 1.197; Table S1b in Supplementary Material).

TABLE 1 Model outputs for pglmm Models 1 and 2 for wing length and body mass.

Variable	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Model 1						
	Wing length (N = 290,412)			Body mass (N = 214,890)		
Intercept	-0.001	-0.022	0.020	-0.183	-0.326	-0.040
Year	-0.023	-0.036	-0.009	-0.077	-0.178	0.025
Average T (spatial)	0.005	-0.009	0.020	0.159	0.032	0.285
Age	-0.002	-0.029	0.025	-0.058	-0.397	0.282
Sex	0.000	-0.027	0.027	-0.007	-0.326	0.311
Hour				1.286	1.206	1.366
SD of species phylogeny RE	0.062	0.001	0.016	1.769	1.724	5.465
SD of year species RE	0.032	0.000	0.011	1.293	0.520	5.518
SD of average T species RE	0.019	0.000	0.001	1.265	0.500	4.923
Model 2						
	Wing length			Body mass		
Intercept	-0.002	-0.025	0.021	-0.234	-0.377	-0.091
T anomaly	-0.020	-0.036	-0.004	-0.215	-0.311	-0.120
Year	-0.016	-0.032	0.000	0.001	-0.107	0.109
Average T (spatial)	0.006	-0.012	0.023	0.123	-0.005	0.252
Age	-0.003	-0.034	0.028	-0.092	-0.420	0.237
Sex	0.000	-0.032	0.032	-0.010	-0.314	0.294
Hour				1.280	1.200	1.360
Year:average T (spatial)	0.016	0.007	0.024	0.212	0.172	0.251
T anomaly:age	0.017	0.000	0.035	0.038	-0.024	0.100
Average T:T anomaly	0.005	-0.003	0.014	-0.069	-0.101	-0.036
SD of species phylogeny RE	0.109	0.003	0.046	1.586	1.149	4.900
SD of T anomaly species RE	0.042	0.001	0.005	1.197	0.471	3.887

Note: Given are model estimates, and the upper and lower limits of the 95% credible intervals (CI). Bold values indicate significant results if the CI does not cross zero. The fixed term hour was only included in the body mass models to account for the time of day when the bird was measured. Random effect (RE) values for all terms present in the models are given in Table S1 in Supplementary Material. T, temperature; (spatial) refers to the average temperature across the time series for each study site, that is the spatioclimatic gradient. For the wing length model, temperature anomaly from the previous winter, while for body mass temperature anomaly of the same winter was included in the model (Table S2 in Supplementary Material).

4 | DISCUSSION

Using a unique large-scale and long-term winter bird ringing data set from two Nordic countries, we show that overwintering birds have decreased in their body size over the last half-century not only with respect to their body mass, as evidenced before (e.g. Husby et al., 2011; Shipley et al., 2022; Weeks et al., 2020; Yom-Tov et al., 2006) but especially their wing lengths. This simultaneous decrease in both body mass and wing length opposes some earlier findings, where often decreasing body mass but increasing wing lengths were reported (e.g. Dubiner & Meiri, 2022; Jirinec et al., 2021; Shipley et al., 2022), while other studies show allometric scaling, where several morphometric traits changed simultaneously and similarly in pace and direction (e.g. Anderson et al., 2019). Making use of accurate ringing locations over 1500km along the latitudinal axis, we further were able to investigate varying response patterns

along the spatioclimatic gradient. As suggested earlier (e.g. Baldwin et al., 2022; Dubiner & Meiri, 2022; McLean et al., 2022; Weeks et al., 2020), climate change, here measured as temperature anomaly, was a strong predictor for the observed body size decrease, and this pattern was found across 24 ecologically diverse species while accounting for an effect of shared ancestry.

Following our first hypothesis (Figure 1a), our study shows that different morphometrics vary in their spatioclimatic pattern, where wing lengths did not show a clear response to the average winter temperature along the latitudinal gradient within our study area. In contrast—and contradicting Bergmann's rule—for body mass, we found that the warmer and more southerly located the birds were, the heavier they were (Table 1, Model 1). Thus, along a spatioclimatic gradient, higher and colder latitudes cost the birds more energy, likely depleting their fat reserves and thus leading to lighter birds (Rogers & Smith, 1993).

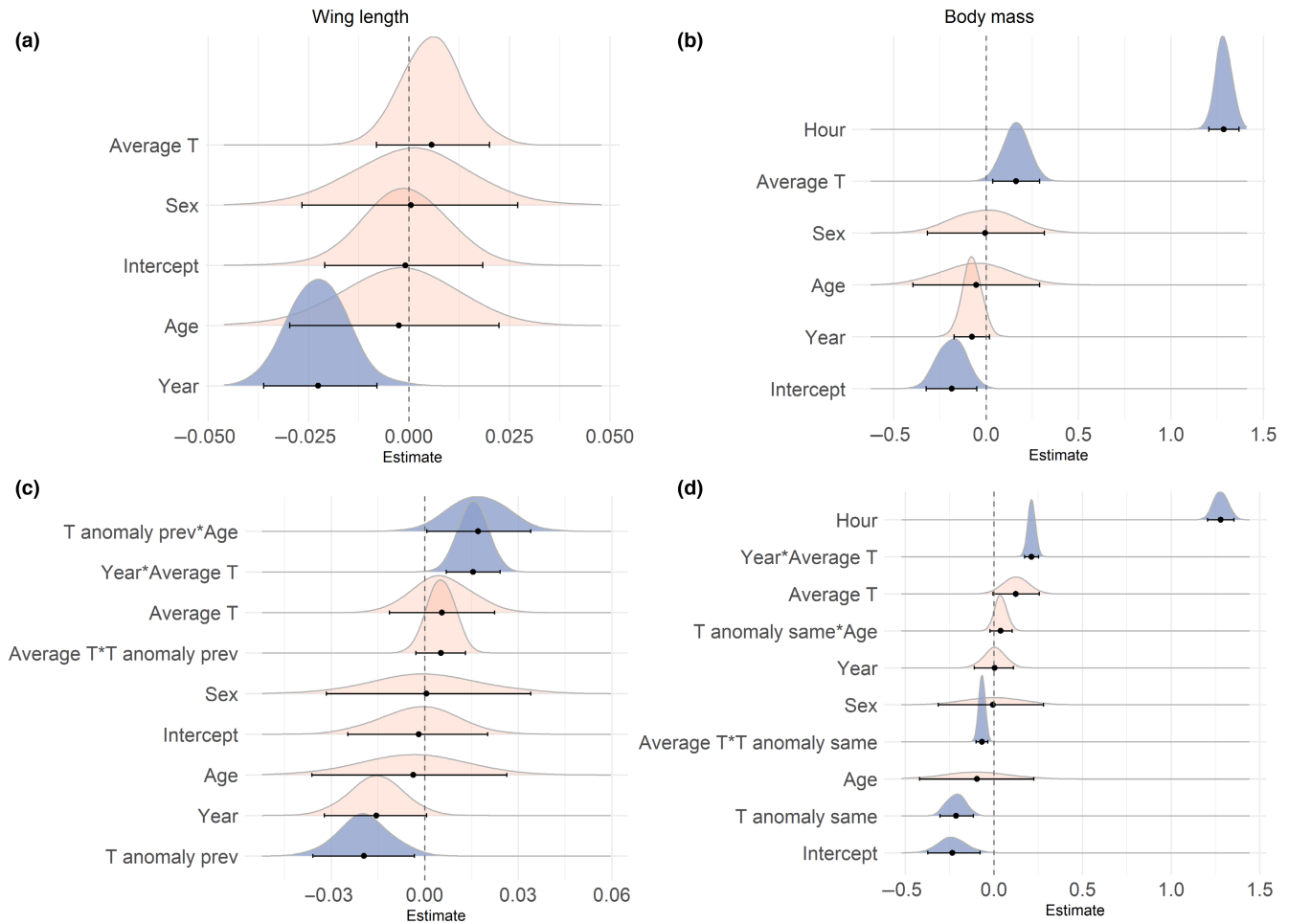


FIGURE 2 Average effects, illustrated as forest plots from the pgImm Models 1 and 2 for wing length (a,c) and body mass (b,d). The posterior mean (black points), 95% credible intervals (CI; error bars) and the posterior distribution mode (shaded areas) are plotted. Blue distributions show significant effects where the CIs do not overlap zero, and orange distributions show nonsignificant effects. Panels a and b show the effect sizes for wing length and body mass, respectively, from Model 1 where year, average winter temperature and the fixed effects age and sex (and hour for the body mass model) were present. Panels c and d show the effect sizes from Model 2 where additionally the temperature anomaly (previous winter for wing length and same winter for body mass) and the interactions between year and average temperature, temperature anomaly and average temperature, and temperature anomaly and age were included. $N = 290,412$ for wing length and $N = 214,890$ for body mass. Age refers to adults compared with young birds, average T, the average winter temperature per study site over the 50 years time series; prev, previous; T, temperature.

Regarding our second hypothesis (Figure 1b), we found that over all species' wing lengths have become smaller during the past half-century, while declines in body mass were less clear (Table 1, Model 1). The bulk of studies on climate change effects on birds are conducted using breeding bird populations, while the nonbreeding season is less well represented (Bosco et al., 2022; Lehikoinen et al., 2021). We here used data on overwintering birds only, where most species are residents, partial or at maximum short-distance migrants and can thus rule out strong selective forces linked to migration abilities (i.e. selection for longer wings enabling longer flight distances, Nowakowski et al., 2014). This is likely to explain our contrasting findings compared with other studies (e.g. Weeks et al., 2020) where they reported decreasing body mass but increasing wing lengths in their breeding bird communities. Migratory birds underlie different selection pressures than resident birds overwintering in the same

or close-by location to the breeding area (Phillips et al., 2018) and are thus likely to differ in terms of adaptations to changing climatic conditions (Rushing et al., 2020). In interaction with time, birds' body size, that is both wing length and body mass, decreased less strongly in southern areas compared with northern birds (Table 1, Model 2). This means that spatially, that is with increasing latitude, birds became smaller at faster rates, likely due to more pronounced temperature increases at higher latitudes (IPCC, 2013; see Figure S3 in Supplementary Material). This is supported by other climate change responses where northern birds shifted their ranges faster than southern birds (Virkkala & Lehikoinen, 2014).

With respect to our third hypothesis on the correlation between body size decrease and temperature warming (Figure 1c), we show that wing length and body mass are strongly negatively associated with the positive anomaly in winter temperatures, where

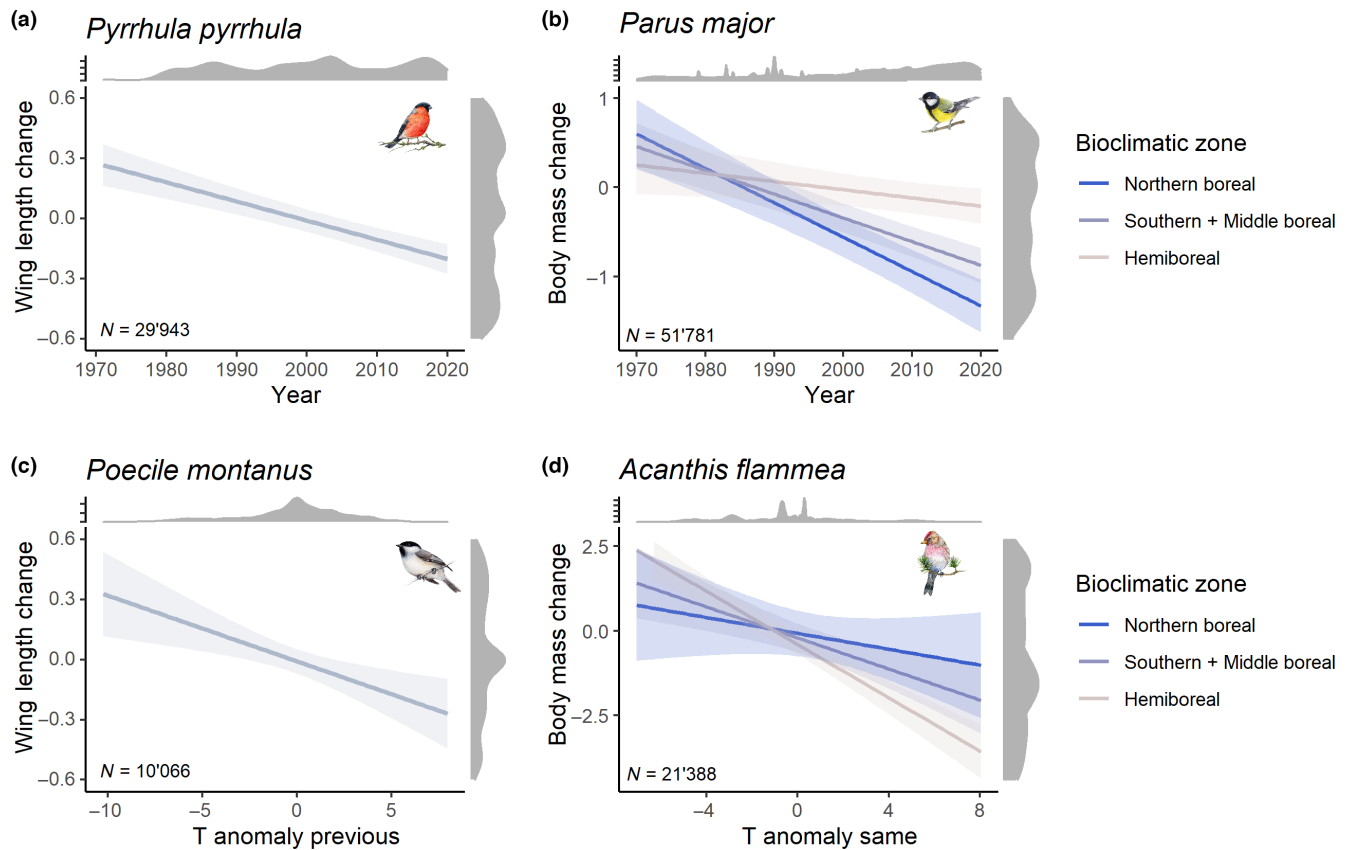


FIGURE 3 Linear regressions for four example species illustrating the significant effects from the pglmm models. The regressions here are based on single species lmer models (including ringer ID as random term, age and sex as fixed effects) showing significant responses of body size change to (a) year for wing length of the bullfinch *Pyrrhula pyrrhula*, (b) year in interaction with average temperature for body mass of the great tit *Parus major*, (c) temperature anomaly measured in the winter previous to the wing length measurement for the willow tit *Poecile montanus* and (d) temperature anomaly (same winter) in interaction with average winter temperature for body mass of the redpoll *Acanthis flammea*. For panels b and d, average winter temperature for three bioclimatic zones was extracted (hemiboreal at latitude $<WGS84\ 60.7 = -1.31^{\circ}C$; southern and middle boreal at latitude $>WGS84\ 60.7$ and $<65.7 = -6.19^{\circ}C$; northern boreal at latitude $>WGS84\ 65.7 = -9.53^{\circ}C$, see also [Figure 1d](#)) to visualize different slopes of wing length change dependent on the spatioclimatic location. Solid lines are the predicted mean, shaded areas the 95% confidence intervals, while other terms present in the models were fixed at their mean. Raw data density distributions are shown on the upper and right side of the plots, and sample sizes per species are given at the bottom of the plots.

wing length shows strong responses to temperature anomalies of the previous winter, while body mass correlates with temperature anomalies of the same winter ([Table 1](#), Model 2). Those findings are in line with previous research based on breeding birds suggesting climate change to drive body size shrinking (e.g. Teplitsky et al., 2008). More immediate and carry-over effects from warmer-than-average temperatures explain decreased mortality of better adapted (or no longer maladapted) birds, where the smaller birds have optimized heat-loss vs. heat-preservation ratios (Rogers & Smith, 1993), optimized fat reserve strategies (i.e. warmer conditions favour birds to store less fat, Gosler, 2002; Rogers & Reed, 2003) and thus increased predator avoidance abilities (Witter & Cuthill, 1993). But for the observed decrease in wing length, the relationship with warming climate could also entail range shifts, where more southern populations of smaller birds shift their ranges northward to follow their climatic niche, leading locally to an overall decline in wing lengths. This hypothesis would involve either northward-biased dispersal, or alternatively, dispersal in all

directions in combination with better survival of northward dispersing individuals. Finally, despite the species being mainly residents, most of them show some kind of migratory movements, and these patterns could arise through phenotypic plasticity in migration distance, if smaller individuals opportunistically head further south during colder winters (immediate effects) and if they on average do what they did the previous winter (lagged effects). We did not find an influence of spring temperatures on birds' body size change, which could either be because the species included in this study are indeed mainly affected by temperature conditions during winter—given that winter temperatures have been increasing faster than during other seasons (Masson Delmotte et al., 2018). On the contrary, many among the 24 species included here are partial migrants or show some movements away from the breeding grounds for overwintering, meaning that our method of using site-specific temperatures from spring based on the wintering location may not make sense for some species and could explain the lack of significance found for spring temperature anomalies.

We further show that body mass (but not wing length) declines in response to temperature warming differed along the spatioclimatic gradient (interaction between temperature anomaly and average winter temperature): birds located in warmer, more southern areas decreased faster in their mass in response to warming temperatures than birds further north (Table 1, Model 2). Along with the above-explained faster decline in body size over time in more northern areas (interaction year and average winter temperature), this could hint at a potential lag behind faster temperature increases in the north compared with southern areas (IPCC, 2013), where species were better able to adapt their body size to changing climatic conditions. In the north, it might be better to have a fat buffer in case of cold spells, whereas in the south birds can shift their body mass more according to climatic conditions and additionally predation risk might be stronger than the risk of cold spells; that is, being smaller and more agile is advantageous for predator avoidance (Witter & Cuthill, 1993). While wing length declines did not show such spatioclimatic patterns in response to warming temperatures, they differed among age groups, where young birds showed stronger declines than adult birds (Table 1, Model 2). This is in line with our hypothesis, confirming that likely inexperienced 1st winter birds are more sensitive to climatic changes than more experienced adults (e.g. Dybala et al., 2013).

When looking into the phylogenetic signal in the models, we found considerable variation in the species-specific slopes for the effects of year and winter temperature anomaly, indicating that some species showed clearer patterns of body size decline over time and in response to climate warming than others. A recent study investigated such interspecific variation in the amount of temporal trait change and found that nontemperature effects were the main drivers suggesting that idiosyncratic responses are not due to different species sensitivities to temperature warming (McLean et al., 2022). Furthermore, several studies showed that species traits explain those interspecific differences with a latest suggestion that bigger-brained birds decline in body size less strongly compared with birds with smaller brains due to increased cognitive capacities (Baldwin et al., 2022). Even though we ruled out strong selection pressures on long-distance migration in our overwintering species sample, some species are short-distance or partial migrants compared with true residents. This could potentially explain why for some species increased wing lengths may be beneficial under conditions of climate change. Thus, taking climate change-driven poleward shifts into account, formerly more southern and resident species, when breeding at higher latitudes might be forced to migrate during winter due to harsh winter conditions further north (Weeks et al., 2020). This in turn might favour the development of longer wings to enable migration (Bowlin & Wikelski, 2008). Idiosyncratic responses may also be explained by dispersal-mediated range shifts where southern phenotypes are displaced northwards, so that the direction of the response in wing lengths is partly derived from unequal spatial variation between species.

Our results highlight a general climate-driven decrease in body size associated with positive anomalies in winter temperature in an overwintering bird community in the high latitudes. However, the responses are not spatially uniform and there is considerable species-specific variation, emphasizing the importance of conducting multispecies, and spatially explicit studies when studying responses to climate change. The mechanisms of decreasing wing length and body mass seem to differ and underline the spatioclimatic pattern of immediate and carry-over effects of temperature warming during the nonbreeding season.

AUTHOR CONTRIBUTIONS

Laura Bosco and Alekski Lehtikoinen formulated the study questions and designed the study. Alekski Lehtikoinen and Thord Fransson provided the data. Markus Piha and Thord Fransson have curated the data and provided guidelines on how it is best analysed, and Laura Bosco and Alekski Lehtikoinen performed all statistical analyses with methodological support from Andreas Lindén. Laura Bosco wrote a manuscript draft, and all authors contributed substantially to the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw ringing data from Finland are freely available online (<https://laji.fi/en/observation/list?sourceId=KE.67>), the Swedish ringing data are available upon request from Swedish Museum of Natural History. The Finnish temperature data was downloaded from the Finnish Meteorological Institute (<https://paituli.csc.fi/download.html>) and the temperature data for Sweden from Copernicus (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land-monthly-means?tab=overview>). The phylogenetic bird trees were downloaded from <http://vertlife.org/phylosubsets/>. The data and modelling code used for the analyses of this paper are stored on zenodo: <https://doi.org/10.5281/zenodo.7961760> (Bosco et al., 2023).

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BIOSKETCH

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SUPPORTING INFORMATION

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