ECOLOGY LETTERS

Ecology Letters, (2019) doi: 10.1111/ele.13434

LETTER

Shared morphological consequences of global warming in North American migratory birds

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The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13434

Abstract

Increasing temperatures associated with climate change are predicted to cause reductions in body size, a key determinant of animal physiology and ecology. Using a four-decade specimen series of 70 716 individuals of 52 North American migratory bird species, we demonstrate that increasing annual summer temperature over the 40-year period predicts consistent reductions in body size across these diverse taxa. Concurrently, wing length – an index of body shape that impacts numerous aspects of avian ecology and behaviour – has consistently increased across species. Our findings suggest that warming-induced body size reduction is a general response to climate change, and reveal a similarly consistent and unexpected shift in body shape. We hypothesise that increasing wing length represents a compensatory adaptation to maintain migration as reductions in body size have increased the metabolic cost of flight. An improved understanding of warming-induced morphological changes is important for predicting biotic responses to global change.

Keywords

Allometry, body size, climate change, migration, morphology.

Ecology Letters (2019)

INTRODUCTION

Body size is an important determinant of animal ecology and life history (Brown 1995; McGill *et al.* 2006), influencing physiological (Hudson *et al.* 2013) and morphological (Gould 1966; Outomuro & Johansson 2017) functions, as well as ecological and social interactions (Yodzis & Innes 2002; McGill *et al.* 2006; Prum 2014). Within species, there is evidence that individuals tend to be smaller in the warmer parts of their ranges, a pattern often interpreted as an intraspecific derivative of Bergmann's rule (Bergmann 1847; Rensch 1938; Mayr 1956; Blackburn *et al.* 1999). This association between warmer temperatures and smaller bodies suggests that anthropogenic climate change may cause intraspecific shifts towards smaller body size in a temporal analog to geographic patterns. However, despite the widespread appreciation of the fundamental importance of body size for ecological and evolutionary processes, the drivers and universality of temperature–body size relationships across space and time remain contested (Watt *et al.* 2010; Forster *et al.* 2011; Gardner *et al.* 2011; Riemer *et al.* 2018). Determining whether rapid body size reductions are occurring in response to increasing temperatures is important for understanding how climate change will influence the phenotypes and ecological dynamics of species in a warming world.

Although the possibility of body size reduction in response to global warming has been suggested for decades (Smith *et al.* 1995; Yom-Tov 2001), empirical support remains mixed (Gardner *et al.* 2014; Salewski *et al.* 2014; Teplitsky & Millien 2014; Dubos *et al.* 2018). This uncertainty may be due, in part, to a scarcity of morphological time series data sets containing sufficiently dense sampling to test the influence of temporal fluctuations in climate on body size (as opposed to simply associating long-term morphological trends with periods of global warming), and to do so across co-distributed species that experience similar climatic regimes. By contrast, those data sets that have sampled large numbers of individuals consistently across time frequently do not have measurements from enough morphological characters to distinguish changes in body size from changes in body shape that may be driven by alternate selection pressures. Consequently, the influence of warming-driven changes in body size on ecologically-important dimensions of body shape remains largely unknown.

Migratory birds are an important but complex system for understanding the morphological responses of biota to increasing temperatures. The extreme energetic demands of long-distance migration have shaped the morphology of migratory birds for efficient flight (Winkler & Leisler 1992; Lockwood *et al.* 1998). Because migratory birds are under strong selection for high site fidelity, perturbations that hinder an efficient return to the breeding grounds are likely to reduce reproductive success (Winger *et al.* 2019). If warming temperatures cause body size reductions in migratory birds, concurrent changes in body shape related to the allometry of flight efficiency may be necessary to maintain migratory patterns. Although migratory species have garnered significant attention from researchers interested in biotic responses to rapid environmental change, particularly as they relate to phenology and geographic range, the extent to which migratory birds are

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changing size and shape in response to anthropogenic global warming remains uncertain (Van Buskirk *et al.* 2010; Goodman *et al.* 2012; Salewski *et al.* 2014; Collins *et al.* 2017a, 2017b; Dubos *et al.* 2018).

A persistent challenge in understanding recent morphological changes in migratory birds is the characterisation of avian size and shape. Frequently used indices to assess changes in avian body size through time, such as mass and wing length, may be problematic in migratory birds; mass is highly variable for migratory species, given rapid fat gains and losses during migration (Alerstam & Lindström 1990; Morris *et al.* 1996), and wing length is positively correlated with migratory distance (Zink & Remsen 1986; Förschler & Bairlein 2011). Nevertheless, studies on recent body size changes in birds in migratory species have often represented body size using wing length or mass (Yom-Tov *et al.* 2006; Salewski *et al.* 2010; Van Buskirk *et al.* 2010; Goodman *et al.* 2012), making it difficult to identify changes in body size and to disentangle them from shifts in shape that may be driven by other factors.

Here, using a large specimen time series of 52 North American migratory bird species with measurements from multiple morphological features, we studied changes in body size and shape between 1978 and 2016. We found remarkably consistent reductions in body size, leading us to test the hypothesis that increases in temperature over this four-decade period are associated with the observed declines in body size. We exploit the densely sampled nature of our data to test the relationship between temperature and body size not only over the whole study period but also across shorter-term fluctuations in temperature.

In addition to decreases in body size, we also found a notable change in body shape: as multiple metrics of body size have declined, wing length has increased among nearly all species in the study. Longer and more pointed wings are associated with more efficient flight in birds, particularly for long distance flights (Pennycuick 2008; Møller *et al.* 2017), suggesting that some aspect of recent global change may be selecting for more efficient flight across this diverse set of migratory birds. Given the consistent trends of decreasing body size that we observed alongside consistent increases in wing length, we hypothesized that these dynamics may be coupled. Specifically, we hypothesised that the observed change in wing allometry may be an adaptive compensation for reductions in body size to efficiently accomplish migration with powered flight. If decreasing body size precipitated selection for longer wings, we predict that species with faster rates of body size decline will exhibit faster rates of increase in wing length. Although morphological responses to climate change can be driven by complex ecological dynamics (Van Gils *et al.* 2016; Bosse *et al.* 2017), selection on allometric relationships that couple changes in size with changes in shape may also be an important dimension of phenotypic responses to climate change.

METHODS

Specimen and data collection

Since 1978, The Field Museum's collections personnel and volunteers have operated a salvage operation to retrieve birds that collided with buildings in Chicago, IL, USA during their spring or fall migrations (Fig. S1). On every individual bird, a single person (David E. Willard) measured: (1) tarsus and bill length using digital calipers; (2) the length of the relaxed wing using a wing rule; and (3) mass using a digital scale. All measurements were taken on fresh or thawed carcasses prior to preparation as specimens, which, given the ease of manipulation, is expected to improve the precision of measurements compared to measurements of live birds or dried specimens. Sex was determined based on gonadal inspection, and skull ossification enabled ageing to Hatch Year (HY; fall birds hatched that summer) or After Hatch Year (AHY; all spring birds and all fall birds at least 1 year old).

We filtered the data set to 70 716 individuals from 52 species from 1978 to 2016 that were consistently sampled and measured across time (for details, see *Supporting Information–Data Filtering*). These species are from 11 families and 30 genera of mostly passerines (Table S1). All species in the data set are migratory. Most breed in boreal or temperate forest or edge habitats, but some species are grassland or marsh specialists, and their winter ranges, habitats, migratory distances, life histories and ecologies are diverse (*Supporting Information–Ecology and Natural History*).

Quantifying change through time

We examined temporal change in four aspects of morphology: tarsus, mass, wing length, and the first axis of a principle component analysis (PCA) of tarsus, wing, bill length and mass. We modelled each aspect of morphology as the dependent variable in a linear mixed-effects model using the 'lmer' function from the R package lme4 (Bates *et al.* 2015) in R (R Core Team 2018). We log transformed each measurement because the 52 species differed in the magnitude of measurements, and to facilitate comparison of relative rates of change among morphological traits. To test the change in each trait through time, we included year (continuous, transformed to start at zero to facilitate model fitting), sex, and age (HY or AHY) as fixed effects, and included a random intercept and slope for year for each species. We assessed significance of parameters using the Satterthwaite method, implemented in the R package lmerTest (Kuznetsova *et al.* 2017). We also conducted analogous multilevel Bayesian models that accounted for phylogenetic relatedness (*Supporting Information–Bayesian Modelling*).

We conducted the PCA using the logarithms of tarsus, wing length, bill length, and the cube root of mass (because it represents a volume) for all specimens with complete data. We used the 'princomp' function in the stats package in R, constructing the axes using a covariance matrix as the scale of variables was similar; the loadings on PC1 were nearly indistinguishable if a correlation matrix was used. We interpreted scores on the first axis of the PCA (PC1) as a metric of body size, following common practice (e.g. Grant & Grant 2008). Because all variables were positively loaded onto PC1 and are expected to scale positively with body size, we interpreted PC1 scores as positively related to body size. We transformed all PC1 scores to be positive (by adding the absolute value of the minimum score, plus 0.01 to all scores).

Testing environmental determinants of morphological change

To test hypotheses on the environmental drivers of changes in body size, we generated species-specific estimates of climatic and environmental variables (temperature, precipitation, and Normalized Difference Vegetation Index [NDVI], a proxy for resource availability) on the breeding and wintering grounds. First, we cropped breeding, wintering and resident ranges for all species (BirdLife International 2015) to exclude unlikely breeding destinations for birds migrating through Chicago (Fig. S1). For each species, we then calculated mean temperature, precipitation, and mean maximum NDVI during June and December of each year for which these environmental data were available (1981–2016) in the region representing each species' likely breeding and wintering grounds, respectively (*Supporting Information–Environmental Data*). We also tested the sensitivity of our results to variation in how ranges were cropped (Fig. S1).

We used linear mixed models to quantify the impacts of these species-specific environmental variables on body size. We considered tarsus length to be the most appropriate and precise univariate metric of intraspecific variation in body size (Rising & Somers 1989; Senar & Pascual 1997), given high variation in mass observed within individuals during migration and the correlation between migratory distance and wing length often observed among individuals (Zink & Remsen 1986; Förschler & Bairlein 2011). We also modelled PC1 as the dependent variable to ensure that our results are robust to different characterisations of body size. In these models, year, the environmental variables (i.e. precipitation, temperature, and NDVI on the breeding and wintering grounds), sex, and season of collection were included as fixed effects and random intercepts were included for each species. Models with random slopes for all environmental variables did not converge, suggesting the data do not support such a complex model (Bates *et al.* 2018); therefore, we made the simplifying assumption that all species are responding similarly to environmental conditions. All environmental variables were scaled to a mean of zero and a standard deviation of one. These models only included AHY birds, as HY birds had not experienced winter conditions, and the environmental covariates from the season immediately prior to collection (i.e. season *t*). In addition, we fitted the model using all age classes but included only the summer environmental variables, and age, as fixed effects. Analogous multilevel Bayesian models that accounted for phylogenetic relatedness were conducted (*Supporting Information–Bayesian modelling*). Because the exact year of birth (and development) for AHY birds is unknown, we tested for the impact of uncertainty in the age of AHY birds by running two alternative models with environmental covariates from each of the two years preceding collection (i.e. seasons *t*-1, and *t*-2, *Supporting Information–Sensitivity of Results to Time Lag*).

Testing environmental predictors of fluctuation in body size

To further explore changes in body size in relation to the climatic and environmental variables, we tested whether fluctuations in tarsus were correlated and temporally synchronised with fluctuations in each of the environmental variables identified as significant (i.e. $P < 0.05$) in the linear mixed-effects models. We fit generalised additive models (GAMs) to each significant variable, modelling them as a function of time and with a random effect for species. We used the 'gam' function in the R package mgcv (Wood 2011) with default smoothing parameters determined by the model fitting.

We used cross correlation analysis (CCA) to analyse the relationships between smoothed fluctuations in the dependent variables through time from the GAMs (that is, to test for synchronised fluctuations in tarsus and the climate variables). In CCA, time series data should be stationary such that after removing any temporal trend, the mean and variance do not change over time. We tested whether the predicted values of the GAMs were stationary using the Kwiatkowski Phillips Schmidt Shin test (Koupidis & Bratsas 2019). All climatic and environmental variables were stationary, but the tarsus data were not, so we used the first differences of the tarsus time series (the differences between tarsus at time *t* and *t*-1) – which were stationary – to compare fluctuations among tarsus and the environmental variables. The CCA was implemented using the 'ccf' function in the R package tseries (Trapletti & Hornik 2017). For visualisation purposes, we also calculated the slope derivatives of the GAMs for summer temperature and tarsus (i.e. the change in slopes of tarsus and environmental variables through time) at 1000 points along the time series, using the 'derivatives' function in the R package gratia (Simpson 2019).

Association between rates of change of wing and tarsus

To test whether rates of change of wing length were associated with rates of change in body size, we tested the correlation between the species-specific rates of change of wing and tarsus from the linear mixed-effects models for wing and tarsus, respectively (Fig. 2, Tables S2 and S5). We used three methods to calculate the correlation in slopes: a linear model, a phylogenetic generalised least squares (pgls) model implemented in the R package ape (Paradis *et al.* 2004; Pinherio et al. 2013), and a pgls approach that treated the standard errors of the random slope estimates in both rates of change of wing length and rates of change of tarsus as sampling error (Ives *et al.* 2007), implemented using the 'pgls.Ives' function from the R package phytools (Revell 2012). We fit the latter model 10 000 times and report the mean parameter results.

RESULTS

Consistent reduction in body size

Despite the ecological and phylogenetic diversity among species, we found consistent reductions in all indices of body size (tarsus, mass, and PC1) across species over the course of the study (Figs 1 and 2). We found significant negative relationships between year and tarsus length (-6.20×10^{-4}, SE 2.93×10^{-5}, $P << 0.001$), mass (-6.94×10^{-4}, SE 1.19×10^{-4}, $P << 0.001$), and PC1 (-1.76×10^{-3}, SE 5.82×10^{-5}, $P << 0.001$); see Tables S2–S4 for full model results. These declines represent a mean decline of 2.4% in tarsus length and 2.6% in mass from 1978 to 2016. Nearly all species-specific changes in tarsus were declines, with standard error estimates that did not overlap with zero, and all species with significant changes in

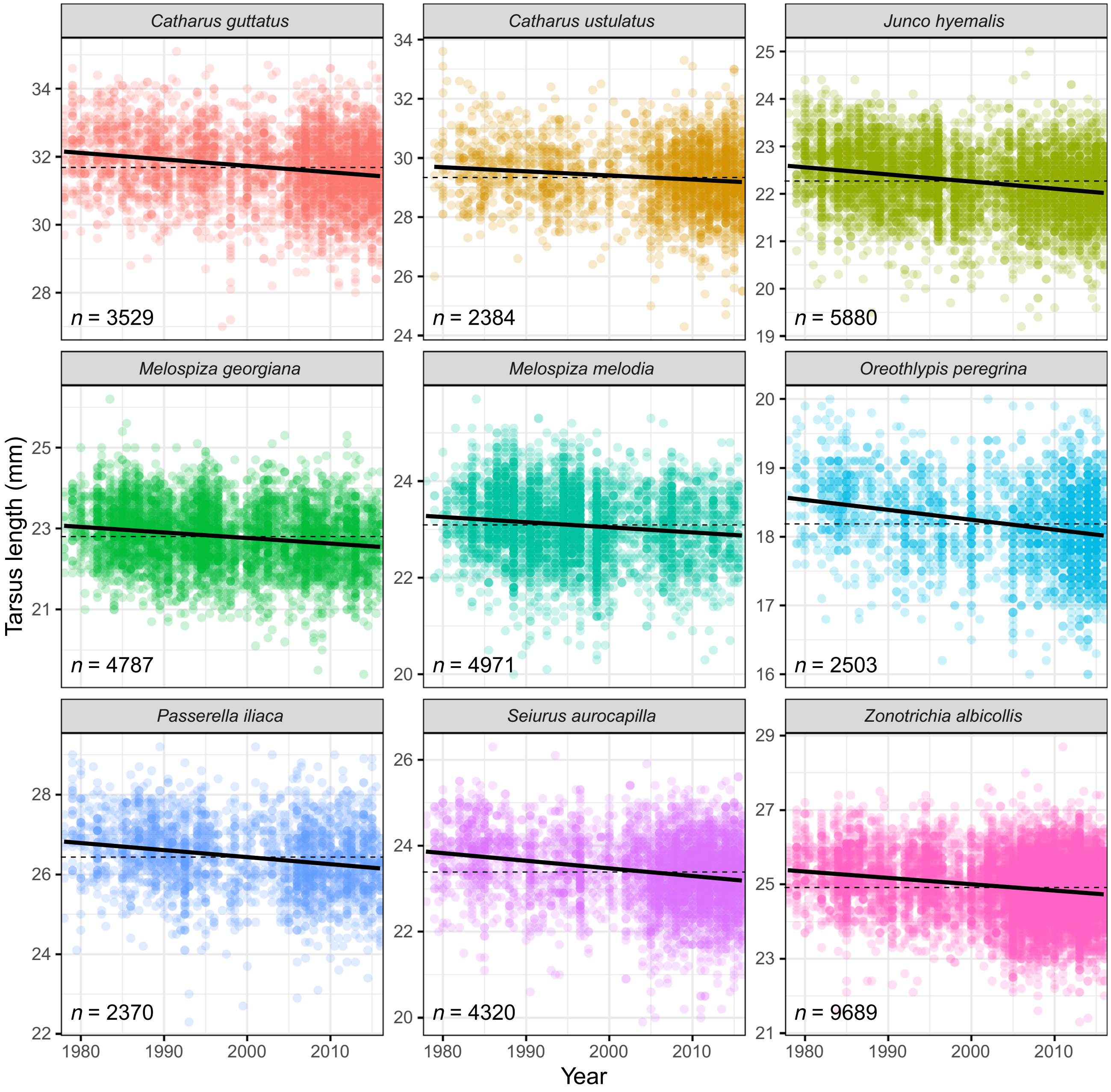

Figure 1 Body size has become smaller through time. Tarsus length declined in nearly all species in the data set (Fig. 2a) with the nine most highly sampled species shown here. Dashed lines have a slope of zero and an intercept equal to the mean tarsus length for each species.

mass and PC1 got smaller (Fig. 2). The consistency among species is reflected in the extremely low (near zero) slope variances of the random year slopes for species across size indices (2.45×10^{-8}, 5.51×10^{-7}, and 1.22×10^{-7}, for tarsus, body mass and PC1, respectively, Table S2–S4). Similar results were obtained using multilevel Bayesian models that accounted for phylogenetic relatedness (Table S6).

CONSISTENT INCREASES IN WING LENGTH RESULTED IN WIDESPREAD CHANGES IN BODY SHAPE

In contrast to tarsus, mass and PC1, wing length increased through time across nearly all species (3.29×10^{-4}, SE 3.35×10^{-5}, $P << 0.001$, see Table S5 for full results; Fig. 2). This reflects an increase in wing length of 1.3% from 1978 to 2016. These shifts were consistent across species in our study (Fig. 2), with a slope variance of the random slopes of 4.19×10^{-8}, Table S5). As with the body size traits, Bayesian analysis that accounted for phylogenetic relatedness yielded similar result (Table S6).

INCREASING SUMMER TEMPERATURES DRIVE BODY SIZE DECLINE

We recovered several significant relationships between climatic and environmental variables and body size. Results presented

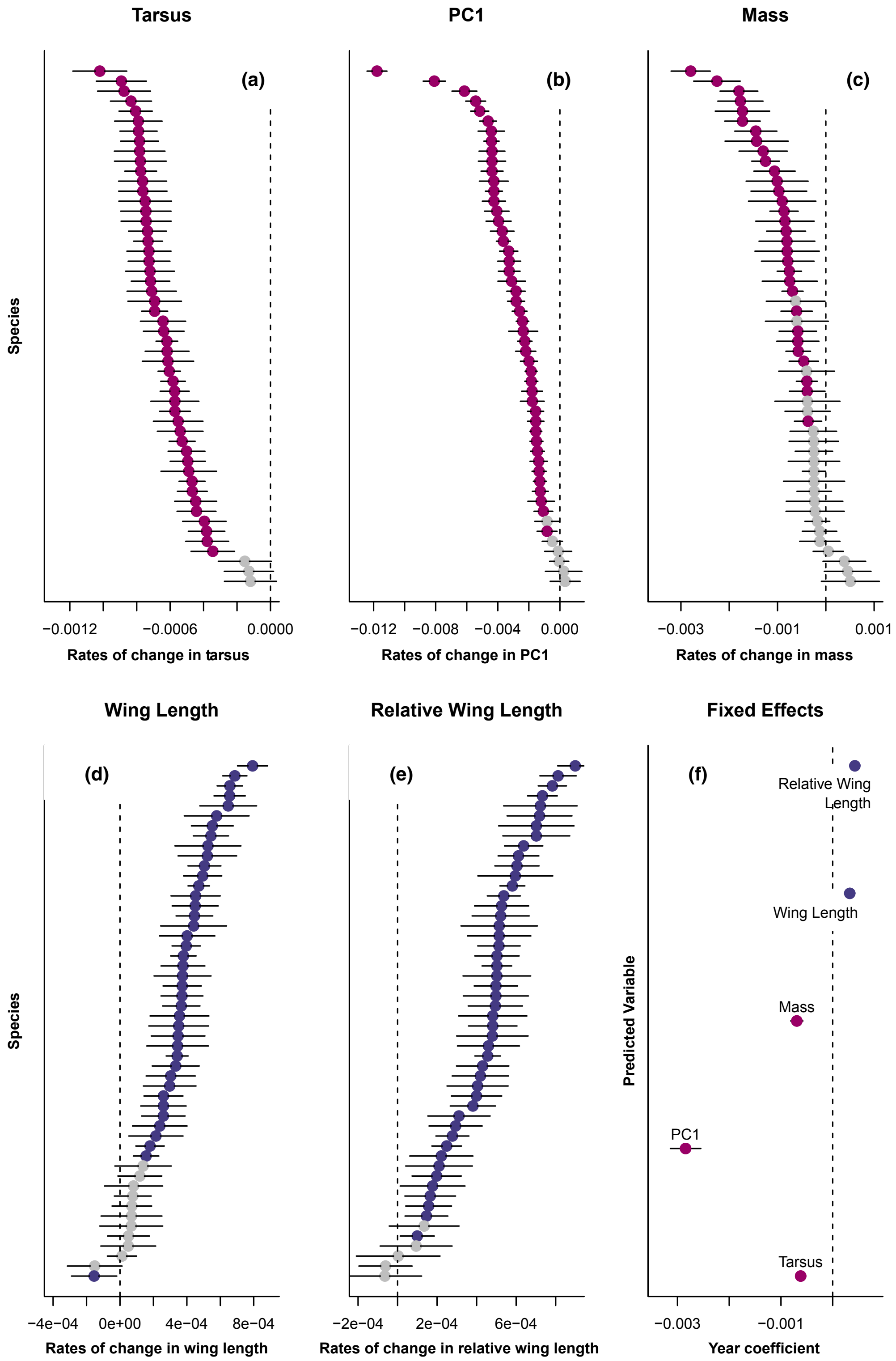

Figure 2 Morphological change has been consistent across species and metrics of body size. Across species, the rates of change in tarsus, PC1, mass, wing length, and relative wing length (represented as log(wing/tarsus)) have been remarkably consistent, with the indicators of body size declining (a–c) and wing length (d) and relative wing length (e) increasing from 1978 to 2016 in nearly all species. Points represent species-specific rates of change in each morphological trait, with the bars showing their respective standard errors, derived from the linear mixed-effects models. Grey points and bars indicate species where the standard error overlaps with zero. Note that due to the properties of ratios, modelling log(wing/tarsus) as a dependent variable is equivalent to modelling log(wing) as the dependent variable and including log(tarsus) as a predictor variable. Fixed effect estimates for year are shown for all response variables (f).

here are for the models that include all winter and summer variables, with tarsus as the index of body size (Table S7); results for PC1 were qualitatively similar (Table S8). Mean temperature on the breeding grounds was significantly negatively associated with body size (-1.22×10^{-3}, SE 1.93×10^{-4}, $P << 0.001$). Neither summer precipitation nor summer NDVI were significantly negatively associated with body size (precipitation: -2.34×10^{-4}, SE 2.36×10^{-4}, $P = 0.32$; NDVI: 1.39×10^{-4}, SE 4.57×10^{-4}, $P = 0.76$). Of the winter variables, there were significant associations between winter temperature and body size (9.39×10^{-4}, SE 1.94×10^{-4}, $P << 0.001$), and winter precipitation and body size (-1.17×10^{-3}, SE 3.74×10^{-4}, $P < 0.01$). Winter NDVI was not significantly associated with body size (-8.71×10^{-5}, SE 2.5×10^{-4}, $P = 0.73$). All results are robust to changes in the environmental variables as a result of different approaches to cropping the breeding ranges (Fig. S1), differences in the modelling approach (Tables S10 and S11), considering both age classes and hence the breeding range covariates only (Tables S7 and S8) and temporal lagging of the variables (Table S9). The predictor variables were not highly correlated with one another (the highest correlation, between summer NDVI and summer precipitation, was 0.56).

The three significant climatic predictors of body size (summer temperature, winter temperature and winter precipitation) also showed temporal fluctuations that are significantly associated with temporal fluctuations in body size. The cross correlation of the GAMs (i.e. short-term fluctuations) of mean summer temperature through time and the first differences of tarsus through time was negative and significant at a time lag of zero (correlation = -0.59, $P < 0.05$), and the correlation at a one-year lag (i.e. comparing tarsus at year t with summer temperatures at year t-1) was even stronger (correlation = -0.63, $P < 0.05$; Fig. 3). The cross correlations of the short-term fluctuations in winter temperature were not significant at a time lag of zero (correlation = 0.29, $P > 0.05$), but were significant and positive (correlation = 0.36, $P < 0.05$) at a one-year lag. Fluctuations in winter precipitation were also significantly correlated with fluctuations in tarsus at a time lag of zero (correlation = 0.61, $P < 0.05$). However, winter precipitation has only changed marginally over the course of the study (*Supporting Information–Climatic and Environmental Variables Through Time*).

Correlated rates of change in tarsus and wing length

As expected if increases in wing length are associated with body size decline, we found evidence that species' rates of change in body size were significantly negatively associated with species' rates of change of wing length (-0.4, SE -0.1, $P = 0.01$; Fig. 4). In other words, species that were getting smaller faster also underwent more rapid increases in wing length over the 40-year period. The slope of this relationship is consistent after correcting for phylogenetic relatedness, however the relationship was not significant (-0.3, SE 0.2, $P = 0.16$; Fig. 4). After controlling for both phylogenetic relatedness and treating the standard error in the random slope estimates as sampling error, we recovered a similar

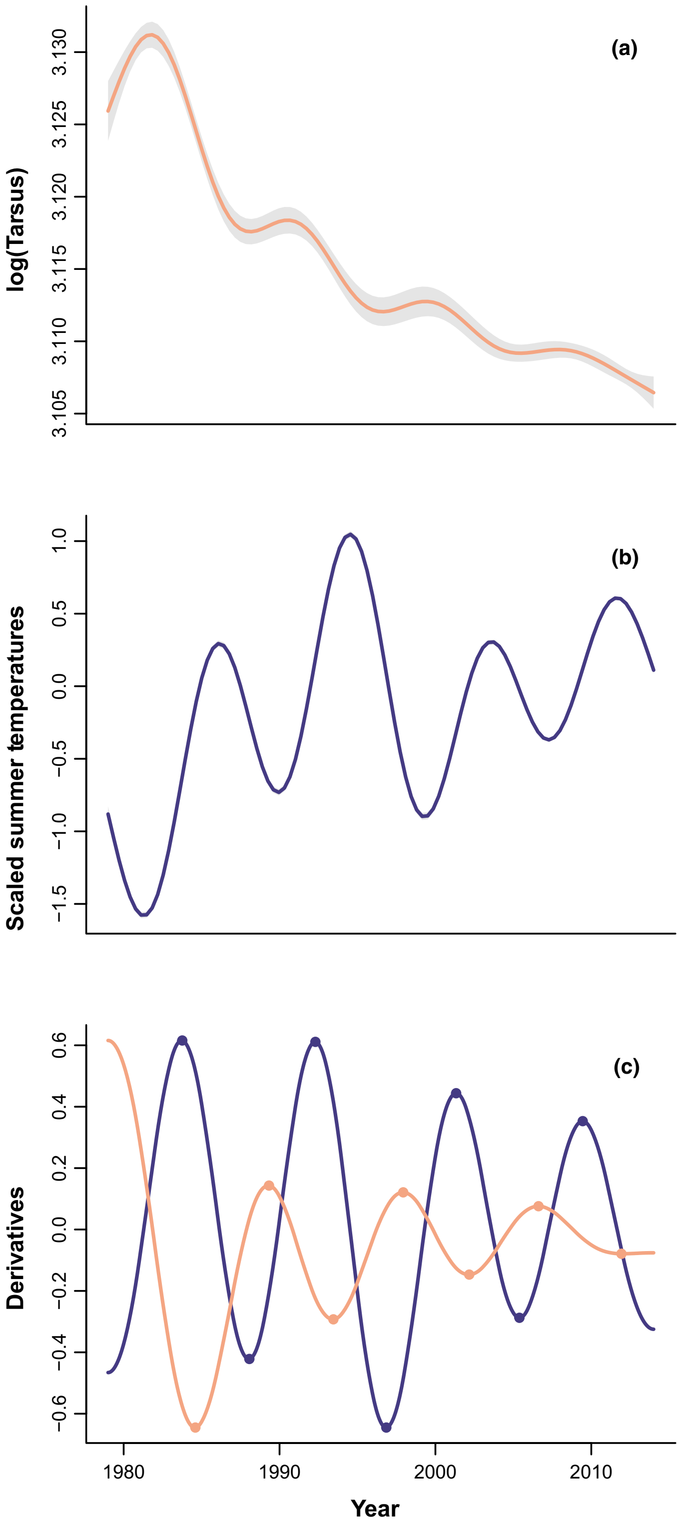

Figure 3 Evidence for temperature-related body size declines. In addition to the long-term negative relationship between summer temperature and tarsus after controlling for climatic and environmental variables, short-term fluctuations in tarsus (a) and summer temperature (b) are significantly inversely correlated. For ease of visualisation, we also present the GAM slope derivatives (c), which show that periods of rapid change in temperature are often followed closely by periods of inverse changes in tarsus. The points depict inflection points in the slopes (c).

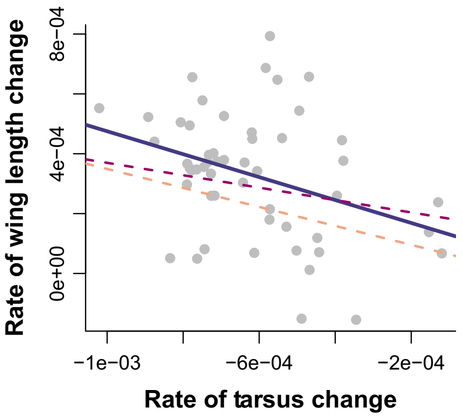

Figure 4 Species that are getting smaller faster are increasing in wing length faster. Species-specific estimates of rates of change in tarsus are significantly associated with species' rates of change in wing length (purple line; $P < 0.05$). Specifically, species with the fastest rates of tarsus declines (more negative slopes) also had higher rates of wing increase (positive slopes). Although this relationship is not significant after accounting for phylogenetic non-independence (peach dashed line) or accounting for both phylogenetic relatedness and error in the slope estimates (magenta dashed line), there is a consistent negative relationship among the models.

slope, however the relationship was not significant (mean slope of −0.2 and $P = 0.77$; Fig. 4).

DISCUSSION

Over the past four decades, for 52 species of migratory North American birds, body size has declined while wing length has increased. Despite the diversity of natural histories, habitats, and geographic distributions represented by the species in our data, these changes were remarkably consistent (Figs 1 and 2). Body size reductions were near-universal across species and were recovered regardless of whether we represented body size with tarsus, mass or PC1 (Fig. 2). In contrast to all other morphological metrics, wing length increased consistently across species (Fig. 2), indicating significant changes in body shape alongside the reductions in body size.

As predicted, based on our hypothesis, our model results showed a significant negative relationship between summer temperature and body size after controlling for plausible alternate environmental and climatic drivers of body size for such a diverse group of species. Additionally, summer temperature and body size show significantly correlated and synchronized shorter-term fluctuations, with changes in temperature consistently followed by changes in body size the following year (Fig. 3), providing further evidence that increasing summer temperature may have an important role in driving reductions in body size. Two additional variables (winter temperature and winter precipitation) were associated with body size in our models, though as we discuss below, the results are more difficult to interpret.

Developmental plasticity and selection on heritable variation represent two potential, non-exclusive mechanisms underlying the observed changes in body size in our data. Experimental studies have shown that higher ambient temperatures during nesting can lead to a reduction in avian adult body size as a result of developmental plasticity during the growth of nestlings (Mariette & Buchanan 2016; Andrew *et al.* 2017). This raises the compelling possibility that the consistent patterns of body size reduction we observe, in concert with the inverse correlation between body size and summer temperature, may be indicative of a plastic response to increased temperatures during development operating across the species in our study. However, the present data alone are not sufficient to distinguish developmental plasticity from changing selection pressures on body size.

Cold weather metabolic demands are often invoked to explain Bergmann's rule (or are considered an integral part of the rule; Watt *et al.* 2010)), with the smaller ratio of surface area to volume that accompanies increased body size considered beneficial in colder climates (Gardner *et al.* 2011; Sheridan & Bickford 2011; Teplitsky & Millien 2014). As such, warming winter temperatures could conceivably relax directional selection for larger body size, indirectly resulting in body size reduction, though we note that the migratory birds in our study vacate the coldest parts of their ranges during the winter, making cold weather selection on body size perhaps less relevant than for non-migratory organisms (Zink & Remsen 1986). In our linear mixed-models, winter temperature was significantly associated with body size and there was some evidence of coincidence in short-term fluctuations in body size and winter temperature (Fig S2). However, the association was positive, with increasing winter temperature predicted to yield larger bodies. Winter precipitation also predicted body size declines over the short- and long- term (Fig. S2 and Tables S7-S8, S10), but winter precipitation changed only subtly over the course of the study (*Supporting Information–Climate and Environmental Variable through Time*). Winter precipitation has been shown to have a positive impact on the food availability and body condition (mass) of birds wintering in precipitation-limited regions of the subtropics (Studds & Marra 2007). However, it is not clear how winter precipitation would lead to increased body size *per se*, and whether such dynamics are relevant across the 52 species in our study that winter in a wide variety of habitats, latitudes and climatic conditions. Thus, the influence of winter temperature and winter precipitation on body size remains uncertain.

More complex ecological dynamics of global change, such as food limitation as a result of climate change-driven phenological mismatches (Both *et al.* 2006; Van Gils *et al.* 2016), may also contribute to body size reduction. Given the observational nature of our data, it is not possible to completely rule out alternative, non-climatic selective pressures (e.g. reduced food availability), particularly if these processes are themselves driven by cyclical fluctuations in temperature. However, because the relationship between summer temperature and body size is evident after controlling for the long-term trends in the data, an alternative mechanism would need to exhibit both a 40-year correlation with body size as well as a significant relationship with body size after controlling for long-term trends. We did not find such a relationship for either winter or summer NDVI. Further, the consistent change in size across the species in our study – which are ecologically diverse and breed and winter in a wide variety of habitats with different phenological dynamics – supports a role for fundamental metabolic or physiological processes (e.g. temperature-body size relationships) influencing the observed trends.

Why has wing length increased as body size has declined in nearly all 52 species in our study? Avian wing length reflects a complex balance of selection pressures ranging from predator avoidance (Witter & Cuthill 1993; Kullberg *et al.* 1996; Swaddle & Lockwood 1998; Martin *et al.* 2018), to foraging behaviour (Norberg 1979; Fitzpatrick 1985), to flight efficiency (Rayner 1988; Pennycuick 2008). One possibility is that increasing selection for proportionately longer wings during the migratory period could be a result of increasing migratory distance through time. Migratory distance is positively correlated with wing length both within and across species in passerines (Winkler & Leisler 1992; Förschler & Bairlein 2011), suggesting that increases in wing length through time could be a response to northward shifts in breeding ranges if lower latitude wintering ranges have remained static. However, trajectories of warming-induced range shifts have been idiosyncratic across North American bird species (Tingley *et al.* 2009), and there is some evidence that the winter ranges of migratory birds may be moving northwards as well (La Sorte & Thompson 2007; Visser *et al.* 2009; La Sorte & Jetz 2012). By contrast, the observed increase in wing length is remarkably consistent across the species in our dataset (Fig. 2). Additionally, our data should be robust to changes in geographic distribution, as has been noted in other studies examining morphological change in migratory species (Van Buskirk *et al.* 2010). This is because all individuals sampled in our study are from populations that breed north of Chicago and winter south of Chicago, meaning that individuals from across the latitudinal breadth of the breeding grounds (Fig. S1) are likely to have been sampled in Chicago. As such, the majority of our data are likely consistently derived from individuals that breed within the core of their species' range (Van Buskirk *et al.* 2010), whereas range shifts should lead to selection for longer wing lengths at the southern and northern edges of the range. However, identifying the geographic provenance of individuals in our data set will be necessary to directly test the relationship between range shifts and morphological change.

Birds that migrate earlier and arrive first on the breeding grounds have been found to have longer wings than birds that arrive later (Bowlin 2007; Hahn *et al.* 2016), raising the possibility that advancing spring phenology may select for longer wings (Møller *et al.* 2017). Additional data are necessary to test this hypothesis. As with range shifts, evidence for phenological changes in timing of migration in North American birds has been variable (Knudsen *et al.* 2011; Mayor *et al.* 2017; Socolar *et al.* 2017; Horton *et al.* 2019), in contrast to the consistently increasing wing lengths observed among the species in our study. Further research should also address the possibility that habitat fragmentation may select for longer winged individuals due to increased distances between migratory stopover points or dispersal distances (Desrochers 2010).

Shifting geographic ranges, phenological changes and habitat fragmentation are plausible and non-exclusive selection pressures that could increase wing length among species. However, we suggest that the near-universal change in wing length across the ecologically diverse species in our data set may be evidence of a more fundamental physiological impact of rapid climate change on migratory birds. Specifically, we propose that longer wings relative to body size confer a selective advantage as body size declines in migratory birds, due to decreased metabolic efficiency (increased energy required per unit mass; Hudson *et al.* 2013) as individuals get smaller, coupled with the increase in flight efficiency associated with longer, more pointed wings (Bowlin & Wikelski 2008; Pennycuick 2008). As expected, if wing length is increasing to compensate for reductions in body size, those species that are getting smaller faster are also the species that are increasing in wing length faster; Fig. 4). The complexities of the physics of flight and their relationship with migration (Alerstam & Lindström 1990; Pennycuick 2008; Møller *et al.* 2017), coupled with the dynamic environmental context of migration as the world changes, preclude definitively identifying a mechanistic link between reductions in body size and an increase in wing length to maintain migration. Understanding if the observed morphological changes in body size and wing length represent a coupled response to global warming – versus decoupled trends driven by alternate forces – is an important avenue of future research, given the consistency with which body size and wing length have changed across this diverse group of species.

CONCLUSIONS

Across 52 species of migratory birds, we find near-universal reductions in size over the past four decades. We identify a significant relationship between summer temperatures and body size after controlling for year and a suite of climatic and environmental factors; in addition, we find correlated and synchronised short-term fluctuations in summer temperature and body size that are consistent with long-term size reduction across species. Taken together, we interpret this as strong evidence that warming temperatures are driving reductions in body size across this diverse group of taxa. The observed concomitant increase in wing length may have expansive ecological implications (Norberg 1990), particularly as the divergent trends in body size and wing length combine to drive a change in shape that may face opposing selective pressures. Should size and shape be a coupled response to increasing temperatures, understanding how these changes interact with macroecological responses to climate change, including shifts in phenology and geographic range, may be an important dimension of predicting biotic responses to global warming.

ACKNOWLEDGEMENTS

We thank the staff, curators and volunteers of the Field Museum, and the Chicago Bird Collision Monitors, for their assistance in salvaging birds. For helpful comments, we thank S. Dubay, N. Senner, J. Bates, S. Hackett, B. Marks, J. Voight, M. Jain, M. Zelditch, S. Cambell, T. Pegan, E. Gulson and two anonymous reviewers. We thank D. Megahan for Fig. S1. For advice on statistical analyses, we thank M. Clark (University of Michigan Center for Statistical Computing and Research).

AUTHORSHIP

BCW and BMW designed the study, performed the research, and wrote the manuscript. DW and MH collected the data. MZ contributed to data analyses. DW, MH, AE, and MW contributed to data development. All authors provided comments on the manuscript.

DATA AVAILABILITY STATEMENT

All morphological data supporting the results will be available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8pk0p2nhw.

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Editor, Ryan Norris
Manuscript received 28 October 2019
Manuscript accepted 30 October 2019