

1 **Title:** Shared morphological consequences of global warming in North American migratory  
2 birds

3  
4 **Short Title:** Recent morphological shifts in migratory birds

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27 **ABSTRACT**

28  
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29 Increasing temperatures associated with climate change are predicted to cause reductions in body  
30 size, a key determinant of animal physiology and ecology. Using a four-decade specimen series  
31 of 70,716 individuals of 52 North American migratory bird species, we demonstrate that  
32 increasing annual summer temperature over the 40-year period predicts consistent reductions in  
33 body size across these diverse taxa. Concurrently, wing length—an index of body shape that  
34 impacts numerous aspects of avian ecology and behavior—has consistently increased across  
35 species. Our findings suggest that warming-induced body size reduction is a general response to  
36 climate change, and reveal a similarly consistent and unexpected shift in body shape. We  
37 hypothesize that increasing wing length represents a compensatory adaptation to maintain  
38 migration as reductions in body size have increased the metabolic cost of flight. An improved  
39 understanding of warming-induced morphological changes is important for predicting biotic  
40 responses to global change.

## 41 INTRODUCTION

42  
43 Body size is an important determinant of animal ecology and life history (Brown 1995;  
44 McGill *et al.* 2006), influencing physiological (Hudson *et al.* 2013) and morphological (Gould  
45 1966; Outomuro & Johansson 2017) functions, as well as ecological and social interactions  
46 (Yodzis & Innes 2002; McGill *et al.* 2006; Prum 2014). Within species, there is evidence that  
47 individuals tend to be smaller in the warmer parts of their ranges, a pattern often interpreted as an  
48 intraspecific derivative of Bergmann’s rule (Bergmann 1847; Rensch 1938; Mayr 1956;  
49 Blackburn *et al.* 1999). This association between warmer temperatures and smaller bodies  
50 suggests that anthropogenic climate change may cause intraspecific shifts toward smaller body  
51 size in a temporal analog to geographic patterns. However, despite the widespread appreciation  
52 of the fundamental importance of body size for ecological and evolutionary processes, the  
53 drivers and universality of temperature-body size relationships across space and time remain  
54 contested (Watt *et al.* 2010; Forster *et al.* 2011; Gardner *et al.* 2011; Riemer *et al.* 2018).  
55 Determining whether rapid body size reductions are occurring in response to increasing  
56 temperatures is important for understanding how climate change will influence the phenotypes  
57 and ecological dynamics of species in a warming world.

58 Although the possibility of body size reduction in response to global warming has been  
59 suggested for decades (Smith *et al.* 1995; Yom-Tov 2001), empirical support remains mixed

60 (Gardner *et al.* 2014; Salewski *et al.* 2014; Teplitsky & Millien 2014; Dubos *et al.* 2018). This  
61 uncertainty may be due, in part, to a scarcity of morphological time series datasets containing  
62 sufficiently dense sampling to test the influence of temporal fluctuations in climate on body size  
63 (as opposed to simply associating long-term morphological trends with periods of global  
64 warming), and to do so across co-distributed species that experience similar climatic regimes. By  
65 contrast, those datasets that have sampled large numbers of individuals consistently across time  
66 frequently do not have measurements from enough morphological characters to distinguish  
67 changes in body size from changes in body shape that may be driven by alternate selection  
68 pressures. Consequently, the influence of warming-driven changes in body size on ecologically-  
69 important dimensions of body shape remains largely unknown.

70         Migratory birds are an important but complex system for understanding the  
71 morphological responses of biota to increasing temperatures. The extreme energetic demands of  
72 long-distance migration have shaped the morphology of migratory birds for efficient flight  
73 (Winkler & Leisler 1992; Lockwood *et al.* 1998). Because migratory birds are under strong  
74 selection for high site fidelity, perturbations that hinder an efficient return to the breeding  
75 grounds are likely to reduce reproductive success (Winger *et al.* 2019). If warming temperatures  
76 cause body size reductions in migratory birds, concurrent changes in body shape related to the  
77 allometry of flight efficiency may be necessary to maintain migratory patterns. Although  
78 migratory species have garnered significant attention from researchers interested in biotic  
79 responses to rapid environmental change, particularly as they relate to phenology and geographic  
80 range, the extent to which migratory birds are changing size and shape in response to  
81 anthropogenic global warming remains uncertain (Van Buskirk *et al.* 2010; Goodman *et al.*  
82 2012; Salewski *et al.* 2014; Collins *et al.* 2017a, b; Dubos *et al.* 2018).

83         A persistent challenge in understanding recent morphological changes in migratory birds  
84 is the characterization of avian size and shape. Frequently used indices to assess changes in avian  
85 body size through time, such as mass and wing length, may be problematic in migratory birds;  
86 mass is highly variable for migratory species, given rapid fat gains and losses during migration  
87 (Alerstam & Lindström 1990; Morris *et al.* 1996), and wing length is positively correlated with  
88 migratory distance (Zink & Remsen 1986; Förschler & Bairlein 2011). Nevertheless, studies on  
89 recent body size changes in birds in migratory species have often represented body size using  
90 wing length or mass (Yom-Tov *et al.* 2006; Salewski *et al.* 2010; Van Buskirk *et al.* 2010;

91 Goodman *et al.* 2012), making it difficult to identify changes in body size and to disentangle  
92 them from shifts in shape that may be driven by other factors.

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

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

## 115 116 **Methods**

117 *Specimen and data collection.*—Since 1978, The Field Museum’s collections personnel  
118 and volunteers have operated a salvage operation to retrieve birds that collided with buildings in  
119 Chicago, IL, USA during their spring or fall migrations (Fig. S1). On every individual bird, a  
120 single person (David E. Willard) measured: 1) tarsus and bill length using digital calipers; 2) the  
121 length of the relaxed wing using a wing rule; and 3) mass using a digital scale. All measurements

122 were taken on fresh or thawed carcasses prior to preparation as specimens, which, given the ease  
123 of manipulation, is expected to improve the precision of measurements compared to  
124 measurements of live birds or dried specimens. Sex was determined based on gonadal inspection,  
125 and skull ossification enabled aging to Hatch Year (HY; fall birds hatched that summer) or After  
126 Hatch Year (AHY; all spring birds and all fall birds at least one year old).

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

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

146 We conducted the PCA using the logarithms of tarsus, wing length, bill length, and the  
147 cube root of mass (because it represents a volume) for all specimens with complete data. We  
148 used the ‘princomp’ function in the stats package in R, constructing the axes using a covariance  
149 matrix as the scale of variables was similar; the loadings on PC1 were nearly indistinguishable if  
150 a correlation matrix was used. We interpreted scores on the first axis of the PCA (PC1) as a  
151 metric of body size, following common practice (e.g. Grant & Grant 2008). Because all variables  
152 were positively loaded onto PC1 and are expected to scale positively with body size, we

153 interpreted PC1 scores as positively related to body size. We transformed all PC1 scores to be  
154 positive (by adding the absolute value of the minimum score, plus 0.01 to all scores).

155 *Testing environmental determinants of morphological change.*— To test hypotheses on  
156 the environmental drivers of changes in body size, we generated species-specific estimates of  
157 climatic and environmental variables (temperature, precipitation, and Normalized Difference  
158 Vegetation Index [NDVI], a proxy for resource availability) on the breeding and wintering  
159 grounds. First, we cropped breeding, wintering and resident ranges for all species (BirdLife  
160 International 2015) to exclude unlikely breeding destinations for birds migrating through  
161 Chicago (Fig. S1). For each species, we then calculated mean temperature, precipitation, and  
162 mean maximum NDVI during June and December of each year (1981-2016) in the region  
163 representing each species' likely breeding and wintering grounds, respectively (*SI Environmental*  
164 *Data*). We also tested the sensitivity of our results to variation in how ranges were cropped (Fig.  
165 S1).

166 We used linear mixed models to quantify the impacts of these species-specific  
167 environmental variables on body size. We considered tarsus length to be the most appropriate  
168 and precise univariate metric of intraspecific variation in body size (Rising & Somers 1989;  
169 Senar & Pascual 1997), given high variation in mass observed within individuals during  
170 migration and the correlation between migratory distance and wing length often observed among  
171 individuals (Zink & Remsen 1986, Förschler & Bairlein 2011). We also modelled PC1 as the  
172 dependent variable to ensure that our results are robust to different characterizations of body  
173 size. In these models, year, the environmental variables (i.e., precipitation, temperature, and  
174 NDVI on the breeding and wintering grounds), sex, and season of collection were included as  
175 fixed effects and random intercepts were included for each species. Models with random slopes  
176 for all environmental variables did not converge, suggesting the data do not support such a  
177 complex model (Bates *et al.* 2015a); therefore, we made the simplifying assumption that all  
178 species are responding similarly to environmental conditions. All environmental variables were  
179 scaled to a mean of zero and a standard deviation of one. These models only included AHY  
180 birds, as HY birds had not experienced winter conditions, and the environmental covariates from  
181 the season immediately prior to collection (i.e., season  $t$ ). In addition, we fitted the model using  
182 all age classes but included only the summer environmental variables, and age, as fixed effects.  
183 Analogous multilevel Bayesian models that accounted for phylogenetic relatedness were

184 conducted (*SI Bayesian modeling*). Because the exact year of birth (and development) for AHY  
185 birds is unknown, we tested for the impact of uncertainty in the age of AHY birds by running  
186 two alternative models with environmental covariates from each of the two years preceding  
187 collection (i.e., seasons  $t-1$ , and  $t-2$ , *SI Sensitivity of Results to Time Lag*).

188 *Testing environmental predictors of fluctuation in body size.*—To further explore changes  
189 in body size in relation to the climatic and environmental variables, we tested whether  
190 fluctuations in tarsus were correlated and temporally synchronized with fluctuations in each of  
191 the environmental variables identified as significant (i.e.  $P < 0.05$ ) in the linear mixed-effects  
192 models. We fit generalized additive models (GAMs) to each significant variable, modeling them  
193 as a function of time and with a random effect for species. We used the ‘gam’ function in the R  
194 package mgcv (Wood 2011) with default smoothing parameters determined by the model fitting.

195 We used cross correlation analysis (CCA) to analyze the relationships between smoothed  
196 fluctuations in the dependent variables through time from the GAMs (that is, to test for  
197 synchronized fluctuations in tarsus and the climate variables). In CCA, time series data should be  
198 stationary such that after removing any temporal trend, the mean and variance do not change  
199 over time. We tested whether the predicted values of the GAMs were stationary using the  
200 Kwiatkowski Phillips Schmidt Shin test (Koupidis & Bratsas 2019). All climatic and  
201 environmental variables were stationary, but the tarsus data were not, so we used the first  
202 differences of the tarsus time series (the differences between tarsus at time  $t$  and  $t-1$ )—which  
203 were stationary—to compare fluctuations among tarsus and the environmental variables. The  
204 CCA was implemented using the ‘ccf’ function in the R package tseries (Trapletti & Hornik  
205 2017). For visualization purposes, we also calculated the derivatives of the GAMs for summer  
206 temperature and tarsus (i.e., the change in slopes of tarsus and environmental variables through  
207 time) at 1,000 points along the time series, using the ‘derivatives’ function in the R package  
208 gratia (Simpson 2019).

209 *Association between rates of change of wing and tarsus.*—To test whether rates of change  
210 of wing length were associated with rates of change in body size, we tested the correlation  
211 between the species-specific rates of change of wing and tarsus from the linear mixed-effects  
212 models for wing and tarsus, respectively (Figure 2, Tables S2 and S5). We used three methods to  
213 calculate the correlation in slopes: a linear model, a phylogenetic generalized least squares (pgls)  
214 model implemented in the R package ape (Paradis *et al.* 2004; Pinherio *et al.* 2013), and a pgls

215 approach that treated the standard errors of the random slope estimates in both rates of change of  
216 wing length and rates of change of tarsus as sampling error (Ives *et al.* 2007), implemented using  
217 the ‘ppls.Ives’ function from the R package phytools (Revell 2012). We fit the latter model  
218 10,000 times and report the mean parameter results.

219

## 220 **RESULTS**

221

### 222 **Consistent reduction in body size**

223 Despite the ecological and phylogenetic diversity among species, we found consistent  
224 reductions in all indices of body size (tarsus, mass, and PC1) across species over the course of  
225 the study (Fig. 1, Fig. 2). We found significant negative relationships between year and tarsus  
226 length ( $-6.20 \times 10^{-4}$ , SE  $2.93 \times 10^{-5}$ ,  $P \ll 0.001$ ), mass ( $-6.94 \times 10^{-4}$ , SE  $1.19 \times 10^{-4}$ ,  $P \ll 0.001$ ),  
227 and PC1 ( $-1.76 \times 10^{-3}$ , SE  $5.82 \times 10^{-5}$ ,  $P \ll 0.001$ ); see Tables S2-S4 for full model results. These  
228 declines represent a mean decline of 2.4% in tarsus length and 2.6% in mass from 1978-2016.  
229 Nearly all species-specific changes in tarsus were declines, with standard error estimates that did  
230 not overlap with zero, and all species with significant changes in mass and PC1 got smaller (Fig.  
231 2). The consistency among species is reflected in the extremely low (near zero) slope variances  
232 of the random year slopes for species across size indices ( $2.45 \times 10^{-8}$ ,  $5.51 \times 10^{-7}$ , and  $1.22 \times 10^{-7}$ ,  
233 for tarsus, body mass and PC1, respectively, Table S2-S4). Similar results were obtained using  
234 multilevel Bayesian models that accounted for phylogenetic relatedness (Table S6).

235

### 236 **Consistent increases in wing length resulted in widespread changes in body shape**

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

243

### 244 **Increasing summer temperatures drive body size decline**



245 We recovered several significant relationships between climatic and environmental  
246 variables and body size. Results presented here are for the models that include all winter and  
247 summer variables, with tarsus as the index of body size (Table S7); results for PC1 were  
248 qualitatively similar (Table S8). Mean temperature on the breeding grounds was significantly  
249 negatively associated with body size ( $-1.22 \times 10^{-3}$ , SE  $1.93 \times 10^{-4}$ ,  $P \ll 0.001$ ). Neither summer  
250 precipitation nor summer NDVI were significantly negatively associated with body size  
251 (precipitation:  $-2.34 \times 10^{-4}$ , SE  $2.36 \times 10^{-4}$ ,  $P = 0.32$ ; NDVI:  $1.39 \times 10^{-4}$ , SE  $4.57 \times 10^{-4}$ ,  $P =$   
252  $0.76$ ). Of the winter variables, there were significant associations between winter temperature  
253 and body size ( $9.39 \times 10^{-4}$ , SE  $1.94 \times 10^{-4}$ ,  $P \ll 0.001$ ), and winter precipitation and body size ( $-$   
254  $1.17 \times 10^{-3}$ , SE  $3.74 \times 10^{-4}$ ,  $P < 0.01$ ). Winter NDVI was not significantly associated with body  
255 size ( $-8.71 \times 10^{-5}$ , SE  $2.5 \times 10^{-4}$ ,  $P = 0.73$ ). All results are robust to changes in the environmental  
256 variables as a result of different approaches to cropping the breeding ranges (Fig. S1),  
257 differences in the modeling approach (Tables S10-S11), considering both age classes and hence  
258 the breeding range covariates only (Tables S7-S8) and temporal lagging of the variables (Table  
259 S9). The predictor variables were not highly correlated (the highest correlation, between summer  
260 NDVI and summer precipitation, was 0.56).

261 The three significant climatic predictors of body size (summer temperature, winter  
262 temperature and winter precipitation) also showed temporal fluctuations that are significantly  
263 associated with temporal fluctuations in body size. The cross correlation of the GAMs (i.e.,  
264 short-term fluctuations) of mean summer temperature through time and the first differences of  
265 tarsus through time was negative and significant at a time lag of zero (correlation =  $-0.59$ ,  $P <$   
266  $0.05$ ), and the correlation at a one-year lag (i.e., comparing tarsus at year  $t$  with summer  
267 temperatures at year  $t-1$ ) was even stronger (correlation =  $-0.63$ ,  $P < 0.05$ ; Fig. 3). The cross  
268 correlations of the short-term fluctuations in winter temperature were not significant at a time lag  
269 of zero (correlation =  $0.29$ ,  $P > 0.05$ ), but were significant and positive (correlation =  $0.36$ ,  $P <$   
270  $0.05$ ) at a one-year lag. Fluctuations in winter precipitation was also significantly correlated with  
271 fluctuations in tarsus at a time lag of zero (correlation =  $0.61$ ,  $P < 0.05$ ). However, winter  
272 precipitation has only changed marginally over the course of the study (*SI Climatic and*  
273 *Environmental Variables Through Time*).

274 *Correlated Rates of Change in Tarsus and Wing Length.*— As expected if increases in  
275 wing length are associated with body size decline, we found evidence that species' rates of

276 change in body size were significantly, negatively associated with species' rates of change of  
277 wing length (-0.4, SE -0.1,  $P = 0.01$ ; Fig. 4). In other words, species that were getting smaller  
278 faster also underwent more rapid increases in wing length over the 40-year period. The slope of  
279 this relationship is consistent after correcting for phylogenetic relatedness, however the  
280 relationship was not significant (-0.3, SE 0.2,  $P = 0.16$ ; Fig. 4). After controlling for both  
281 phylogenetic relatedness and treating the standard error in the random slope estimates as  
282 sampling error, we recovered a similar slope, however the relationship was not significant (mean  
283 slope of -0.2 and  $P = 0.77$ ; Fig. 4).

284

## 285 **DISCUSSION**

286

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

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

304 Developmental plasticity and selection on heritable variation represent two potential,  
305 non-exclusive mechanisms underlying the observed changes in body size in our data.  
306 Experimental studies have shown that higher ambient temperatures during nesting can lead to a

307 reduction in avian adult body size as a result of developmental plasticity during the growth of  
308 nestlings (Mariette & Buchanan 2016; Andrew *et al.* 2017). This raises the compelling  
309 possibility that the consistent patterns of body size reduction we observe, in concert with the  
310 inverse correlation between body size and summer temperature, may be indicative of a plastic  
311 response to increased temperatures during development operating across the species in our study.  
312 However, the present data alone are not sufficient to distinguish developmental plasticity from  
313 changing selection pressures on body size.

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

334 More complex ecological dynamics of global change, such as food limitation as a result  
335 of climate change-driven phenological mismatches (Both *et al.* 2006; Van Gils *et al.* 2016), may  
336 also contribute to body size reduction. Given the observational nature of our data, it is not  
337 possible to completely rule out alternative, non-climatic selective pressures (e.g., reduced food

338 availability), particularly if these processes are themselves driven by cyclical fluctuations in  
339 temperature. However, because the relationship between summer temperature and body size is  
340 evident after controlling for the long-term trends in the data, an alternative mechanism would  
341 need to exhibit both a 40-year correlation with body size as well as a significant relationship with  
342 body size after controlling for long-term trends. We did not find such a relationship for either  
343 winter or summer NDVI. Further, the consistent change in size across the species in our study —  
344 which are ecologically diverse and breed and winter in a wide variety of habitats with different  
345 phenological dynamics — supports a role for fundamental metabolic or physiological processes  
346 (e.g., temperature-body size relationships) influencing the observed trends.

347 Why has wing length increased as body size has declined in nearly all 52 species in our  
348 study? Avian wing length reflects a complex balance of selection pressures ranging from  
349 predator avoidance (Witter & Cuthill 1993; Kullberg *et al.* 1996; Swaddle & Lockwood 1998;  
350 Martin *et al.* 2018), to foraging behavior (Norberg 1979; Fitzpatrick 1985), to flight efficiency  
351 (Rayner 1988; Pennycuick 2008). One possibility is that increasing selection for proportionately  
352 longer wings during the migratory period could be a result of increasing migratory distance  
353 through time. Migratory distance is positively correlated with wing length both within and across  
354 species in passerines (Winkler & Leisler 1992; Förschler & Bairlein 2011), suggesting that  
355 increases in wing length through time could be a response to northward shifts in breeding ranges  
356 if lower latitude wintering ranges have remained static. However, trajectories of warming-  
357 induced range shifts have been idiosyncratic across North American bird species (Tingley *et al.*  
358 2009), and there is some evidence that the winter ranges of migratory may be moving northwards  
359 as well (La Sorte & Thompson 2007; Visser *et al.* 2009; La Sorte & Jetz 2012). By contrast, the  
360 observed increase in wing length is remarkably consistent across the species in our dataset (Fig.  
361 2). Additionally, our data should be robust to changes in geographic distribution, as has been  
362 noted in other studies examining morphological change in migratory species (Van Buskirk *et al.*  
363 2010). This is because all individuals sampled in our study are from populations that breed north  
364 of Chicago and winter south of Chicago, meaning that individuals from across the latitudinal  
365 breadth of the breeding grounds (Fig. S1) are likely to have been sampled in Chicago. As such,  
366 the majority of our data are likely consistently derived from individuals that breed within the  
367 core of their species' range (Van Buskirk *et al.* 2010), whereas range shifts should lead to  
368 selection for longer wing lengths at the southern and northern edges of the range. However,

369 identifying the geographic provenance of individuals in our dataset will be necessary to directly  
370 test the relationship between range shifts and morphological change.

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

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

400

401 **Conclusions**

402

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

416

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602

## 603 **Figure Legends**

604 **Fig. 1. Body size has become smaller through time.** Tarsus length declined in nearly all  
605 species in the dataset (Fig. 2A) with the nine most highly sampled species shown here. Dashed  
606 lines have a slope of zero and an intercept equal to the mean tarsus length for each species.  
607

## 608 **Fig. 2. Morphological change has been consistent across species and metrics of body size.**

609 Across species, the rates of change in tarsus, PC1, mass, wing length, and relative wing length  
610 (represented as  $\log(\text{wing}/\text{tarsus})$ ) have been remarkably consistent, with the indicators of body  
611 size declining (a-c) and wing length (d) and relative wing (e) length increasing from 1978-2016  
612 in nearly all species. Points represent species-specific rates of change in each morphological  
613 trait, with the bars showing their respective standard errors, derived from the linear mixed-effects  
614 models. Grey points and bars indicate species where the standard error overlaps with zero. Note  
615 that due to the properties of ratios, modelling  $\log(\text{wing}/\text{tarsus})$  as a dependent variable is  
616 equivalent to modelling  $\log(\text{wing})$  as the dependent variable and including  $\log(\text{tarsus})$  as the

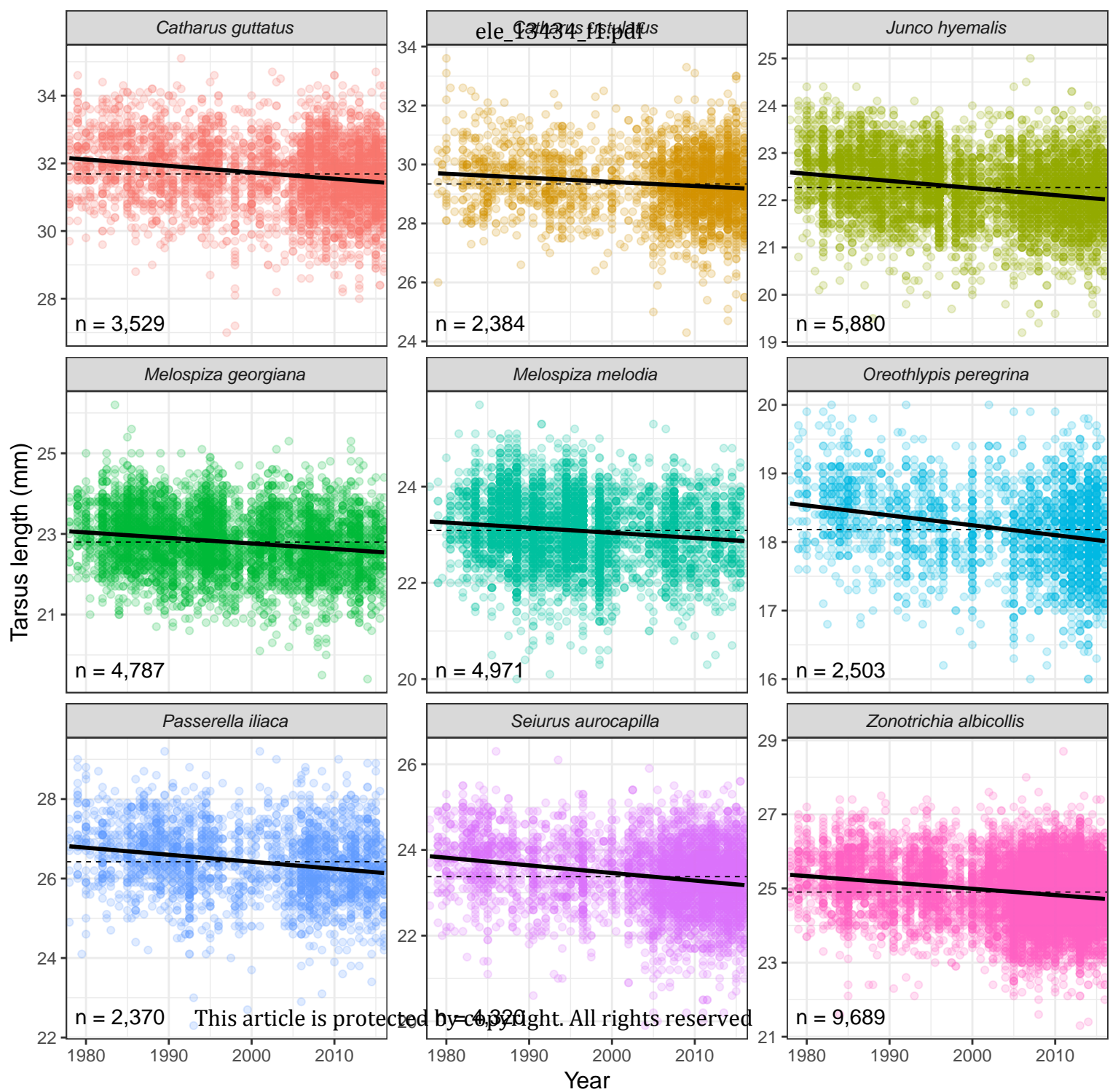
617 predictor variable. Fixed effect estimates for year are shown for all response variables (f).

618

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

626

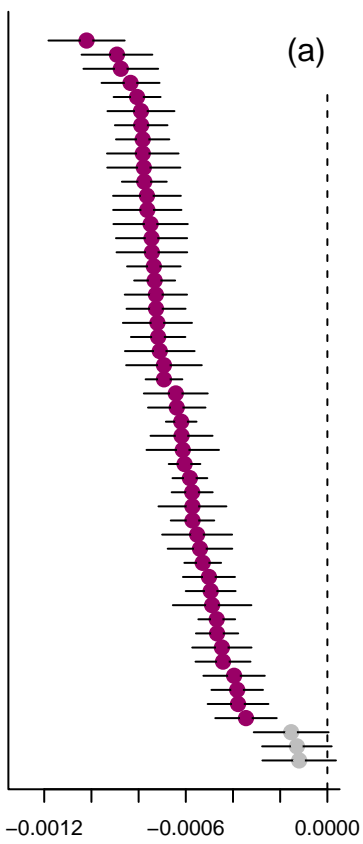
627 **Fig. 4. Species that are getting smaller faster are increasing in wing length faster.** Species-  
628 specific estimates of rates of change in tarsus are significantly associated with species' rates of  
629 change in wing length (purple line;  $P < 0.05$ ). Specifically, species with the fastest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



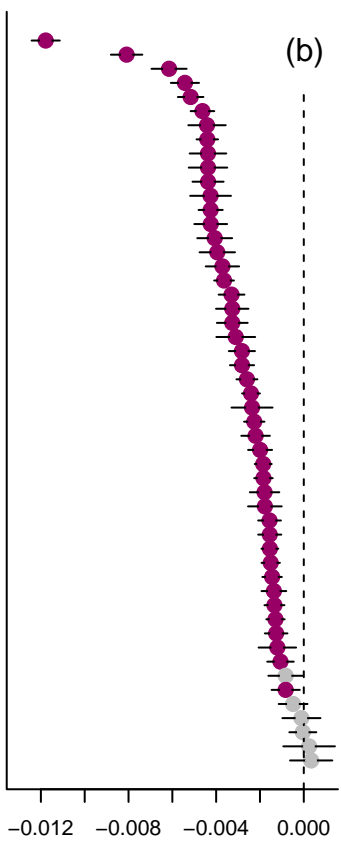
Tarsus

Mass

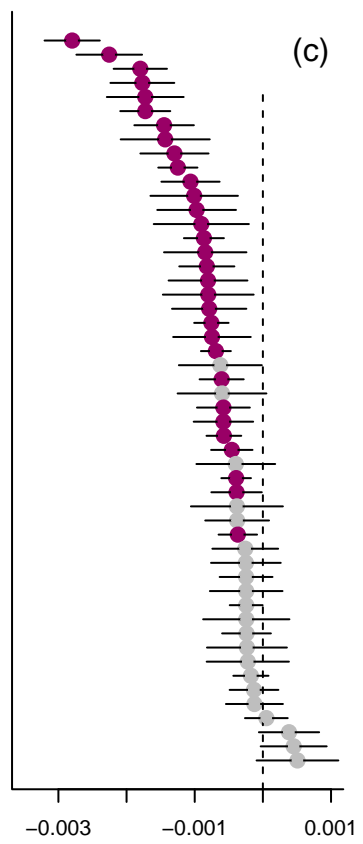
Species



(a)



(b)



(c)

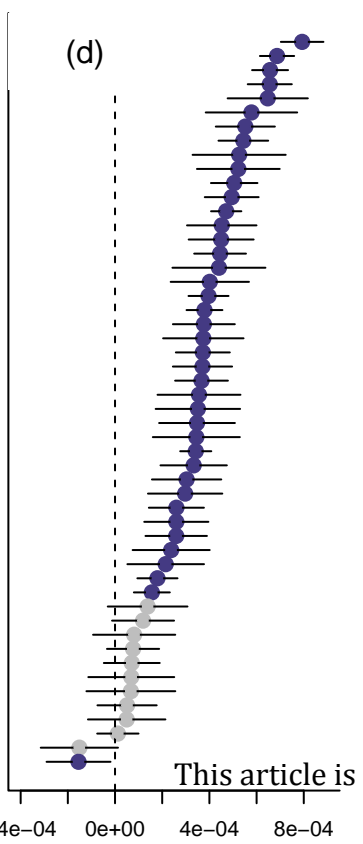
Wing Length

Relative Wing Length

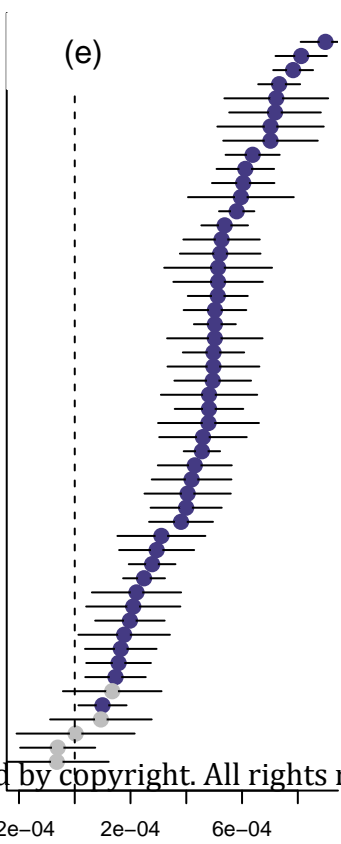
Fixed Effects

Species

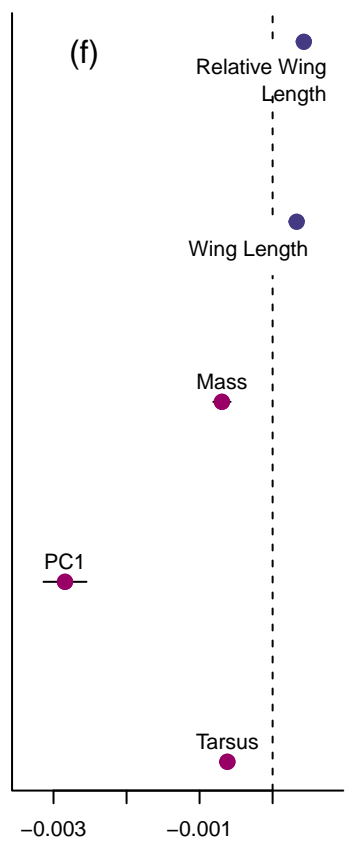
Predicted Variable



(d)



(e)



(f)

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Rates of Change in Wing Length

Rates of Change in Relative Wing Length

Year Coefficient

