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Heterogeneous changes in avian body size across and within species

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Abstract Contemporary climate change has been linked to widespread changes in phenology and in the geographic distribution of species. Based on Bergmann's rule, body sizes of birds have been predicted to decline as global temperatures increase. We examined changes in body size of 20 resident and short-distance migrant passerine species in eastern North America between 1980 and 2012, and how changes in resident species related to annual mean summer and mean winter temperatures. We found that wing length generally increased and that fat-free mass did not change significantly. Fat score, a measure of body condition, declined over time. However, changes in wing length, fat-free mass, and fat score all showed significant variation across species. For resident species, increasing mean summer temperatures were generally associated with shorter wing lengths, but were not related to fat-free mass or fat score. Increasing mean winter temperatures were associated with reduced fat-free mass but not with wing length or fat score. Temperature effects did not vary significantly across species for any of the three measures. Across resident species, the magnitude of body size change over time was not related to the influence of mean winter or mean summer temperatures, and may have been driven by other factors. Our findings contrast with those from a study at a nearby bird banding station, in which widespread

decreases in wing length and fat-free mass were observed. Our results demonstrate that populations of the same species can exhibit opposing changes in body size over short geographic distances (<250 km). We conclude that changes in body size are heterogeneous over short time scales and can vary across and within species over short distances. Continued advances in understanding how body size changes relate to climate change must embrace this inherent complexity and consider alternative hypotheses.

Keywords Bergmann's rule · Climate change · Body mass · Morphology · Passerine · Wing length

Zusammenfassung

Heterogene Veränderungen in der Körpergröße von Vögeln zwischen und innerhalb von Arten

Der momentane Klimawandel wurde in Verbindung gebracht mit weitverbreiteten Veränderungen in der Phänologie und der geographischen Verbreitung von Arten. Auf der Grundlage von Bergmanns Regel wurde vorausgesagt, dass die Körpergröße bei Vögeln mit der weltweiten Zunahme der Temperatur abnehmen sollte. Wir untersuchten zwischen 1980 und 2012 die Körpergröße von 20 nicht-ziehenden und Kurzstrecken-ziehenden Singvögeln im östlichen Nordamerika, und wie deren Änderung sich zu jährlichen Sommer- und Wintermitteln der Temperatur verhält. Wir fanden, dass die Flügelänge sich generell vergrößerte und sich die fettfreie Masse nicht signifikant änderte. Der Fettwert, ein Maß für die körperliche Gesundheit, nahm über die Zeit ab. Allerdings zeigten sowohl die Änderungen der Flügelänge, als auch die fettfreie Masse und der Fettwert signifikante Unterschiede im Artvergleich. Bei den nicht-ziehenden Arten standen

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steigende Sommertemperaturen generell in Verbindung mit kleinerer Flügellänge, aber hatten keinen Zusammenhang mit fettfreier Masse oder Fettwert. Eine geringere fettfreie Masse, nicht aber Flügellänge oder Fettwert, stand im Zusammenhang mit steigenden Temperaturen im Wintermittel. Die Temperatureffekte unterschieden sich für keines der drei Maße signifikant zwischen Arten. Über alle nicht-ziehenden Arten hinweg war das Ausmaß der Veränderung der Körpergröße über die Zeit nicht korreliert mit dem Einfluss der mittleren Winter- oder Sommertemperatur und könnte durch andere Faktoren bedingt sein. Unsere Ergebnisse stehen im Kontrast zu denen einer nahegelegenen Beringungsstation, in der weitreichende Abnahmen in der Flügellänge und der fettfreien Körpermasse beobachtet wurden. Unsere Ergebnisse zeigen, dass Populationen einer einzigen Art über kurze Entfernungen (<250 km) entgegengesetzte Veränderungen in der Körpergröße aufweisen können. Wir schließen daraus, dass Veränderungen in der Körpergröße über kurze Zeiträume heterogen sind und sich innerhalb von und zwischen Arten auch über kurze Entfernungen unterscheiden können. Ständige Fortschritte im Verständnis des Zusammenhangs zwischen Veränderungen in der Körpergröße und Klimawechsel müssen die Komplexität erfassen und alternative Hypothesen ins Gespräch bringen.

Introduction

Mounting evidence continues to demonstrate that the Earth's climate is changing rapidly (Jones et al. 2001; Karl and Trenberth 2003; Hansen et al. 2006; IPCC 2014). Particularly for birds and other endotherms, climate change has been linked to changes in phenology (Crick 2004; Torti and Dunn 2005; Macmynowski et al. 2007; Miller-Rushing et al. 2008; Végvári et al. 2010), morphology (Yom-Tov et al. 2006; Van Buskirk et al. 2010; Gardner et al. 2011; Goodman et al. 2012), geographic distribution (Graves 1991; Parmesan and Yohe 2003; Tingley et al. 2009; Thomas 2010), and population size (Jiguet et al. 2010; Ozgul et al. 2010). Body size has been predicted to change with increasing temperatures based on Bergmann's (1847) rule, a biogeographic pattern that relates larger body sizes of endothermic animals to increasing latitude (a correlate of decreasing temperature). Although originally formulated for homeotherms, some poikilotherm vertebrates may adhere, at least in part, to the general trends associated with Bergmann's rule (Olalla-Tárraga et al. 2006; Caruso et al. 2014), and some invertebrate taxa may also follow this pattern (Cushman et al. 1993; Atkinson 1994; Arnett and Gotelli 1999; Ray 2005). Although most bird species adhere to Bergmann's rule (Blackburn and Gaston 1996;

Ashton 2002), both the generality of the rule and its causal mechanism remain controversial (Blackburn et al. 1999; Olson et al. 2009; Watt et al. 2010; Meiri 2011). Several causal mechanisms have been proposed (Blackburn et al. 1999), including the heat conservation hypothesis, the resource availability hypothesis, and the starvation resistance hypothesis.

A larger body mass reduces the loss of thermal energy, which would benefit an endotherm living in colder environments (Bergmann 1847; Mayr 1956). The heat conservation hypothesis predicts that the warming temperatures associated with climate change will result in reduced body sizes. Rosenzweig (1968) and Geist (1987) hypothesized that primary productivity sets an upper limit to body size and that Bergmann's rule has resulted not from thermal efficiency, but from latitudinal differences in productivity. The productivity hypothesis predicts that the influence of climate change on body size will depend on how climate change affects productivity (Yom-Tov and Geffen 2011). Bumpus (1899) observed that more severe weather events occur at higher latitudes and proposed starvation resistance as a likely mechanism underlying Bergmann's rule. More recent studies have shown that severe weather events can exert directional selection pressures, favoring heavier mass and larger size (Jaramillo and Rising 1995; Brown and Brown 1999; Ashton 2002; Acquarone et al. 2004). Some extreme weather events, such as heat waves and the number of heavy precipitation events, might increase in both frequency and severity as a result of climate change (Easterling et al. 2000; Meehl and Tebaldi 2004; Stouffer and Wetherald 2007; Min et al. 2011). However, other events, such as cold temperature extremes, are likely to decrease (IPCC 2014), and there is not high confidence in predictions that relate extreme weather events to climate change (IPCC 2014). Consequently, the starvation resistance hypothesis predicts that climate change could result in either larger or smaller body sizes. These mechanisms are not mutually exclusive, and could influence morphological changes simultaneously (Yom-Tov et al. 2002) and in a context-dependent manner (Yom-Tov and Geffen 2011).

Paleontological studies have shown clear patterns between temperature and body size over time. Kurtén (1968) showed that body sizes of European mammals oscillated over thousands of years, with larger sizes occurring during colder climates and smaller sizes during warmer interglacial periods. Davis (1981) found similar patterns in mammals of Israel during the Holocene. Morphological changes to recent climate change over much shorter periods of decades to a century are less clear, however, and studies of the possible effect of climate change on avian body size have yielded conflicting results. Van Buskirk et al. (2010) found that migrating birds

captured in western Pennsylvania have exhibited decreasing fat-free mass (mass when fat score is zero) and wing length since 1961, and noted that this trend was consistent with a response to a warming climate. In contrast, Salewski et al. (2010) found no general trend for body size changes in response to climate change between 1972 and 2006 for 12 central European passerines. In a study of 11 bird species in Germany, Salewski et al. (2014) found that morphological changes between 1889 and 2010 were not consistent either within or across species, and that observed changes were not associated with temperature.

In addition to these inconsistent results, Goodman et al. (2012) found that body sizes of birds in California increased between 1983 and 2009, and attributed these changes to increases in primary productivity or climatic variation. Thus, although climate change has been associated with morphological responses in birds, observed changes have varied across species and across studies (Gardner et al. 2011). Given the myriad factors that can influence body size (Peters 1983; Calder 1984) and the complex interaction between climate and body size (Ozgul et al. 2009, 2010; Chown 2012; Huey et al. 2012), observed heterogeneity in the magnitude and direction of body size responses to climate change should not be surprising (Millien et al. 2006). Here, we examine whether avian body size changes also vary regionally within species and ask whether populations of the same species exhibit differing changes in body size over time. Our objectives in this exploratory analysis were to (1) examine how body sizes of resident and short-distance migratory birds have changed in Laurel, Maryland, from 1980 to 2012, (2) evaluate whether observed morphological changes in locally breeding birds are influenced by mean summer or mean winter temperatures, and (3) examine the spatial scale at which body sizes can change by comparing our findings to those obtained from a site 235 km away.

Methods

Data sets

We captured birds in mist nets in the fall (August–November) between 1980 and 2012 (excluding 2004–2006) at the USGS Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland, USA (elevation 50 m; 39.05 N, 76.81 W). We used 12-m, 30-mm-gauge mist nets, and generally opened 26 nets 25 min before sunrise and kept nets open for 3–4 h. Habitat near the banding includes a transmission line in 2–3-m dense shrubbery dominated by native shrub species with scattered grassy areas. Birds were identified to species and aged and

sexed according to Pyle (1997). We measured wing length (± 1 mm), mass (± 0.1 g), and fat score (on a scale of 0–4). We used wing length and fat-free mass as our measures of body size. There is no widespread agreement as to the best measure of body size for birds (Rising and Somers 1989; Freeman and Jackson 1990; Gosler et al. 1998), but wing length is the most common measure (Ashton 2002), and body mass is also examined frequently. Fat-free mass is obtained with covariance analysis and is the estimated mass when the fat score is zero.

We obtained regional temperature data from the United States Cooperative Observing Network for all 39 weather stations within 200 km of PWRC (http://cdiac.ornl.gov/e pubs/ndp/ushcn/usa_monthly.html). These data are corrected for changes in method, equipment, and urbanization (Van Buskirk et al. 2010). We calculated annual mean summer (May–July) temperature and annual mean winter (December–February) temperature, with each station's contribution weighted by the inverse of its distance from PWRC. These data show increasing mean summer ($b = 0.0155$ °C/year \pm 0.0040 SE; $P < 0.001$) and winter ($b = 0.0254$ °C/year \pm 0.0078 SE; $P = 0.001$) temperatures from 1895 to 2011.

Statistical analyses

We captured 87,832 individuals of 121 species. We excluded Neotropical migrants and analyzed only species that winter in North America (residents and short-distance migrants), because Neotropical migrants escape winter weather and might be less influenced by climate (Meiri and Dayan 2003). We also excluded repeated captures of an individual within a season, individuals of unknown age, and species that had fewer than 300 captured individuals; 20 species comprising 36,017 individuals met our criteria for inclusion.

Overall trends in body size were determined with generalized linear mixed models (GLMMs; West et al. 2006) with the GLIMMIX procedure in SAS version 9.3 software (2011; SAS Institute Inc., Cary, NC, USA). We analyzed wing length and fat-free mass separately and weighted species by sample size. We used \ln (wing length) and \ln (fat-free mass) of individual birds as our response variables to examine proportional changes across species. Fixed effects were year and capture date (Julian day) as continuous variables, and age and sex as categorical variables. Species was included as a random effect (nesting species in genus nested in family was not significant and was removed from the analyses). To test whether species differed in their slopes, we compared models with and without the heterogeneity in slopes (i.e., with and without species on the RANDOM statement) with a likelihood ratio test (West et al. 2006). For analyses of fat-

free mass, time of day and fat score were also included as fixed continuous variables.

For each of the 20 species included in the GLMM, we estimated the morphological change (i.e., change in wing length and change in fat-free mass over years) using the MIXED procedure in the SAS program. We included age, sex, year, and Julian day as fixed effects. For analyses of fat-free mass, we also included time of day and fat score.

We examined the influence of annual temperature variation only on resident species, because short-distance migrants might be less impacted by regional temperatures that were used as explanatory variables. We added mean summer temperature (SumTemp) and mean winter temperature (WintTemp) as continuous fixed effects to the two GLMMs (for wing length and fat-free mass) described previously. To test whether species differed in their slopes to SumTemp and WintTemp, we compared models with and without the heterogeneity in slopes with a likelihood ratio test (West et al. 2006). Significance of effects was determined from *F*-tests (Type III SS). We estimated the influence of mean summer and mean winter temperature on each species separately by adding SumTemp and WintTemp to the MIXED models described previously.

To examine overall changes in body condition between 1980 and 2012, we used GLMM to model fat score as a function of year, time of day, Julian date, age, and sex with the GLIMMIX procedure in SAS. To test whether species differed in their slopes, we compared models with and without the heterogeneity in slopes with a likelihood ratio test (West et al. 2006). We examined changes in fat score for each species separately with the MIXED procedure, with year, time, Julian date, age, and sex as explanatory variables.

Long-term declines in body size could indicate deteriorating environmental conditions (Teplitsky et al. 2008). Environmental degradation could reduce the quality and availability of food, resulting in smaller and less healthy individuals, which could scale up to population declines. To examine this possibility, we examined Pearson correlation coefficients between changes in body size (wing length and fat-free mass), changes in body condition (fat score), and changes in population size across species. Positive correlations could indicate environmental degradation (Van Buskirk et al. 2010). Winter population density was obtained from the Christmas Bird Count (www.audubon.org/bird/cbc/index.html); we selected US ENTIRE United States for the County/Region. Breeding population density was estimated from Breeding Bird Survey data using the New England/Mid-Atlantic Coast region for local breeders. For northern breeders, we used the Atlantic Northern Forest region; when a species population trend was not found in this region, we used Boreal Hardwood Transition or consulted range maps

from Birds of North America species accounts to select a suitable region.

Results

Morphological changes over time

Mean wing length across species increased between 1980 and 2012 ($F_{1, 35311} = 13.00, P < 0.001$, Table 1).

Table 1 Summaries of generalized linear mixed models (GLMMs) to examine morphological changes (log-transformed wing length, log-transformed fat-free mass, and fat score) for 20 resident and short-distance migrant species from 1980 to 2012

Source of variation	Estimate	SE	<i>F</i> value	<i>P</i>
Wing length				
Year	0.000129	0.000036	13.00	<0.001
Julian day	0.000198	0.000011	328.41	<0.001
Age				
AHY	0.01921	0.000454	1791.56	<0.001
HY	0			
Sex				
Female	-0.02607	0.00076	4227.10	<0.001
Male	0.03445	0.00077		
Unknown	0			
Fat-free				
Year	-0.000060	0.000088	0.43	0.51
Time	0.000058	0.000003	295.27	<0.001
Julian day	0.000713	0.00002	1238.65	<0.001
Age				
AHY	0.00858	0.00082	110.86	<0.001
HY	0			
Sex				
Female	-0.02976	0.00137	1554.50	<0.001
Male	0.03619	0.00137		
Unknown	0			
Fat			1406.37	<0.001
Fat score				
Year	-0.00525	0.00035	224.83	<0.001
Time	0.00029	0.00003	98.08	<0.001
Julian day	0.00693	0.000171	1634.40	<0.001
Age				
AHY	0.04073	0.007099	32.91	<0.001
HY	0			
Sex				
Female	-0.00785	0.01189	17.29	<0.001
Male	-0.05959	0.01194		
Unknown	0			

Estimates are coefficients; negative coefficients indicate declining size and positive coefficients indicate increasing size

SE standard error

Although significant, the mean magnitude of change in wing length was just 0.41 % over the course of the study. Change in wing length differed significantly across species ($\chi^2 = 116,282.7$, $df = 1$, $P < 0.001$) and ranged from -0.90 to $+2.47$ %. Of the 20 species examined, 16 exhibited an increasing trend in wing length ($P = 0.012$, two-tailed binomial test, Table 2). Of species with a significant trend, 10 of 11 exhibited increases in wing length ($P = 0.003$, two-tailed binomial test, Table 2), with only Dark-eyed Juncos (*Junco hyemalis*) showing a significant decrease.

Fat-free mass showed a negative but non-significant trend across years ($F_{1, 33481} = 0.43$, $P = 0.51$, Table 1), but species varied significantly in change in fat-free mass ($\chi^2 = 145,264.4$, $df = 1$, $P < 0.001$), ranging from -4.11 to $+5.22$ % between 1980 and 2012. Fat-free mass of Blue Jays (*Cyanocitta cristata*, -4.11 %), Ruby-crowned Kinglets (*Regulus calendula*, -1.18 %), and White-throated Sparrows (*Zonotrichia albicollis*, -0.73 %) decreased significantly, and fat-free mass of three species (Eastern Phoebe, *Sayornis phoebe*, 5.22 %; Gray Catbird, *Dumetella carolinensis*, 0.66 %; and Tufted Titmouse,

Table 2 Changes in log-transformed wing length and log-transformed fat-free mass ($\times 10,000$) and change in fat score on a 0–4 scale ($\times 10,000$) 1980–2012

Family Common name	Species code	Scientific name	Wing		Fat-free mass		Fat score	
			Est.	SE	Est.	SE	Est.	SE
Cardinalidae								
Northern Cardinal	NOCA	<i>Cardinalis cardinalis</i>	7.63 [‡]	1.63	4.71	3.41	-1.7	6.9
Corvidae								
Blue Jay	BLJA	<i>Cyanocitta cristata</i>	-2.80	2.39	-13.10*	5.37	-27.8	17.9
Emberizidae								
Dark-eyed Junco	SCJU	<i>Junco hyemalis</i>	-2.00 [‡]	0.36	-1.60	0.86	-27.8 [‡]	7.5
Swamp Sparrow	SWSP	<i>Melospiza georgiana</i>	-0.01	1.41	1.17	2.79	-80.6 [‡]	22.2
Song Sparrow	SOSP	<i>Melospiza melodia</i>	0.11	1.12	-1.90	2.04	-56.2 [‡]	14.7
Fox Sparrow	FOSP	<i>Passerella iliaca</i>	0.40	2.07	-7.10	3.69	4.1	32.3
Eastern Towhee	EATO	<i>Pipilo erythrophthalmus</i>	1.78	2.01	0.27	1.91	-67.7 [‡]	16.0
Field Sparrow	FISP	<i>Spizella pusilla</i>	4.39*	1.78	2.00	2.75	3.6	22.2
White-throated Sparrow	WTSP	<i>Zonotrichia albicollis</i>	-0.20	0.43	-2.30*	0.97	-65.7 [‡]	8.8
Mimidae								
Gray Catbird	GRCA	<i>Dumetella carolinensis</i>	2.71 [‡]	0.55	2.05*	0.84	-57.0 [‡]	7.5
Paridae								
Tufted Titmouse	TUTI	<i>Baeolophus bicolor</i>	6.64 [‡]	1.63	8.48*	3.47	-11.6	6.3
Carolina Chickadee	CACH	<i>Poecile carolinensis</i>	3.84*	1.75	4.61	3.42	-22.1*	8.8
Parulidae								
Yellow-rumped Warbler	MYWA	<i>Setophaga coronata</i>	7.02 [‡]	0.83	3.31	2.11	14.0	17.8
Regulidae								
Ruby-crowned Kinglet	RCKI	<i>Regulus calendula</i>	1.32*	0.63	-3.70 [†]	1.39	-45.9 [†]	16.4
Golden-crowned Kinglet	GCKI	<i>Regulus satrapa</i>	0.72	0.80	-0.30	2.01	-111.1 [‡]	23.7
Troglodytidae								
Carolina Wren	CARW	<i>Thryothorus ludovicianus</i>	7.38 [†]	2.24	10.04	5.19	-8.0	12.6
House Wren	HOWR	<i>Troglodytes aedon</i>	2.57	1.49	-5.30	4.68	-33.1	23.8
Winter Wren	WIWR	<i>Troglodytes hiemalis</i>	5.79 [†]	1.90	4.44	4.07	-90.1*	35.6
Turdidae								
Hermit Thrush	HETH	<i>Catharus guttatus</i>	0.58	0.98	-1.10	1.56	-55.8 [‡]	15.5
Tyrannidae								
Eastern Phoebe	EAPH	<i>Sayornis phoebe</i>	7.35*	2.89	15.91*	6.37	-4.3	19.1

Estimates are coefficients; negative coefficients indicate declining size and positive coefficients indicate increasing size

SE standard error

P values are denoted by symbols: * indicates $P < 0.05$, † indicates $P < 0.01$, and ‡ indicates $P < 0.001$

Baeolophus bicolor, 2.75 %) increased significantly, from 1980 (Table 2). Across species, change in wing length and change in fat-free mass were positively correlated ($r = 0.82$, $N = 20$, $P < 0.001$, Fig. 1).

Across all species, fat scores decreased between 1980 and 2012 ($F_{1, 35272} = 224.83$, $P < 0.001$, Table 1), with a decrease of 0.17 (on a 0–4 scale) over the course of the study. Species exhibited significant variation in fat score change over time ($\chi^2 = 3704.65$, $df = 1$, $P < 0.001$, Table 2), ranging from -0.36 to $+0.04$ over 32 years. Eleven of the 20 species exhibited a significant decline in fat score, and none showed a significant increase ($P < 0.001$, two-tailed binomial test, Table 2).

Body size changes and annual temperature variation

Wing length

Across resident species, increasing mean summer temperatures were associated with shorter wing lengths ($F_{1, 6654} = 5.77$, $P = 0.016$, Table 3). Although significant, the magnitude of wing change was small (-0.26 %/°C). The association between mean summer temperature and wing length ranged from -0.63 % to $+0.15$ %/°C but

did not differ significantly across species ($\chi^2 = 3.9$, $df = 1$, $P = 0.10$, Table 4). Eastern Towhees (*Pipilo erythrophthalmus*) and Northern Cardinals (*Cardinalis cardinalis*) exhibited significantly shorter wings with increases in mean summer temperature, and no species had significantly longer wings (Table 4). Increasing mean winter temperatures were not related to wing lengths of residents ($F_{1, 6654} = 0.03$, $P = 0.87$, Table 3) and did not vary significantly across species ($\chi^2 = 1.4$, $df = 1$, $P = 0.37$), but Eastern Phoebes had significantly lower fat-free mass with warmer mean winter temperatures (Table 4).

Fat-free mass

Fat-free mass of residents was not associated with mean summer temperature ($F_{1, 6217} = 3.08$, $P = 0.08$, Table 3). Change in fat-free mass did not vary significantly across species ($\chi^2 = 0.06$, $df = 1$, $P = 0.59$) and declined significantly in only Northern Cardinals and Eastern Towhees (Table 4). Fat-free mass declined with increasing mean winter temperature ($F_{1, 6217} = 8.63$, $P = 0.003$, Table 3) at a rate of 0.19 %/°C. This relationship did not vary significantly across species ($\chi^2 = 0.00$, $df = 1$, $P = 1.0$), and no species was individually significant (Table 4).

Fig. 1 Annual change in fat-free mass ($\times 10,000$) vs. annual change in wing length ($\times 10,000$) between 1980 and 2012 for 20 bird species ($r = 0.82$, $N = 20$, $P < 0.001$). Species codes are defined in Table 2

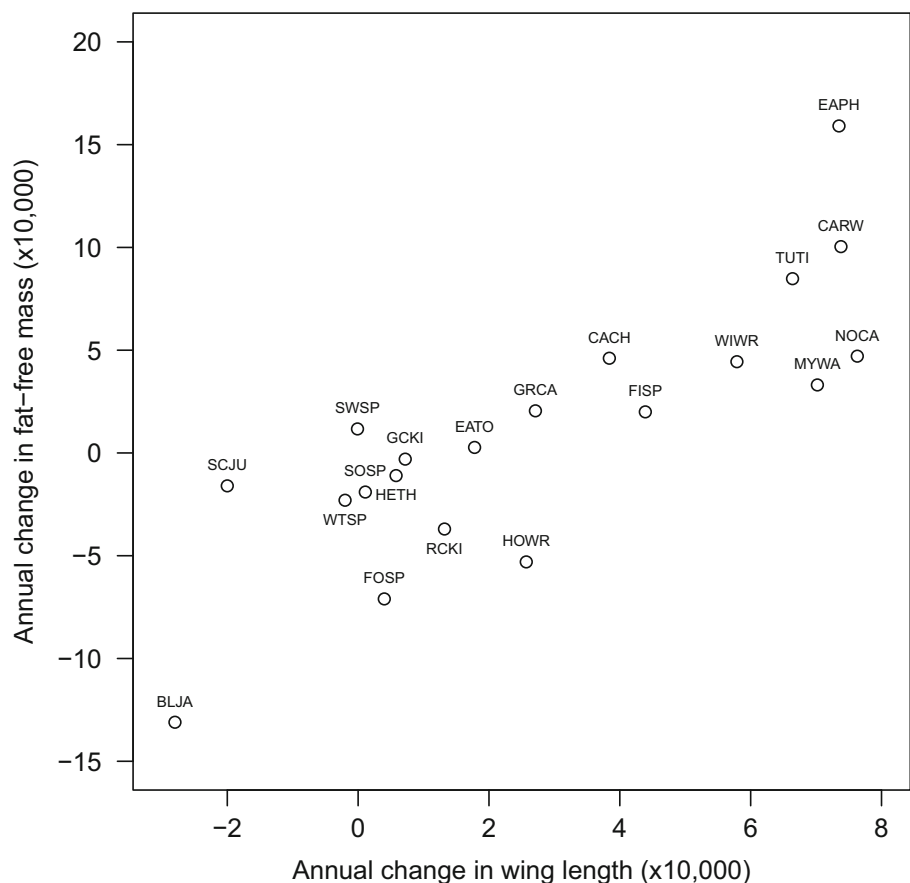


Table 3 Summaries of generalized linear mixed models (GLMMs) for log-transformed wing length, log-transformed fat-free body mass, and fat score for 9 resident species from 1980–2012

Source of variation	Estimate	SE	F value	P
Wing length				
Year	0.000372	0.000082	20.55	<0.001
Julian day	0.000207	0.000022	89.93	<0.001
Age				
AHY	0.02201	0.001468	224.64	<0.001
HY	0			
Sex				
Female	−0.01659	0.00474	223.98	<0.001
Male	0.02731	0.00486		
Unknown	0			
SumTemp	−0.00257	0.00107	5.77	0.016
WintTemp	0.000091	0.000548	0.03	0.87
Fat-free mass				
Year	0.00023	0.000158	2.11	0.15
Time	0.000057	0.000008	50.90	<0.001
Julian day	0.000509	0.000034	229.09	<0.001
Age				
AHY	0.01898	0.002209	73.87	<0.001
HY	0			
Sex				
Female	−0.02288	0.00715	219.73	<0.001
Male	0.04268	0.00733		
Unknown	0			
Fat			49.53	<0.001
SumTemp	−0.00227	0.001293	3.08	0.079
WintTemp	−0.00188	0.000639	8.63	0.003
Fat score				
Year	−0.00343	0.000617	30.92	<0.001
Time	0.000182	0.000047	15.23	<0.001
Julian day	0.001442	0.000194	55.00	<0.001
Age				
AHY	0.02982	0.01286	5.38	0.020
HY	0			
Sex				
Female	−0.02176	0.03860	2.81	0.061
Male	−0.06121	0.03959		
Unknown	0			
SumTemp	0.000068	0.006282	0.00	0.99
WintTemp	−0.00911	0.004775	3.64	0.056

Estimates are coefficients, and SE is standard error

Fat score

Fat score of residents was not associated with increasing mean summer temperature ($F_{1, 6629} = 0.00, P = 0.99$, Table 3) and did not vary significantly across species ($\chi^2 = 0.08, df = 1, P = 0.87$). Fat score did not vary with

mean winter temperature ($F_{1, 6629} = 3.64, P = 0.06$), and the relationship with mean winter temperature did not vary significantly across species ($\chi^2 = 1.95, df = 1, P = 0.27$). Fat score of Song Sparrows (*Melospiza melodia*) decreased with increasing mean winter temperature (Table 4).

Correlated morphological changes and annual temperature variation

Across resident species, the effects of mean summer temperature on wing length and on fat-free mass were not correlated ($r = 0.44, N = 9, P = 0.24$, Fig. 2). The effects of mean winter temperature on wing length and fat-free mass were positively correlated ($r = 0.80, N = 9, P = 0.01$, Fig. 3). Wing responses to increasing summer temperature and to increasing winter temperature were not correlated ($r = 0.04, N = 9, P = 0.93$). Change in fat-free mass with increasing summer temperature was also not correlated with change in fat-free mass with increasing winter temperature ($r = 0.44, N = 9, P = 0.24$).

Body size changes over time and annual temperature variation

Across resident species, change in wing length over time was not correlated with response to mean summer temperature ($r = -0.60, N = 9, P = 0.09$) or to mean winter temperature ($r = -0.27, N = 9, P = 0.48$). Change in fat-free mass over time was not correlated with response to mean summer temperature ($r = 0.26, N = 9, P = 0.50$) or to mean winter temperature ($r = -0.60, N = 9, P = 0.09$).

Assessment of deteriorating environmental conditions

Changes in wing length and fat score over time were weakly positively correlated across species ($r = 0.45, N = 20, P = 0.045$, Fig. 4), but these morphological responses were not correlated with any measure of population change ($N = 20, P > 0.07$ for all tests, Table 5). Change in mass over time was weakly correlated with change in breeding population density since 1980 ($r = 0.45, N = 20, P = 0.049$, Fig. 5; Table 5), but not with change in winter population density ($r = 0.26, N = 20, P = 0.27$, Table 5).

Discussion

We document widespread increases in wing length, but not in fat-free mass, across 20 resident and short-distance migrant species between 1980 and 2012. Annual

Table 4 Change in log-transformed wing length and log-transformed fat-free mass ($\times 10,000$) and change in fat score ($\times 10,000$) on a 0–4 scale with mean annual summer temperature (SumTemp) and mean annual winter temperature (WintTemp)

Family Common name	Wing length				Fat-free mass				Fat score				
	SumTemp		WintTemp		SumTemp		WintTemp		SumTemp		WintTemp		
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	
Cardinalidae													
Northern Cardinal	-57.1 [‡]	16.8	7.3	9.8	-88.1 [*]	34.8	-31.0	20.6	0.0	7.2	-1.7	4.2	
Corvidae													
Blue Jay	15.0	25.5	1.8	13.0	-69.5	51.9	-15.7	27.0	-35.8	18.2	10.7	9.3	
Emberizidae													
Song Sparrow	1.0	12.2	11.4	7.1	0.2	21.6	5.0	12.6	21.9	16.2	-29.4 [†]	9.4	
Eastern Towhee	-62.8 [†]	23.7	15.0	13.1	-61.6 [†]	21.7	-18.3	12.0	-20.0	18.6	-16.6	10.2	
Field Sparrow	-13.7	16.9	-16.6	11.2	-10.6	25.5	-27.0	17.1	12.6	21.2	9.3	14.1	
Paridae													
Tufted Titmouse	-25.1	13.6	-7.9	8.0	-37.9	30.0	-34.3	17.7	-3.1	5.5	1.4	3.2	
Carolina Chickadee	-8.9	20.4	0.0	12.0	2.2	39.8	-13.1	23.0	1.0	10.3	-10.7	6.1	
Troglodytidae													
Carolina Wren	-22.5	21.3	19.6	12.8	24.7	48.9	-11.6	29.7	-1.7	11.8	-11.0	7.1	
Tyrannidae													
Eastern Phoebe	-46.6	26.8	-32.3 [*]	15.4	-46.2	59.8	-60.3	34.1	-10.9	18.3	-14.9	10.5	

Estimates are coefficients, and SE is standard error

P values are denoted by symbols: * indicates $P < 0.05$, † indicates $P < 0.01$, and ‡ indicates $P < 0.001$

Fig. 2 Morphological response to increasing mean summer temperature for 9 resident bird species between 1980 and 2012. Graph shows change in fat-free mass ($\times 10,000$) vs. change in wing length ($\times 10,000$) for each degree increase in mean summer temperature ($r = 0.44$, $N = 9$, $P = 0.24$). Species codes are defined in Table 2

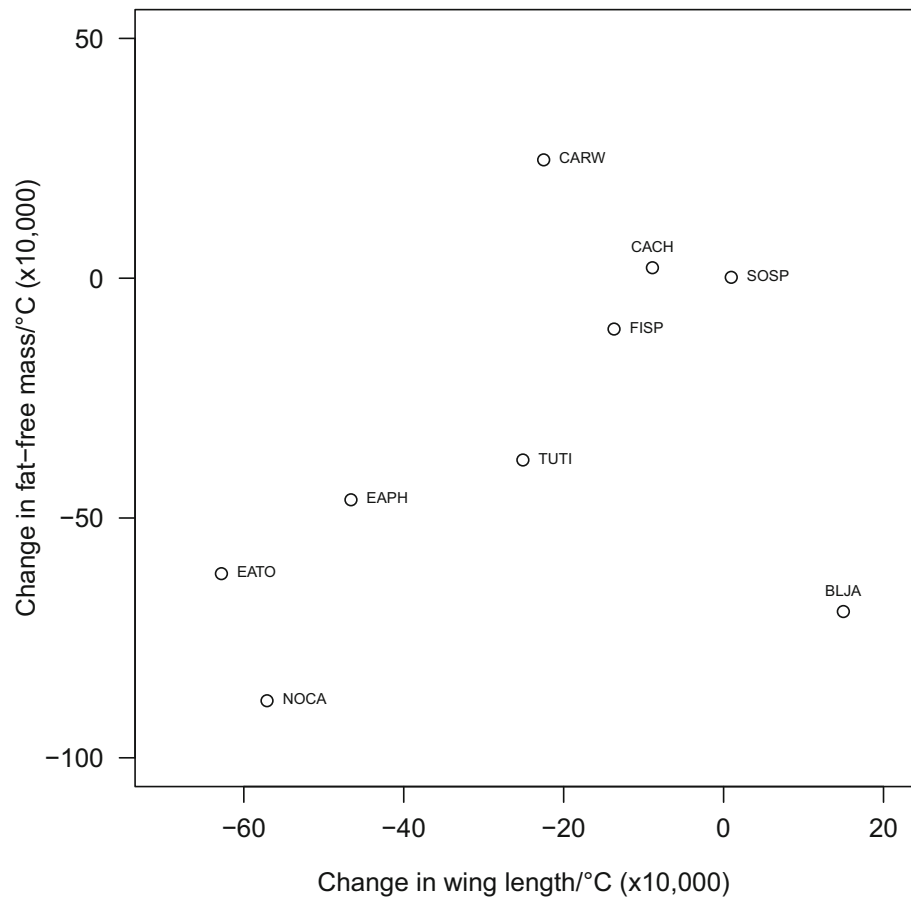
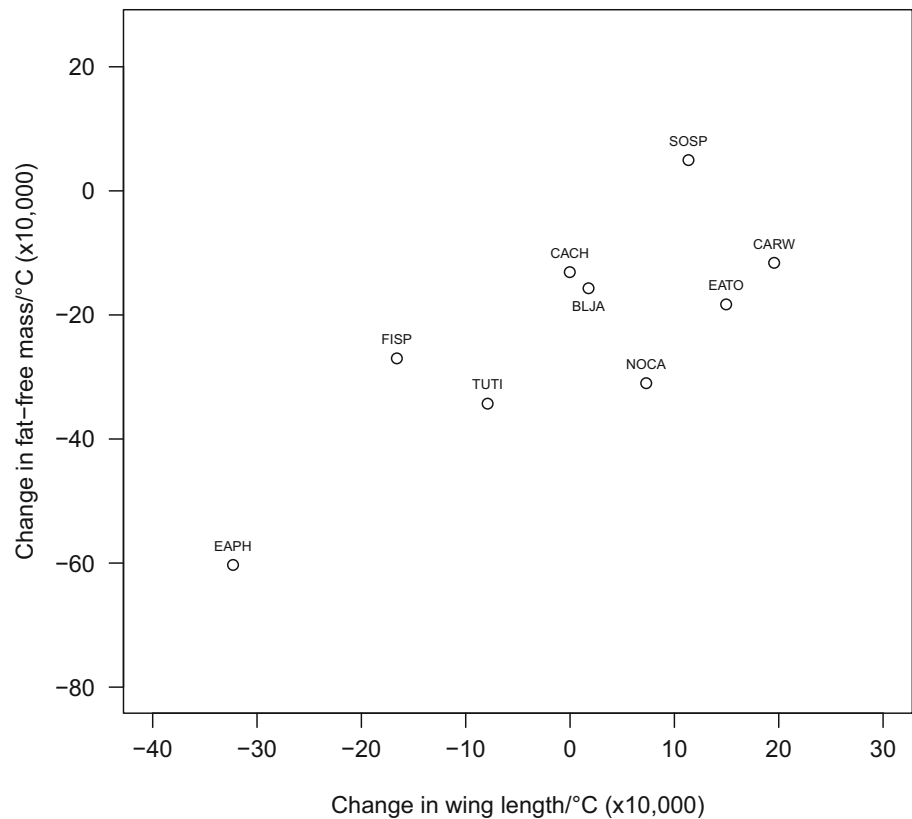


Fig. 3 Morphological response to increasing mean winter temperature for 9 resident bird species between 1980 and 2012. Graph shows change in fat-free mass ($\times 10,000$) vs. change in wing length ($\times 10,000$) for each degree increase in mean winter temperature ($r = 0.80$, $N = 9$, $P = 0.01$). Species codes are defined in Table 2



temperature variation was associated with some changes in body size, but the magnitude and direction of change depended on the trait examined. In contrast, Van Buskirk et al. (2010) found that wing length and fat-free mass of passerines had decreased since 1961 in western Pennsylvania, and McCoy (2012) found that mean wing length of three of six resident species in Connecticut declined between two sampling periods, 1874–1952 and 1958–2010. These results suggest that changes in avian body size can exhibit different patterns over regional spatial scales, and suggest either that the influence of broad-scale climatic change on body size depends on local factors or that factors other than climate change drive these morphological trends.

In California, Goodman et al. (2012) showed that wing length and mass increased between 1983 and 2009, and hypothesized that these trends were driven by climatic variability or changes in primary productivity. Although Van Buskirk et al. (2010) and Goodman et al. (2012) found opposing trends in body size, changes in body size were consistent within each study, with wing length and fat-free mass showing similar patterns. In our study, wing length increased significantly, but fat-free mass showed a negative but non-significant trend. Our results show that body size changes depend on the morphological trait examined (Salewski et al. 2014).

In our study, fat scores of 11 species decreased over time and none increased. Fat scores can change rapidly and are not reliable measures of body size. Declining fat scores could indicate reduced food availability and less favorable environmental conditions (Teplitsky et al. 2008), but changes in fat scores across species were not correlated with changes in population size estimated from either Breeding Bird Survey (BBS) or Christmas Bird Count (CBC) data. In direct contrast, declining fat scores could also reflect favorable conditions with increased food availability, because a perceived reduction in starvation risk might reduce the optimal level of fat deposition (McNamara and Houston 1990). Shorter migration distances due to climate change might also select for lower fat levels. We do not think that these declines in fat scores are due to differences across banders in scoring fat levels. One of us (DB) was the primary bander in 1980–1986 and again after 2006, and data from these periods also show decreased fat scores. We are unaware of other studies that have shown long-term declines in fat scores across species, and this pattern merits further investigation.

Changes in both wing length and fat-free mass over time were species-specific. Van Buskirk et al. (2010) and Goodman et al. (2012) also found significant variation across species. In all three studies, magnitudes of change

Fig. 4 Annual change in wing length ($\times 10,000$) vs. annual change in fat score ($\times 10,000$) 1980–2012 ($r = 0.45$, $N = 20$, $P = 0.045$). Species codes are defined in Table 2

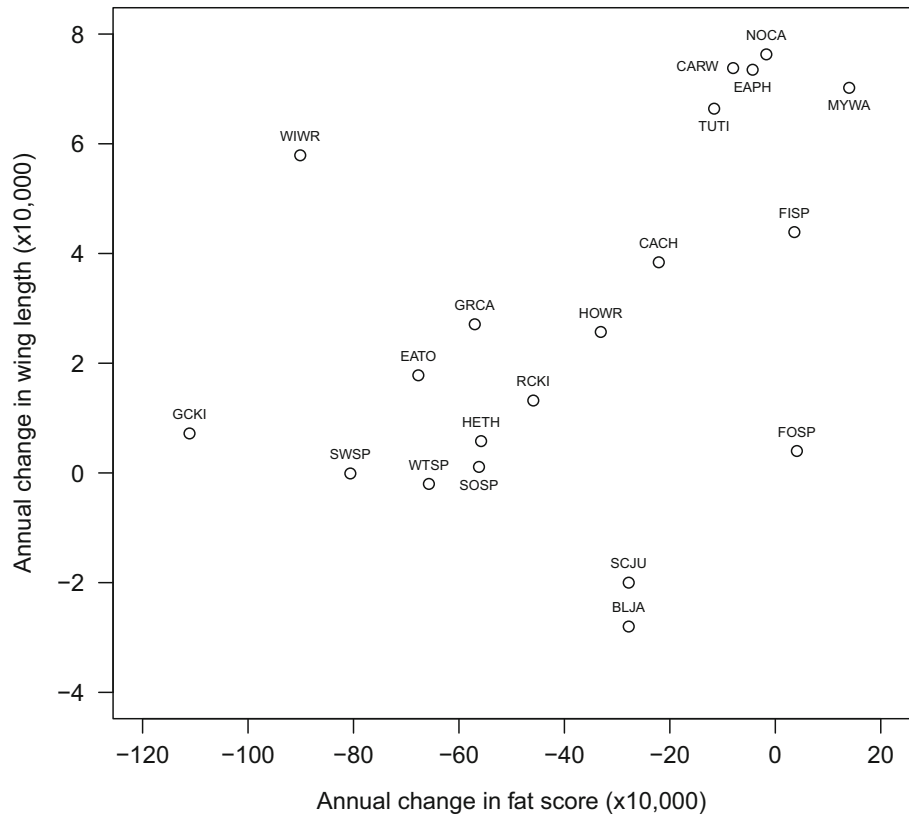


Table 5 Correlations between changes in population size (BBS for summer population size and CBC for winter population size) and annual changes in morphology (percentage wing length, percentage fat-free mass, and percentage fat score)

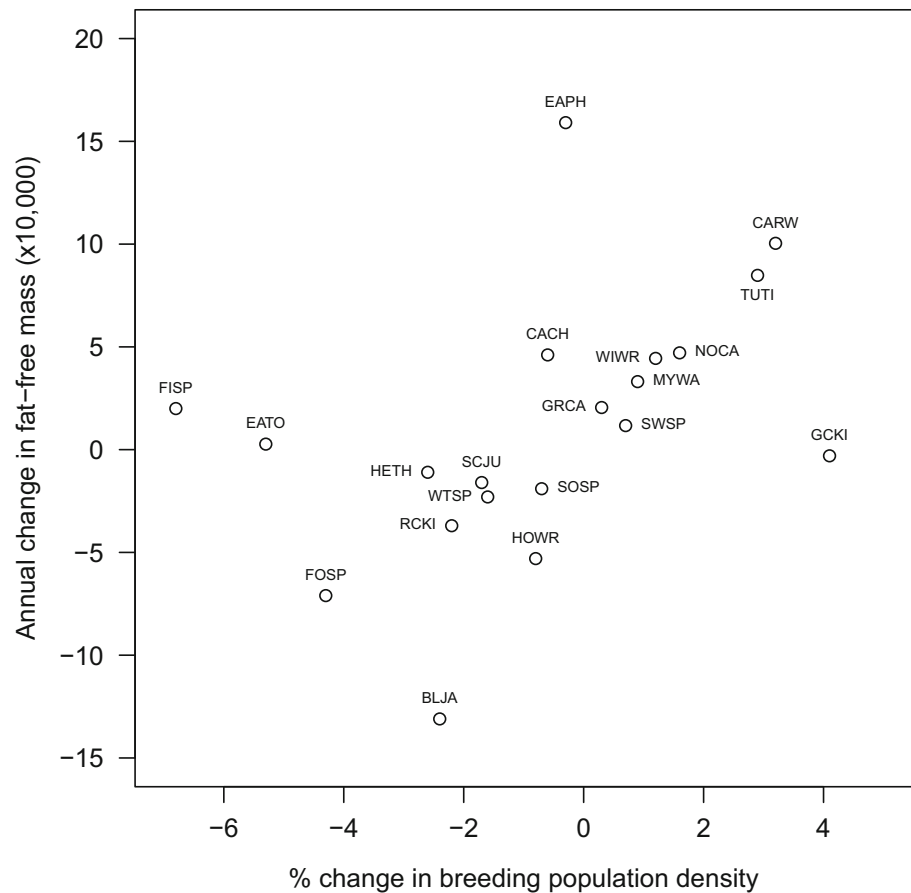
	Wing	Mass	Fat
BBS			
r	0.40	0.45	-0.19
P	0.08	0.05	0.41
CBC			
r	-0.02	0.26	-0.04
P	0.93	0.27	0.86

For each correlation, we report Pearson's r and P . Sample size was 20 for all correlations

were small: -0.13 to $+0.16$ %/year in our study, -0.08 to $+0.02$ %/year in Van Buskirk et al. (2010), and -0.03 to $+0.08$ %/year in Goodman et al. (2012). In our study, 16 of 20 species showed a trend of increasing wing length, and 10 of these trends were statistically significant. Van Buskirk et al. (2010) analyzed 19 of the 20 species in our study (all except Carolina Chickadee [*Poecile carolinensis*]) and found that wing length decreased significantly in 12 species and did not increase significantly in any species. Dark-eyed Juncos, the only species that showed significantly shorter wing length in our study, did not show a significant trend in theirs. McCoy's (2012) findings also show that species can exhibit differing body size changes. Wing lengths of Blue Jays, the only species in common with our study, decreased

significantly in Connecticut, but did not change significantly in our study. Van Buskirk et al. (2010) analyzed all six species examined by McCoy (2012). Only Purple Finches (*Haemorhous purpureus*), which decreased in both locations, and White-breasted Nuthatches (*Sitta carolinensis*), which showed no significant trend, exhibited consistent patterns. Some species showed significant decreases in western Pennsylvania, but no significant change in Connecticut, and these discrepancies might be attributable to larger sample sizes and greater statistical power from western Pennsylvania. But not all differences between these studies can be explained by statistical power: wing lengths of Common Grackles (*Quiscalus quiscula*) decreased significantly in Connecticut but increased significantly in western Pennsylvania. Changes in fat-free mass also differed within species between Maryland and western Pennsylvania. In our study, five species (Blue Jay, Eastern Phoebe, Gray Catbird, Tufted Titmouse, and White-throated Sparrow) exhibited significant changes in fat-free mass, but none of these five showed the same significant trend in Pennsylvania. Fat-free mass of Eastern Phoebes and Gray Catbirds increased significantly in our study but decreased in western Pennsylvania (Van Buskirk et al. 2010), whereas fat-free mass of White-throated Sparrows decreased in our study but increased in the study by Van Buskirk et al. (2010).

Fig. 5 Annual change in fat-free mass ($\times 10,000$) 1980–2012 vs. percent change in population density estimated from BBS routes, 1966–2010 ($r = 0.45$, $N = 20$, $P = 0.049$). Species codes are defined in Table 2



Together, these findings demonstrate that the opposing body size trends documented between our study and that of Van Buskirk et al. (2010) are not due to sampling different species between sites, but that populations of a single species can exhibit opposing body size changes and that these patterns can differ over short distances (<250 km). Others have also noted that body size changes can differ across species (Millien et al. 2006; Gardner et al. 2011, 2014b; Teplitsky and Millien 2014), but few studies have documented variation in morphological changes across populations of the same species (see Desrochers (2010) for an example).

Several possible explanations could resolve why numerous species show opposing changes in body size between our study in Maryland and that of Van Buskirk et al. (2010) in western Pennsylvania. First, climate change may differ between the two sites. It is possible, for example, that warming trends have been less pronounced at our site, perhaps owing to its proximity to the Atlantic Ocean. Comparing changes in annual mean summer temperatures between western Pennsylvania and Maryland does not support this hypothesis. Van Buskirk et al. (2010) reported an annual increase of $0.017\text{ }^{\circ}\text{C}/\text{year} \pm 0.008$, and we found $0.016\text{ }^{\circ}\text{C}/\text{year} \pm 0.004$ since 1895. Mean

summer temperature showed a similar but non-significant trend at our site since 1980 ($b = 0.016\text{ }^{\circ}\text{C}/\text{year} \pm 0.028\text{ SE}$; $P = 0.58$), but this difference, by itself, seems unlikely to explain opposing changes within species between locations. Extreme weather events can influence avian body size (Jaramillo and Rising 1995; Brown and Brown 1999). It is possible that changes in the frequency or intensity of these events or in other measures of climate might differ between these sites, but we have no evidence to suggest that the opposing changes in body size between western Pennsylvania and Maryland reflect differing climatic changes between these locations.

A second possible explanation for opposing changes in body size is that strong context dependence causes the influence of warming temperatures on body size to differ between locations. The effects of increased temperatures, for example, might depend on other climatic variables. Increasing temperatures might affect body size indirectly, through its influence on productivity and food availability (Yom-Tov and Geffen 2011), and increases in temperature might increase productivity in areas with high rainfall, but decrease productivity in drier locations where higher temperatures increase water stress. James (1970) demonstrated that geographic variation in wing length is more closely

associated with wet-bulb temperature, a measure that incorporates temperature and humidity, than with temperature alone. We found that annual variation in mean summer and mean winter temperatures was related to some measures of body size of residents. Increasing mean summer temperatures were associated with shorter wing lengths and reduced fat-free mass in residents. This finding mirrors the findings of Van Buskirk et al. (2010); thus residents at the two sites exhibited similar trends of variation in mean summer temperature. However, observed increases in wing length of residents in our study are not explained by increasing mean summer temperatures. In addition, observed species-specific changes in wing length and fat-free mass of residents at our site were not correlated with species-specific associations with increasing temperatures. Species-specific changes in body size over time in our study are not easily explained by temperature, but our results must be interpreted with caution. Even for resident species, most individuals were likely captured while migrating from more northern locations, because birds that breed at the site learn to avoid the nets (D. Bystrak, pers. obs.). Consequently, we do not know where these individuals spent the summer or how closely our climate measures match the conditions encountered by captured birds. With this caveat, we have no evidence that context dependence results in differing effects of climate change on body size between banding stations.

Third, changes in body size documented in our study may not reflect climate change. The magnitudes of body size changes in our study were comparable to or greater than those reported in other studies (see Van Buskirk et al. 2010; Goodman et al. 2012; Gardner et al. 2014a), but observed changes were small, ranging between -0.13 and 0.16 %/year. Increasing trends in mean summer and mean winter temperatures since 1980 were non-significant and modest. Although a strong, clear relationship exists between climate and body size over much longer periods (Kurtén 1968; Davis 1981), body size changes over shorter periods might not be driven by climate change, particularly when only minor increases in temperature have occurred. Body size affects many physiological and ecological processes, and can influence fitness (Peters 1983; Calder 1984). For example, decreased migration distances due to climate change (Visser et al. 2009) might select for shorter wing lengths. Desrochers (2010) found that wing pointedness in North American songbirds in the eastern USA changed predictably in response to forest loss and fragmentation, and that some species showed regional differences. In addition to these other factors, changes in one aspect of body size can influence other measures of body size; a reduction in mass, for example, might influence changes in wing length due to allometric responses and aerodynamic selection pressures (Yom-Tov et al. 2006).

Because changes in body size reflect the combined selective forces of these factors, the influence of climate on body size might be swamped by other factors when climatic change is mild. In our study, warmer summer temperatures were associated with shorter wings in residents, but rather than decrease, wing length increased since 1980. Warmer mean winter temperatures were associated with reduced fat-free mass of residents, but fat-free mass did not decrease over time. As with density-vague dynamics (Strong 1986), climate might drive morphological changes only when climate change is more pronounced.

Our findings build on those of other researchers (Salewski et al. 2010; Van Buskirk et al. 2010; Goodman et al. 2012; Salewski et al. 2014) and demonstrate that morphological changes in birds can vary over short time scales. Body size changes are not consistent across studies (cf. Van Buskirk et al. 2010; Gardner et al. 2011; Goodman et al. 2012, this study), and species within studies can show opposing trends (Yom-Tov et al. 2006; Salewski et al. 2010; 2014, Gardner et al. 2011, 2014b, this study). We show that populations of the same species can exhibit variable changes in body size over short distances. In our study, the wing length of some species increased over time, but these trends varied across species, and species-specific changes were not related to annual variation in mean summer or mean winter temperatures. We found no evidence of widespread declines in body size (cf. Daufresne et al. 2009), and conclude that body size changes in our study are likely driven by factors other than temperature (Salewski et al. 2014).

Predictions for how body size is likely to respond to climate change that are based on a biogeographic pattern such as Bergmann's rule (Daufresne et al. 2009), or on a single mechanism such as the heat conservation hypothesis, do not explain the variability in body size changes observed in our study and by others. Other factors might drive body size changes over short periods. Rather than thinking of declining body size as a universal response to climate change (Daufresne et al. 2009), we suggest that ecologists embrace the heterogeneity of body size changes and evaluate alternate hypotheses for these changes. This endeavor will require better climatic data that include not just mean temperatures but also extreme weather events of temperature and rainfall, and estimates of primary productivity that are not usually available (but see Yom-Tov and Geffen 2006; Gardner et al. 2014b). Detailed autecological investigations would be valuable for understanding observed heterogeneity in body size changes over short time scales.

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