Neotropical Migrants Exhibit Variable Body-Size Changes Over Time and Space

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Abstract - Recent changes in the Earth's climate have been linked to changes in phenology, geographic distributions, and morphology of species, and warming temperatures associated with climate change have been predicted to result in decreases in avian body sizes. We examined changes in wing length and fat-free mass of 34,844 fall migrants from 31 neotropical migratory species captured at Patuxent Wildlife Research Center in Maryland between 1980 and 2012. Body size changes varied across species, but wing length and fat-free mass increased significantly over time in the pooled sample of all species. Magnitudes of change were small and similar to other studies, with mean wing length increasing 0.55% and mean fat-free mass increasing 1.30% across all species. General morphological changes at our site differed from those at a banding station located 235 km away. Across species, changes in wing length were weakly correlated between stations, and changes in fat-free mass were uncorrelated. Populations of some species showed opposite morphological changes, demonstrating that morphological changes can vary regionally. Over short time scales, factors other than climate might drive observed changes in body size of neotropical migrants, and alternative hypotheses for body size changes should be considered.

Introduction

Abundant evidence has documented rapid changes in the Earth's climate (Field et al. 2014, Hansen et al. 2006, Jones et al. 2001, Karl and Trenberth 2003), and climate change has been linked to observed changes in phenology (Crick 2004, Macmynowski et al. 2007, Miller-Rushing et al. 2008, Torti and Dunn 2005, Végvári et al. 2010), morphology (Gardner et al. 2011, Goodman et al. 2012, Van Buskirk et al. 2010, Yom-Tov et al. 2006), geographical distributions (Graves 1991, Parmesan and Yohe 2003, Thomas 2010, Tingley et al. 2009) and population size (Jiguet et al. 2010, Ozgul et al. 2010). Body sizes of birds and other endotherms have been predicted to decrease with rising temperatures based on Bergmann's (1847) rule (Daufresne et al. 2009, Kirchman and Schneider 2014, Van Buskirk et al. 2010). Bergmann's rule states that body sizes of endotherms increase with latitude. Because latitude is negatively correlated with temperature, climate change is predicted to result in smaller body sizes. This prediction is based largely on the heat-conservation hypothesis, which argues that larger endotherms would have an advantage in colder environments because a larger body would reduce the loss of heat energy (Bergmann 1847, Mayr 1956). However, Bergmann's rule is also seen in some poikilotherm

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vertebrates (Caruso et al. 2014, Olalla-Tárraga et al. 2006) and in some invertebrates (Arnett and Gotelli 1999, Atkinson 1994, Cushman et al. 1993, Ray 2005). Most bird species adhere to Bergmann's rule (Ashton 2002, Blackburn and Gaston 1996), but how widespread the pattern is and its underlying cause remain unresolved (Blackburn et al. 1999, Meiri 2011, Olson et al. 2009, Watt et al. 2010).

Based on Bergmann's rule and the mechanistic heat-conservation hypothesis, Daufresne et al. (2009) hypothesized that decreasing body sizes would be a third universal ecological response to global warming, with the first 2 responses being geographic range shifts toward higher latitudes and elevations and changes in phenology (seasonality). Over time scales of several millennia, clear patterns exist between temperature and body sizes. Body sizes of mammals, for example, oscillate, becoming smaller during warmer interglacials and increasing during colder periods (Davis 1981). This pattern, however, is not entirely clear over shorter time scales, and studies on the effect of recent climate change on body sizes of birds have produced conflicting results. In a study of migrating birds in western Pennsylvania, Van Buskirk et al. (2010) found that changes in wing length and fat-free mass (mass when fat score is zero) differed across species and have steadily decreased since 1961 and concluded that these changes were consistent with a response to warmer climates. In contrast, Salewski et al. (2010) found that morphological changes of 12 European passerines did not show consistent patterns. Salewski et al. (2014) found variable body size trends in 11 bird species in Germany and showed that observed changes were not related to temperature. Teplitsky and Millien (2014) reviewed the literature on body size and climate change and found only mixed evidence that body sizes have decreased, with 60% of avian cases and 7% of mammalian cases showing decreases. Some studies have found increases in avian body sizes (Goodman et al. 2012). Thus, observed changes in avian body size in response to recent climate change have been variable and inconsistent (Gardner et al. 2011). Because many factors can influence body size (Calder 1984, Peters 1983) and the relationship between climate and body size can be complicated (Chown 2012; Huey et al. 2012; Ozgul et al. 2009, 2010), heterogeneous responses of avian body sizes to climate change should not be surprising (Millien et al. 2006).

Our study aims (1) to examine how body sizes of neotropical migrants have changed in Laurel, MD, between 1980 and 2012; (2) to determine which particular species show significant changes in body size; and (3) to compare our findings to those from another banding station in the eastern United States to examine whether changes in body size show variation at regional spatial scales.

Field-Site Description

Our banding station was located at the USGS Patuxent Wildlife Research Center (PWRC) in Laurel, MD (elevation 50 m; 39.05°N, 76.81°W). Habitat near the banding site included a transmission line in 2–3-m–tall dense shrubbery dominated by native shrub species with scattered grassy areas. The site has seen very little vegetation change since 1980 (D. Bystrak, USGS PWRC, Laurel, MD, pers. comm.)

Methods

Between 1980 and 2012 (excluding 2004–2006), we captured birds in 12-m, 30-mm–gauge mist nets in the fall (August through November). We generally deployed 26 nets 25 minutes before sunrise for 3–4 hours on the days we banded. We identified individuals to species and aged and sexed birds using skulling (examination of the extent of bone pneumatization in the skull) and molt limits (see Pyle 1997). We measured wing length (as unflattened wing chord ± 1 mm), mass (± 0.1 g), and fat score (on a scale of 0–4) and used wing length and fat-free mass as our measures of body size. Wing length is the most common measure of avian body size (Ashton 2002), and fat-free mass, the estimated mass when fat is zero, is obtained with covariance analysis by including fat score as a covariate. Over the course of the study, 10 banders measured the vast majority of birds, and 2 individuals measured about 2/3 of all captured birds.

Statistical analyses

We captured 87,832 individuals of 121 species. Here, we examine only neotropical migrants and exclude species that winter primarily in North America (residents and short-distance migrants). We excluded from our analyses species with fewer than 300 captured individuals, repeated captures of an individual within a season, and individuals of unknown age; 34,844 individuals of 31 species met our criteria for inclusion.

We used generalized linear mixed models (GLMMs; West et al. 2006) with the "GLIMMIX" procedure in SAS 9.3 (SAS Institute, Inc. 2011) and examined the main effect of year to determine overall or universal (sensu Daufresne et al. 2009) trends in body size. We analyzed wing length and body mass separately, and our response variables were ln(wing length) and ln(mass) of individual birds. Fixed effects were year and capture date (Julian day) as continuous variables and age and sex as categorical variables. We included species as a random effect. To test whether species or ages 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 likelihood ratio tests (West et al. 2006). For analyses of mass, we also included fat score and time of day as fixed continuous variables.

For each of the 31 species included in the GLMM, we used the "MIXED" procedure in SAS to estimate the species' change in wing length and change in mass over years. We included age, sex, year, and Julian day as covariates and the age*year interaction. For analyses of mass, we also included time of day and fat score.

Results

Body-size changes

For all species combined, wing length increased between 1980 and 2012 ($F_{1, 34060}$ = 46.06, $P < 0.001$, Table 1). While highly significant, the magnitude of the change in wing length (after back-transforming) was small at 0.55% ± 0.08% (mean ± SE) over the course of the study. Change in wing length differed significantly across

species (χ^2 = 119664.2, df = 1, P < 0.001) and ranged from -2.03% to +2.00%. Wing length increased significantly in 9 species (*Geothlypis trichas* [Common Yellowthroat], *Mniotilta varia* [Black-and-white Warbler], *Seiurus aurocapilla* [Ovenbird], *Setophaga caerulescens* [Black-throated Blue Warbler], *Catharus fuscescens* [Veery], *Catharus minimus* [Gray-cheeked Thrush], *Catharus ustulatus* [Swanson's Thrush], and *Vireo olivaceus* [Red-eyed Vireo]) and decreased significantly in 3 (*Setophaga discolor* [Prairie Warbler], *Empidonax flaviventris* [Yellow-bellied Flycatcher], and *Empidonax minimu*s [Least Flycatcher]) (Table 2). Change in wing length did not differ between Hatch Year (HY) and After Hatch Year (AHY) age classes (χ^2 = 2.0, df = 1, P = 0.26).

For all species combined, fat-free mass increased 1.30% ± 0.20% between 1980 and 2012 ($F_{1, 32369}$ = 42.37, P < 0.001, Table 1). Species varied significantly in change in fat-free mass over time (χ^2 = 116447.94, df = 1, P < 0.001), ranging from -2.87% to +3.69% between 1980 and 2012. Fat-free mass increased significantly in 6 species (Common Yellowthroat, Black-and-white Warbler, Ovenbird, Prairie Warbler, Veery, and Red-eyed Vireo) and decreased in only *Setophaga virens* (Black-throated Green Warbler) (Table 2). Across species, change in wing length and change in fat-free body mass were positively correlated (r = 0.49, n = 31, P = 0.005; Fig. 1).

Spatial variation in body-size changes

For all species combined, change in wing length over time at our site in Maryland was weakly correlated with change in wing length from 1961 to 2006 at a

Table 1. Summaries of generalized linear mixed models (GLMMs) to examine morphological changes (log-transformed wing length and log-transformed fat-free mass) for 31 neotropical migratory species from 1980-2012. Estimates are coefficients. Negative coefficients indicate declining size and positive coefficients indicate increasing size. SE is standard error.

Source of variation		Estimate	SE	*F* value	*P*
Wing length					
Year		0.000171	0.000025	46.06	<0.001
Julian day		0.000136	0.000011	165.93	<0.001
Age	AHY	0.022810	0.000371	3777.15	<0.001
	HY	0.000000			
Sex	Female	-0.021540	0.000519	7984.38	<0.001
	Male	0.034030	0.000518		
	Unknown	0.000000			
Fat-free mass					
Year		0.000405	0.000062	42.37	<0.001
Time		0.000061	3.50 E-6	300.95	<0.001
Julian day		0.000340	0.000026	177.63	<0.001
Age	AHY	0.018890	0.000852	491.52	<0.001
	HY	0.000000			
Sex	Female	-0.017030	0.001193	1050.47	<0.001
	Male	0.029150	0.001189		
	Unknown	0.000000			
Fat				4537.02	<0.001

Table 2. Changes in log-transformed wing length and log-transformed fat-free mass (change x10000/year). Sample size is given by n. Estimates are coefficients; negative coefficients indicate declining size and positive coefficients indicate increasing size. SE is standard error. * indicates $P < 0.05$, † indicates $P < 0.01$, and ‡ indicates $P < 0.001$.

Family/ common name	Species code	Scientific name	n	Wing Est.	Wing SE	Fat-free mass Est.	Fat-free mass SE
Cardinalidae							
Indigo Bunting	INBU	*Passerina cyanea* (L.)	407	2.76	1.69	-2.90	4.07
Scarlet Tanager	SCTA	*Piranga olivacea* (Gmelin)	313	1.33	2.22	2.53	4.48
Parulidae							
Canada Warbler	CAWA	*Cardellina canadensis* (L.)	860	-1.40	1.01	4.70	2.58
Common Yellowthroat	COYE	*Geothlypis trichas* (L.)	4443	4.90‡	0.58	8.74‡	1.28
Black-and-white Warbler	BAWW	*Mniotilta varia* (L.)	939	2.95†	0.94	5.91*	2.41
Connecticut Warbler	CONW	*Oporornis agilis* (Wilson)	404	2.04	1.97	6.76	4.50
Tennessee Warbler	TEWA	*Oreothlypis peregrina* (Wilson)	1427	-0.60	0.68	0.88	1.64
Nashville Warbler	NAWA	*Oreothlypis ruficapilla* (Wilson)	347	3.60*	1.72	2.57	4.31
Ovenbird	OVEN	*Seiurus aurocapilla* (L.)	1962	2.49‡	0.75	4.72†	1.71
Northern Parula	NOPA	*Setophaga americana* (L.)	399	-2.20	1.61	-5.20	3.58
Black-throated Blue Warbler	BTBW	*Setophaga caerulescens* (Gmelin)	1525	2.15†	0.72	3.43	1.87
Bay-breasted Warbler	BBWA	*Setophaga castanea* (Wilson)	573	-0.80	1.66	1.22	3.26
Hooded Warbler	HOWA	*Setophaga citrina* (Boddaert)	539	3.15	1.61	3.86	3.44
Prairie Warbler	PRAW	*Setophaga discolor* (Vieillot)	361	-5.70*	2.30	11.31*	4.81
Magnolia Warbler	MAWA	*Setophaga magnolia* (Wilson)	4274	-0.20	0.40	0.90	0.97
Chestnut-sided Warbler	CSWA	*Setophaga pensylvanica* (L.)	738	-1.00	1.18	2.70	2.79
American Redstart	AMRE	*Setophaga ruticilla* (L.)	1679	-1.00	0.78	-3.70	1.99
Blackpoll Warbler	BLPW	*Setophaga striata* (Forster)	418	-1.10	1.71	3.34	3.93
Black-throated Green Warbler	BTNW	*Setophaga virens* (Gmelin)	805	0.80	0.93	-4.70*	2.29

Table 2, continued.

Family/ common name	Species code	Scientific name	n	Wing Est.	Wing SE	Fat-free mass Est.	Fat-free mass SE
Polioptilidae							
Blue-gray Gnatcatcher	BGGN	*Polioptila caerulea* (L.)	314	-3.80	3.01	-6.30	5.51
Turdidae							
Veery	VEER	*Catharus fuscescens* (Stephens)	752	4.14[†]	1.41	9.90[‡]	2.90
Gray-cheeked Thrush	GCTH	*Catharus minimus* (Lafresnaye)	533	6.20[‡]	1.80	7.21	3.90
Swainson's Thrush	SWTH	*Catharus ustulatus* (Nuttall)	2151	2.67[‡]	0.64	-0.30	1.61
Wood Thrush	WOTH	*Hylocichla mustelina* (Gmelin)	455	2.64	1.83	2.95	3.97
Tyrannidae							
Eastern Wood-Pewee	EAWP	*Contopus virens* (L.)	294	-1.60	2.63	0.42	6.12
Yellow-bellied Flycatcher	YBFL	*Empidonax flaviventris* (Baird and Baird)	400	-5.00[*]	2.09	1.89	5.23
Least Flycatcher	LEFL	*Empidonax minimus* (Baird and Baird)	310	-6.40[†]	2.21	-9.10	6.38
Traill's Flycatcher	TRFL	*Empidonax* sp.	695	-2.20	1.49	-1.10	3.20
Acadian Flycatcher	ACFL	*Empidonax virescens* (Vieillot)	407	-1.90	2.42	-4.90	4.41
Vireonidae							
White-eyed Vireo	WEVI	*Vireo griseus* (Boddaert)	504	1.71	1.51	3.93	2.96
Red-eyed Vireo	REVI	*Vireo olivaceus* (L.)	5616	2.91[‡]	0.34	8.61[‡]	1.13

station in western Pennsylvania, 235 km away ($r = 0.37$, $n = 30$, $P = 0.043$; Fig. 2). Change in fat-free mass was not correlated between banding stations ($r = 0.27$, $n = 30$, $P = 0.16$; Fig. 3).

Discussion

We documented changes in wing length and fat-free mass across 31 neotropical migratory bird species between 1980 and 2012 at the USGS Patuxent Wildlife Research Center (PWRC) in Laurel, MD. While highly statistically significant, overall general changes in body size were small, amounting to a 0.55% mean increase in wing length and a 1.30% mean increase in fat-free mass over the course of the study. Changes in both measures of body size varied between species, and species-
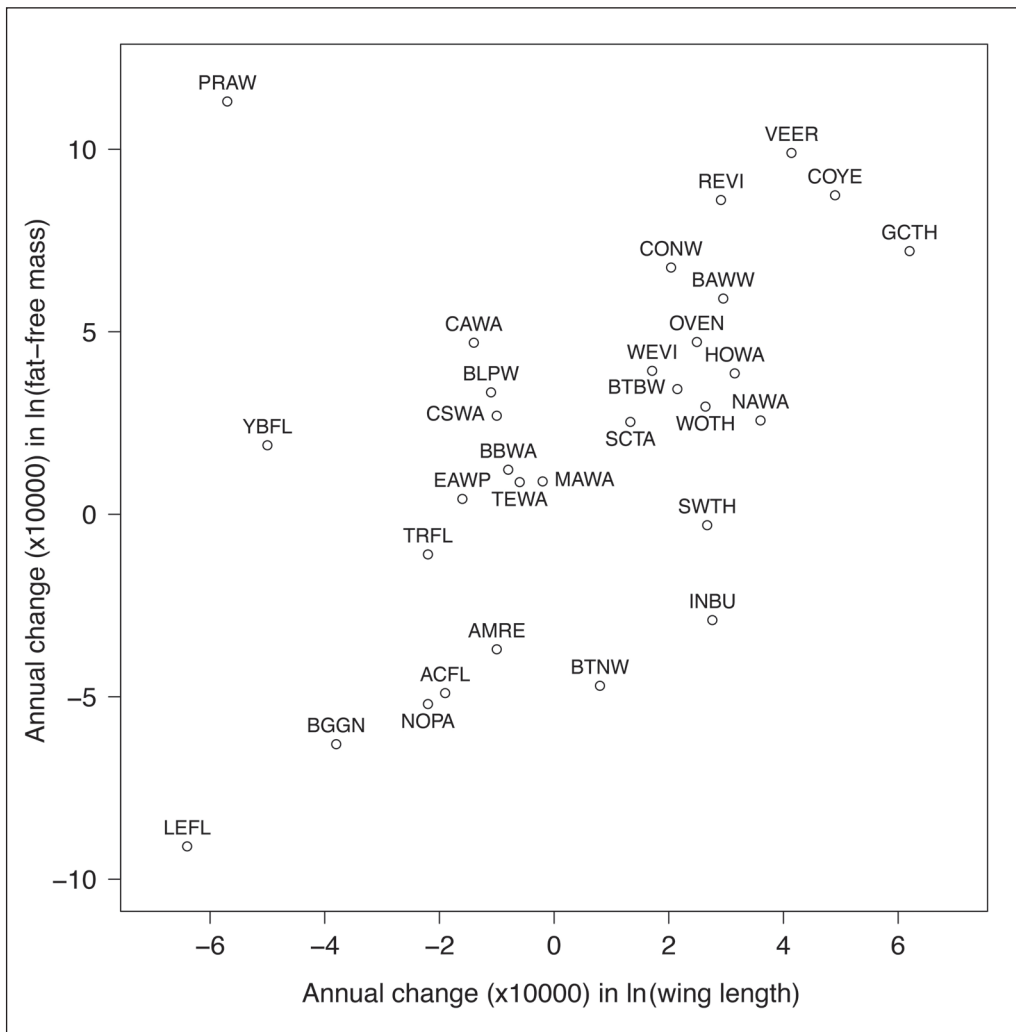
Figure 1. Annual change (x10000) of ln(fat-free mass) and ln(wing length) between 1980 and 2012 for 31 neotropical migratory bird species ($r = 0.49$, $n = 31$, $P = 0.005$). Estimates are for the separate models for each species. Species codes are defined in Table 2.

specific changes sometimes swamped the general trend. For example, despite a general increase in wing length and fat-free mass across species, 3 species showed significant decreases in wing length, and 1 exhibited a significant decline in fat-free mass. Wing length and fat-free mass increased significantly in 9 and 6 species, respectively. Species in the same family sometimes showed similar changes in body size (Table 2). Two of the 3 species with significant decreases in wing length were flycatchers (Tyrannidae), and the other 3 species of flycatcher showed decreasing but nonsignificant changes in wing length. In thrushes (Turdidae), wing lengths increased significantly in 3 of 4 species, and the fourth species showed a positive but nonsignificant trend. When examined individually, many migratory species did not exhibit significant changes in body size: 19 species showed no significant change
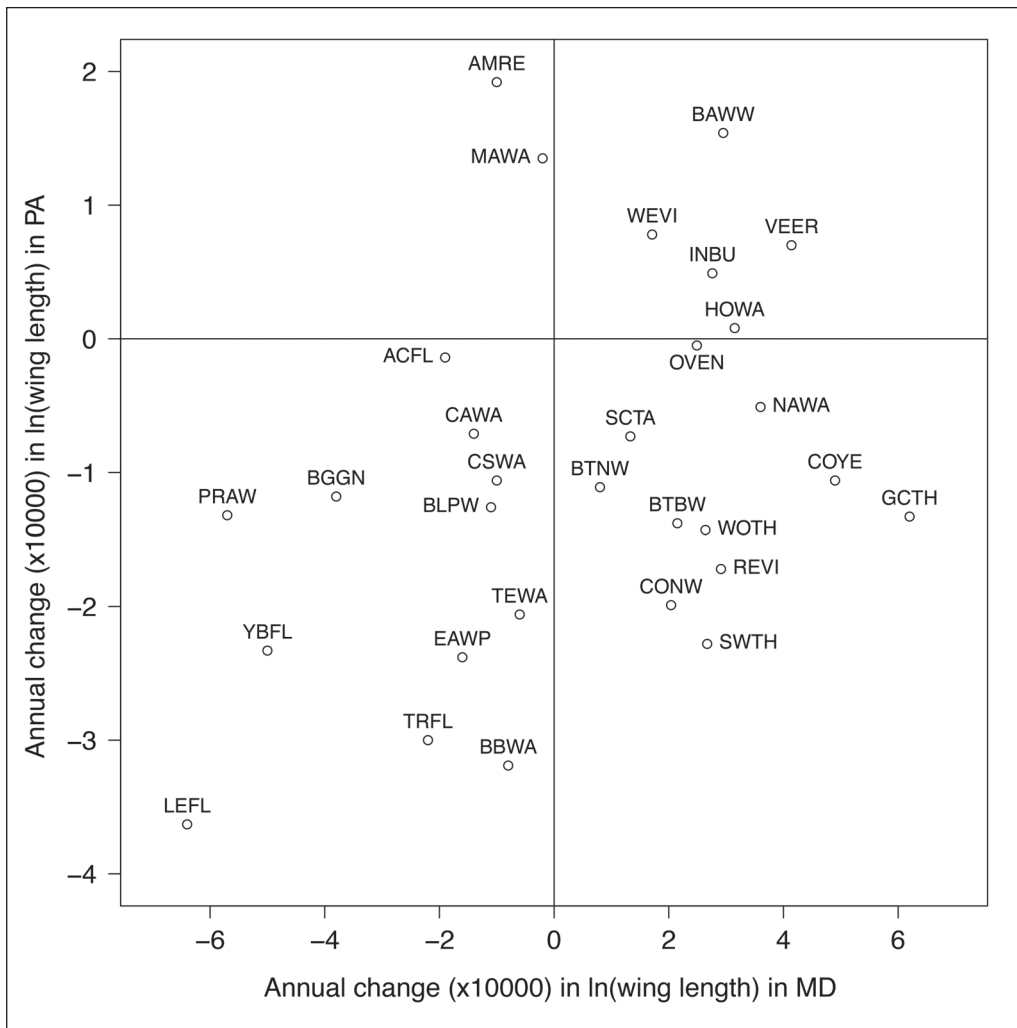

Figure 2. Across species, annual change (x10000) in ln(wing length) in our study from 1980 to 2012 and a study in western Pennsylvania from 1961 to 2006 are weakly correlated ($r = 0.37$, $n = 30$, $P = 0.043$). We excluded Northern Parula because this species was not caught in the fall in Pennsylvania. Species codes are defined in Table 2.

in wing length, and 24 species showed no significant change in fat-free mass. Most of the individuals captured in our study likely belonged to northerly populations and were caught during migration. Consequently, our samples likely consist of individuals from different breeding populations. It is possible that changes in body size have occurred at finer spatial scales, but that opposing patterns result in no net effect at broader scales. At the spatial scale examined here, neotropical migrants have largely shown individualistic changes in body size at PWRC between 1980 and 2012, and we find no evidence for widespread declines in body size as a universal response to climate change as posited by Daufresne et al. (2009).

Our findings that wing length and fat-free mass have generally increased contrast with those of Van Buskirk et al. (2010). Van Buskirk et al. (2010) found widespread declines in wing length and fat-free mass of passerines in western Pennsylvania
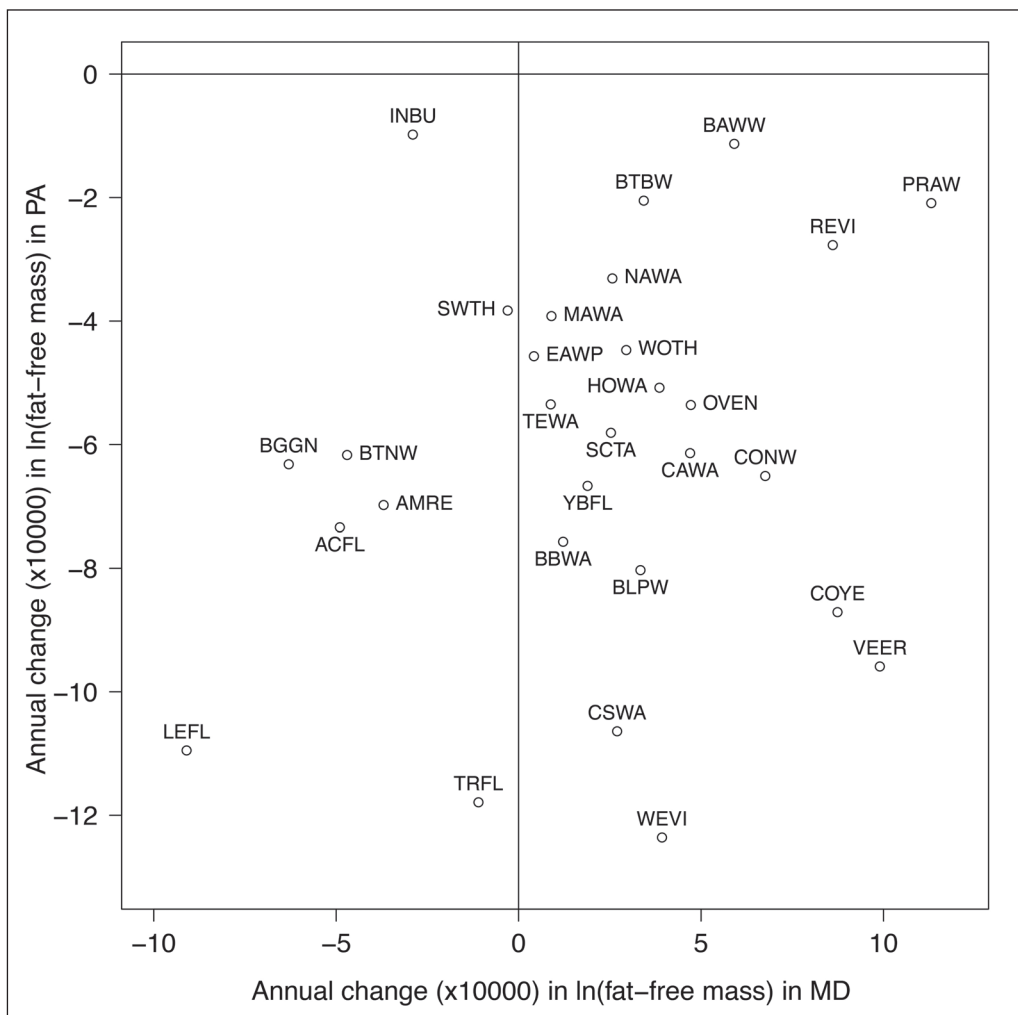

Figure 3. Across species, annual change (x10000) in ln(fat-free mass) is not correlated between banding stations ($r = 0.27$, $n = 30$, $P = 0.16$). Gray-cheeked Thrush (6.2, 6.51) is not shown. Species codes are defined in Table 2.

between 1961 and 2006 and noted that these changes were consistent with a response to a warming climate. In contrast, Goodman et al. (2012) documented increases in wing length and in fat-free mass between 1983 and 2009 in California, and Collins et al. (2017) found increases in wing length but not in fat-free mass for 20 resident and short-distant migrant passerine species at PWRC. Goodman et al. (2012) hypothesized that increases in body size reflected increases in climatic variability or primary productivity. Bumpus (1899) proposed that more severe weather at higher latitudes might drive Bergmann's rule by selecting for larger individuals with increased fasting endurance. This starvation resistance hypothesis has been supported by studies that have demonstrated that severe weather events can favor larger body sizes (Ashton 2002, Brown and Brown 1999, Jaramillo and Rising 1995). Climate change is predicted to increase the frequency and severity of some extreme weather events, such as heat waves and the number of heavy precipitation events, (Easterling et al. 2000, Meehl and Tebaldi 2004, Min et al. 2011, Stouffer and Wetherald 2007) while decreasing other events, such as cold-temperature extremes. Consequently, this hypothesis predicts that climate change may result in either larger or smaller body sizes.

Our study, Van Buskirk et al. (2010), Goodman et al. (2012), and Collins et al. (2017) all found that changes in body size differed between species, and magnitudes of species change were similarly small in all 3 studies: -0.09% to +0.11% per year in our study, -0.08 to +0.02% per year in Van Buskirk et al. (2010), -0.03 to +0.08% per year in Goodman et al. (2012), and -0.13 to +0.16% per year in Collins et al. (2017). Across species, change in wing length was correlated with change in fat-free mass at our site (Fig. 1). One species, Prairie Warbler, showed a significant decrease in wing length but a significant increase in fat-free mass. Our findings agree with those of Salewski et al. (2014) and demonstrate that observed body size changes depend on the species and morphological trait examined.

That we documented general increases in body size while Van Buskirk et al. (2010) found widespread declines is particularly surprising given the proximity of study sites and the similarity of the 2 studies. Only 235 km separate our banding station in Maryland from theirs in western Pennsylvania. Both studies used wing length and fat-free mass as measures of body size and examined a similar set of species over comparable times and durations (32 years vs. 46). In both studies, large sample sizes allowed inclusion of covariates such as age, sex, and date of capture into statistical models. Of the 31 species examined in our study, Van Buskirk et al. (2010) analyzed fall banding records for all species except *Setophaga americana* (Northern Parula). Both studies found significant change over time for all species combined, but when comparing the changes in individual species, the change in wing length in our study was only weakly correlated with change in wing length in western Pennsylvania (Fig. 2). In addition, 6 species (Common Yellowthroat, *Catharus minimus* [Gray-cheeked Thrush], *Oreothlypis ruficapilla* [Nashville Warbler], Ovenbird, Red-eyed Vireo, and *Catharus ustulatus* [Swainson's Thrush]) that showed significant decreases in wing length in western Pennsylvania increased significantly in our study. Similarly, changes in fat-free

mass were not correlated between banding stations (Fig. 3), and in 4 species (Common Yellowthroat, Ovenbird, Red-eyed Vireo, and Veery), fat-free mass increased in our study but decreased in western Pennsylvania. Together, these findings demonstrate that changes in body size over time are species-specific, that these relative and absolute changes vary across space, and that populations of a species can exhibit opposite changes in body size over regional spatial scales.

Several explanations can account for differing body sizes changes in neotropical migrants between studies. Most of these neotropical migratory species have large breeding populations north of our banding stations. In our study, even for species that breed locally, most captured individuals likely belonged to northerly populations and were caught during migration. It is possible that the 2 banding stations caught birds from different breeding areas and that climate change differed between areas. It is also plausible that morphological responses to climate change differed between breeding populations. Context dependence could cause the influence of warming temperatures on body sizes to differ between breeding populations (Yom-Tov and Geffen 2011) and lead to variable or contrasting trends in body size over time. Interactions between climatic variables are one possible mechanism of context dependence. For example, summer temperatures might affect fat-free mass indirectly, through its influence on productivity and food availability (Yom-Tov and Geffen 2011), and warming temperatures might increase productivity and avian body sizes in wetter areas but cause water stress and decrease productivity and body sizes in drier locations. Identification of breeding areas would permit analyses of climate data and examination of morphological responses to climate change to test these hypotheses for differing trends in body sizes of neotropical migants. One could use stable isotopes to identify breeding areas (Rubenstein and Hobson 2004), but this approach would require feather or tissue samples, which we did not collect.

Another hypothesis for the differing changes in body size of neotropical migrants between the 2 studies is that observed changes in body size were not driven by climate change in at least 1 site. Patterns between climate and body size over long periods of millenia are unambiguous: body sizes become smaller during periods with warmer climates (Davis 1981, Kurtén 1968). But, this pattern might not hold over shorter time scales. Salewski et al. (2014) found that morphological changes in 11 bird species in Germany over the last century were not related to temperature, and Collins et al. (2017) found that species-specific body-size changes in resident birds and short-distance migrants at PWRC were not driven by mean summer or mean winter temperatures. Although magnitudes of body-size change that we recorded in neotropical migrants were comparable to or greater than those reported from other studies (Gardner et al. 2014, Goodman et al. 2012, Van Buskirk et al. 2010), observed changes were small, ranging between -0.09% and 0.11% per year. Many physiological and ecological processes are influenced by body size (Calder 1984, Peters 1983), and many selective pressures can contribute to changes in body size. For example, warming temperatures associated with climate change have decreased migration distances (Visser et al. 2009), and shorter migration distances

might select for shorter wing lengths. Moreover, a change in one morphological trait can influence other morphological traits. Decreased mass, for example, might select for reduced wing length due to allometric responses and selective pressures associated with aerodynamics (Yom-Tov et al. 2006). Changes in body size reflect the combined selective forces of these factors, so over shorter periods with only moderate increases in temperature, other forces might drive changes in body size. If so, then climate would drive changes in body size only when climate change is more extreme or prolonged.

Our work adds to a growing literature on the effect of recent climate change on avian body sizes (Goodman et al. 2012; McCoy 2012; Salewski et al. 2010, 2014; Van Buskirk et al. 2010) and demonstrates that morphological changes in neotropical migratory birds were highly variable since 1980. We find no evidence for widespread declines in wing length or fat-free mass. Species exhibited inconsistent and variable changes in body size across space, and some species displayed opposite morphological changes between banding stations in Maryland and western Pennsylvania. While variable and conflicting body size trends might arise between sites due to regional differences in climate change or to differing effects of climate change on avian body sizes through context dependence, factors other than climate might drive observed changes in body size of neotropical migrants, and alternative hypotheses for body-size changes over short time scales should be considered.

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