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

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 despecies (G^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 minimus* [Least Flycatcher]) (Table 2). Change in wing length did not differ between Hatch Year (HY) and After Hatch Year (AHY) age classes (G^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 (G^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 $P < 0.001$.

				Wing		Fat-free mass	
Family/ common name	Species code	Scientific name	*n*	Est.	SE	Est.	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	$4.90^{\ddagger}$	0.58	$8.74^{\ddagger}$	1.28
Black-and-white Warbler	BAWW	*Mniotilta varia* (L.)	939	$2.95^{\dagger}$	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	$2.49^{\ddagger}$	0.75	$4.72^{\dagger}$	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	$2.15^{\dagger}$	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	$4.14^{\dagger}$	1.41	$9.90^{\ddagger}$	2.90
Gray-cheeked Thrush	GCTH	*Catharus minimus* (Lafresnaye)	533	$6.20^{\ddagger}$	1.80	7.21	3.90
Swainson's Thrush	SWTH	*Catharus ustulatus* (Nuttall)	2151	$2.67^{\ddagger}$	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	$-6.40^{\dagger}$	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	$2.91^{\ddagger}$	0.34	$8.61^{\ddagger}$	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 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

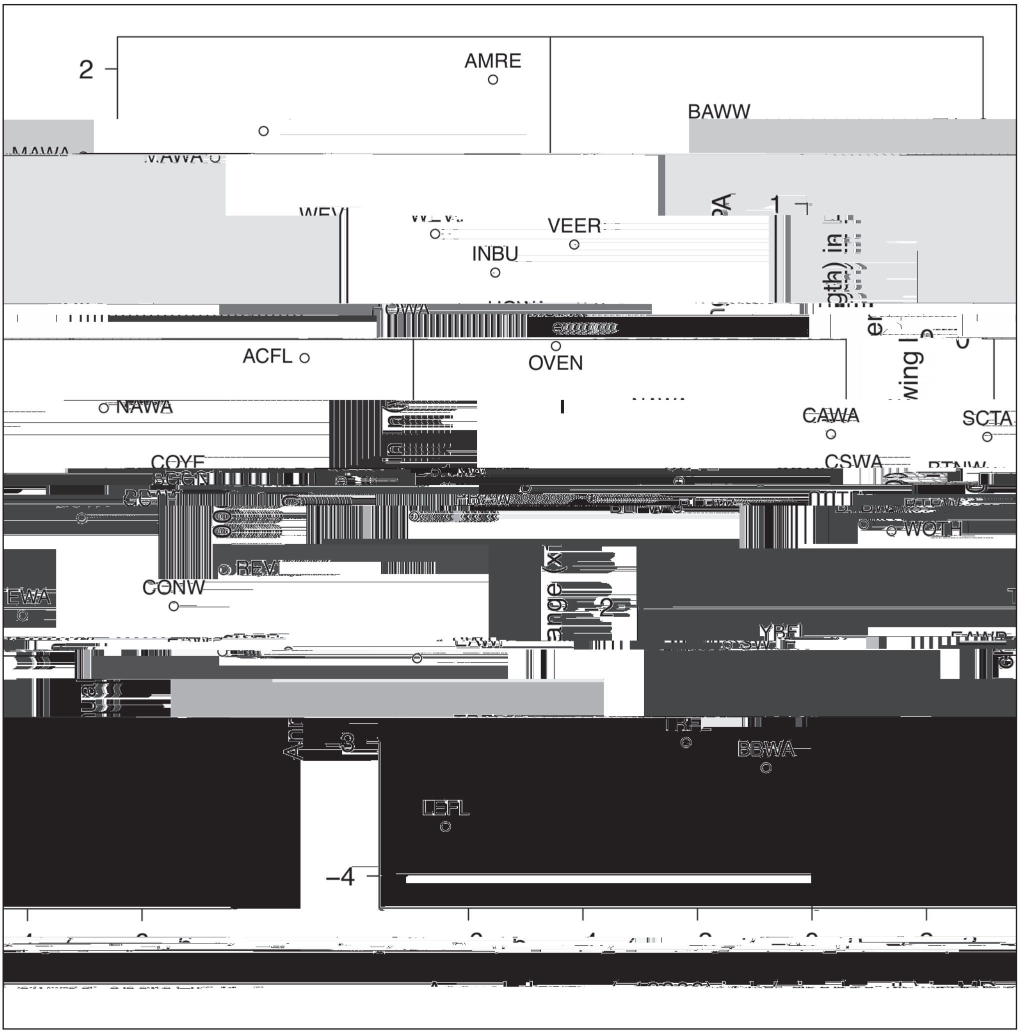

Figure 2. Across species, annual change (x10000) in ln(wing length) in our study from 1980 to 2012 and a study in western Pennsylvania from 1961 to 2006 are weakly correlated (r = 0.37, n = 30, P = 0.043). We excluded Northern Parula because this species was not caught in the fall in Pennsylvania. Species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

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

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