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Declining body sizes in North American birds associated with climate change

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Recent climate change has caused comparatively rapid shifts in the phenology and geographic distributions of many plants and animals. However, there is debate over the degree to which populations can meet the challenges of climate change with evolutionary or phenotypic responses in life history and morphology. We report that migrating birds captured at a banding station in western Pennsylvania, USA, have exhibited steadily decreasing fat-free mass and wing chord since 1961, consistent with a response to a warmer climate. This confirms that phenotypic responses to climate change are currently underway in entire avian assemblages. Declines in body size were not explained by an index of habitat condition within the breeding or wintering distributions. Instead, size was negatively correlated with temperature in the previous year, and long-term trends were associated with the direction of natural selection acting on size over the winter: species undergoing the strongest selection favoring small wing chord showed the most rapid long-term declines in wing. Phenotypic changes are therefore in line with the prevailing selection regime.

The rate of change in the Earth's climate over the past few decades is very high in comparison with recent millennia (Hansen et al. 2006). Many important features of biological populations, such as geographic distributions, life history traits, and the timing of events such as migration and reproduction, are showing directional changes associated with rapid environmental change (Parmesan 2006, Cleland et al. 2007, Van Buskirk et al. 2009). Our study focuses on recent trends in body size because this trait is clearly predicted to change as temperature increases. The rationale begins with the observation, known as Bergmann's rule, that body size is smaller in populations occupying warmer climates (Rensch 1936, Mayr 1956, James 1970). The cause of Bergmann's rule was originally taken to involve energy metabolism, thermoregulation, and surface-area-to-volume ratios (Bergmann 1847, Rensch 1936), but this has been cast into doubt by two observations. First, many poikilotherms, in addition to endotherms, are smaller in warm climates (Millien et al. 2006), and body size decreases over time even within experimental insect populations held at warm temperature (Anderson 1973, Partridge et al. 1994). Second, even though larger organisms have lower surface area for their body size, the strength of Bergman's rule is unrelated to size (Ashton et al. 2000, Ashton 2002). Even without a well-accepted mechanism, however, Bergmann's rule itself is so consistent that it clearly justifies the prediction that body size will decline as the climate warms in the Northern Hemisphere, particularly for tetrapods (Millien et al. 2006).

Early tests of this prediction have yielded mixed results. The best example comes from work on *Neotoma* woodrats in southwestern North America. Smith et al. (1995) and Smith and Betancourt (2006) discovered that the sizes of fecal pellets, which are related to the animal's body size, closely corresponded to the late Quaternary temperature record. Over a period of 25 000 years, woodrats were large during cool periods and small during warm periods. In other mammal species, however, body size trends in recent decades are just as often positive as negative, and therefore do not uphold the expectation based on Bergmann's rule (Yom-Tov et al. 2003, 2006a, 2008, Hill et al. 2008, Meiri et al. 2009). Results for birds are also mixed, with examples both of species that have declined in size (Monahan 2008, Teplitsky et al. 2008) and increased in size over the second half of the 20th century (Kanuscak et al. 2004, Guillemain et al. 2005, Yom-Tov et al. 2006b). It is difficult at this stage to draw generalities from these studies, if only because rather few species have been studied. Therefore, we included in our analysis a large number of bird species, in order to discern dominant patterns of change in body size that might not be evident in just one or a few species.

The relative contributions of plasticity and evolved genetic change to phenotypic responses is an important issue in the study of biotic impacts of climate change (Gienapp et al. 2008). A definitive answer requires quantitative genetic analyses or long-term studies of marked individuals. But studies that observe natural selection congruent with the phenotypic shift can at least argue that a prerequisite for genetic change is present (Etterson 2004, Charmantier et al. 2008). We adopt this approach here. First we document long-term trends in body size of a large sample of bird species; then we test whether differential survival with respect to size is consistent with the observed phenotypic change. Although our data cannot demonstrate that body size is evolving under climate change, they do show that the response is correlated with natural selection and may therefore be adaptive.

Methods

The data set

We studied the body sizes of birds captured in mist-nets and traps between June 1961 and November 2006 at Powdermill Nature Reserve (PNR), a field station operated by Carnegie Museum of Natural History in Pennsylvania, USA (elevation 400 m; 40°10'N, 79°16'W). The 10-ha study area was characterized by small fields, marshland and low scrub habitats. About 35 12-m mist nets (30 mm and 36 mm mesh) were operated each day, 5–6 days per week during spring and autumn migration. A reduced number of nets was used during summer, and winter banding employed only wire traps when the temperature was below freezing. Our study site is not located in an exceptional geographic situation, such as along a coastline or mountain ridge, and therefore the results may be broadly representative of bird communities in the Appalachian region of eastern North America. The banding methods and locations of the traps and nets remained largely unchanged, and the majority of birds were processed by just two people (RCL and RSM), whose measurements were continually calibrated against one another during the study.

We included birds captured as summer and winter residents and during spring and autumn migrations. Predicted changes in body size may differ among seasons, depending on the time of year during which adaptation to temperature occurs and whether other modes of response to climate change are available. For example, breeding and wintering species can adjust their migration distances or shift their geographic distributions northward (La Sorte and Thompson 2007, Zuckerberg et al. 2009), and therefore may not show a decline in size at PNR. However, for migrants that breed entirely to the north, a shift in breeding range would have no effect on the size of individuals captured at PNR because the banding station 'samples' the entire latitudinal distribution of the species.

We defined summer residents as adults captured during the months of June and July, including only species known to breed within the study area. Winter residents included birds captured during December, January and February. We determined migratory periods separately for each species by inspecting its overall distribution of captures. The completion of spring migration was marked by the disappearance of unbanded individuals; the onset of autumn migration was the point at which increasing numbers of unbanded birds appeared. The Supplementary material Appendix 1 lists the species included in the study.

Three measurements were available for each individual: unflattened wing chord (±0.5 mm; method a in Van Balen 1967, page 5), mass (±0.1 g), and fat score (on a scale of 0–3; Mulvihill et al. 2004). Our measures of body size were wing chord and fat-free mass, which is the mass when fat score is zero estimated by covariance analysis. Wing and fat-free mass are positively but imperfectly correlated within species (Chandler and Mulvihill 1992) ($n = 75$ autumn migrant species in our sample, mean $r = 0.35$, $SD = 0.14$, average sample size within species was 3904 individuals). Wing chord can change with age and feather wear (Stewart 1963, Mulvihill et al. 2004) but is nevertheless the most common measure of body size in studies of birds (Ashton 2002). In our dataset, the repeatability of wing was higher than that of mass (wing 0.895, fat-free mass 0.692; $n = 43$ species and 4060 individuals recaptured at least three times in autumn migration).

Statistical analyses

A species was included only if we captured it in at least seven different years over a >25-year period. The dataset included 19 097 individuals of 61 species caught in summer, 42 439 individuals of 26 species in winter, 132 962 individuals of 83 species in spring migration, and 291 705 individuals of 75 species in autumn.

Long-term trends in body size were estimated using mixed-effects linear models, separately for the four seasons. The response variables were ln(wing chord) and ln(mass) of individual birds. Fixed effects were year, time of day, fat score (for analyses of mass) and date of passage (for migrants) as continuous variables; sex, breeding range and migration distance as categorical variables; and interactions between year and breeding range and migration distance. Breeding range and migration distance were included because some studies have suggested that Bergmann's rule applies most strongly to sedentary species, perhaps because migrants are less influenced by temperature during stressful seasons (Rensch 1936, Zink and Remsen 1986, Ashton 2002). 'Breeding range' differentiated species that breed in the vicinity of PNR from those that breed entirely to the north or at higher elevation; this effect was included in analyses of wintering birds and migrants. 'Migration distance' differentiated species that winter mostly in the southern United States from those that winter entirely south of North America; this effect was included in analyses of breeding birds and migrants. Information on breeding range and migration distance came from Poole (2008) and the North American Breeding Bird Survey (BBS; www.mbr-pwrc.usgs.gov/bbs/). Sex, time of day, fat score and date of passage were included because they are potentially important for predicting body size. For example, mass is known to increase during the day (Lehikoinen 1987, Dunn 2001), during migratory stop-over (Schaub and Jenni 2001), with increasing fat level (Mulvihill et al. 2004), and differs among age- or sex-classes that migrate at different times (Stewart 1963). Significance of fixed effects was judged from F-tests (type III SS), with the denominator DF equal to the number of species in the analysis minus one. The random component of the model included species (treated as subjects) and the interactions between species and year, sex, fat, time of day and date of passage. Significance of random effects was evaluated from likelihood ratio tests comparing nested models with and without each variance component.

If an individual was captured more than once within a season, we used only the first capture. Models were implemented in SAS proc mixed (Littell et al. 1996).

We also tested whether body size in local breeding birds was associated directly with temperature. Regional temperature data, adjusted for changes in equipment, methodology, and urbanization, came from the 25 weather stations of the United States Cooperative Observing Network within 200 km of PNR (http://cdiac.ornl.gov/epubs/ndp/ushcn/usa_monthly.html). We calculated annual mean temperature during the breeding season (May–July), with each weather station's contribution weighted by the inverse of the distance between the station and PNR. These data showed an increasing trend over the duration of our study ($b = 0.0167$°C $\text{year}^{-1} \pm 0.0075$ SE, $p = 0.0311$). The two linear models described above (on wing chord and mass of breeding species) were then re-fitted with three additional covariates: temperature in the current year, in the previous year, and two years ago. Lagged temperatures were included because adult body size may be determined early in development or during the prebasic molt of the preceding year (Pehrsson 1987, Searcy et al. 2004).

A long-term decline in body size could be caused by deteriorating conditions during some part of the life cycle. We evaluated this possibility by calculating the correlation between the change in size for each species, its change in breeding population density estimated from the BBS, and its change in wintering population density estimated from the Christmas Bird Count (www.audubon.org/bird/cbc/index.html). Analyses were repeated for body size trends in all four seasons, and for species that breed locally (using the Allegheny Plateau BBS region) and to the north (Northern spruce-hardwoods and Closed boreal forest BBS regions combined). The rationale was that population trends reflect conditions during some stage of the annual cycle; a positive correlation would indicate that size decreases are associated with poor conditions.

An evolved adaptive response of body size to environmental change is possible only if there is directional selection favoring a shift in size. We therefore checked for natural selection on body size, following Johnston et al. (1972), by comparing fat-free mass and wing chord of spring migrants (post-selection) with the same measures during the previous autumn (pre-selection). This comparison was made for each species averaging across all years. Size measures were corrected for sex, migration date, and time of day, but not for age class because most individuals could not be aged in spring. The analysis of wing excluded seven species that molt their primary feathers during winter (Poole 2008). This approach would not be suitable for estimating selection between spring and autumn because a new cohort of juveniles is produced over the summer and most species replace their remiges during the prebasic molt. Finally, we tested whether the long-term body size trend in spring migration was correlated with the mean overwinter selection coefficient, as expected if body size is evolving in response to selection. A positive correlation would suggest that size-related survival within cohorts is associated with the long-term process of size change measured across many cohorts and years. The Discussion evaluates assumptions underlying this method.

Results

There were widespread declines in fat-free mass of birds sampled at PNR during all four seasons, and in wing chord during spring and autumn migration. Figure 1 depicts results for all seasons and both measures of body size; statistical analyses are presented in Table 1 (mass) and Supplementary material Appendix 2 (wing chord). In summer, 51 of 65 breeding species had negative slopes of mass against year ($p < 0.0001$, two-tailed binomial test); 20 of 26 wintering species had negative slopes ($p = 0.0025$); 60 of 83 spring migrants had negative slopes ($p < 0.0001$); and 66 of 75 autumn migrants had negative slopes ($p < 0.0001$). For wing chord, breeding species showed a non-significant decline, wintering species exhibited longer wings through time, 60 of 83 spring migrant species had negative slopes of wing against year ($p < 0.0001$), and 52 of 75 autumn migrants had negative slopes ($p = 0.0004$). Although highly significant, the absolute magnitude of body size decline was never large. For example, the average change in mass of the 83 spring migrants over 46 years was only –1.3% (range –9.2% to +18%). Average mass loss was highest in winter (3.6% decline over 46 years). Changes in wing chord were similarly modest, ranging from –0.6% in spring and autumn to +1% in winter (Supplementary material Appendix 2).

Different categories of species showed different trends in body size change, with the steepest declines observed in species that migrate long distances and winter to the south of North America (Fig. 1, Table 1, Supplementary material Appendix 2). The difference was not large, but it caused significant interactions between migration distance and year for mass during autumn migration and wing length during both migration seasons. Main effects of migration distance arose from the generally larger sizes of short-distance migrants; weak effects of breeding range occurred because local breeders were slightly larger than northern breeders. There were also overall differences in wing between sexes, and the significant effects of date of migration were probably caused by size differences between age classes that migrate at different times (Stewart 1963, Mulvihill et al. 2004). Random effects were always important (Table 1). Especially relevant here was the species-by-year interaction in all seasons, reflecting extensive variation among species in their body size changes over 46 years. Relationships between size and year for individual species are reported in Supplementary material Appendix 1. Other significant random effects reflected heterogeneity among species in the way body size depended on sex, fat score, time of day and date of passage.

Decreasing size was associated with warming summer temperatures, at least for species that bred locally. When regional temperature was included along with year in the analyses of breeding adults, mass decreased significantly with increasing temperature in the current and the preceding year (Fig. 2; temperature this year: -4.35 ± 0.76 SE (all coefficients $\times 10^{-3}$), $F_{1,60} = 32.7$, $p = 0.0001$; temperature last year: -3.35 ± 0.77, $F_{1,60} = 19.0$, $p = 0.0001$; temperature two years ago: 0.88 ± 0.73, $F_{1,60} = 1.45$, $p = 0.23$). The effect of year was negative but no longer significant (-0.28 ± 0.14, $F_{1,60} = 1.70$, $p = 0.18$). Wing chord also declined significantly with temperature in the preceding year, and year itself was

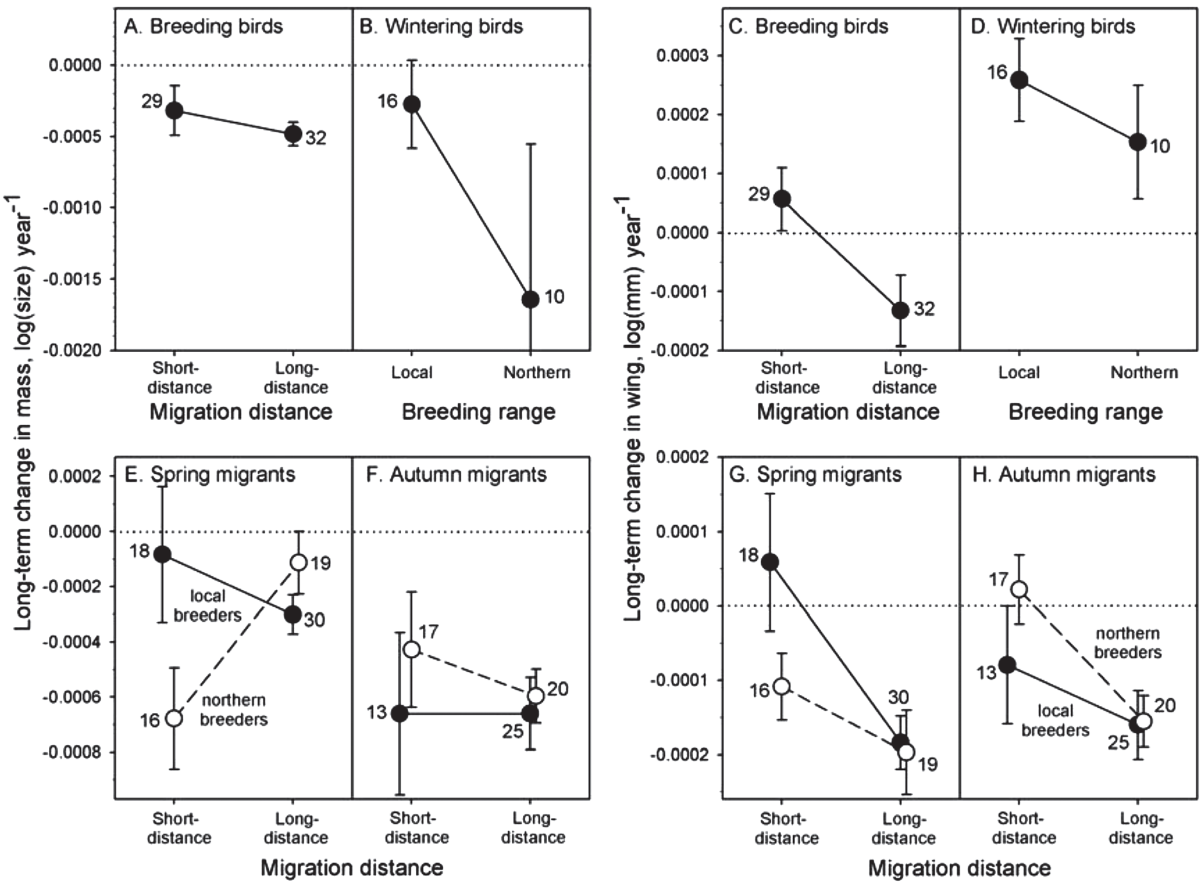

Figure 1. Mean (±1 SE) of the long-term change in fat-free mass (left side) and wing chord (right side) of resident (upper panels) and migrant (lower panels) birds captured at PNR between 1961 and 2006. Numbers beside the points indicate the number of species; the fine dotted line represents no change in size. Over all species, mass declined significantly in all samples and wing declined in migrants (Table 1, Supplementary material Appendix 2). Long-distance migrant species tended to become smaller more rapidly than short-distance migrants.

non-significant (temperature this year: –0.33 ± 0.36, $F_{1,60}$ = 0.84, p = 0.36; temperature last year: –0.87 ± 0.35, $F_{1,60}$ = 5.97, p = 0.0175; temperature two years ago: 0.10 ± 0.34, $F_{1,60}$ = 0.09, p = 0.77; year: –0.06 ± 0.07, $F_{1,60}$ = 0.01, p = 0.92). Estimated slopes indicate that mass declined 0.34% and wing chord declined 0.09% for each degree of increase in temperature during the preceding summer. Thus, the wing chord and fat-free mass of breeding birds reflect to some extent local temperature during the previous breeding season, and adult mass is further related to current conditions.

Data from population trends indicate that declines in body size were not associated with deteriorating conditions, at least during the winter season or on the breeding grounds. For wing chord, there were no significant correlations between the long-term change observed at PNR and trends in breeding and wintering population densities estimated from the Breeding Bird Survey and Christmas Bird Count (Table 2). For body mass, one of the 12 correlations was significant, but not in the predicted direction: species with declining winter population densities showed increasing fat-free mass at PNR during the autumn migration. Assuming that population trends reflect the overall condition of habitat, the data in Table 2 give no indication that species becoming smaller at PNR were the same as those experiencing deteriorating habitat in summer or winter.

Cohorts of individuals showed a shift in body size between autumn and spring migrations in many species. For mass, 31 of 70 species were of significantly different size in spring than in autumn ($p < 0.0001$, binomial test against the null hypothesis of 5% significant). Of these, 16 species were smaller in spring, 15 were larger, and there was no net overwinter change in mass across all species (Fig. 3a). For wing chord, 12 of 63 species showed a significant change, and all of these were positive. A significant fraction of species had a longer wing chord in spring than in the previous autumn (Fig. 3b; 48 of 63 species; $p < 0.0001$, binomial test). Here we interpret overwinter changes in mass and wing chord as measures of natural selection acting on body size between autumn and spring; the Discussion considers alternative interpretations. Our results suggest that selection on size within cohorts was associated with long-term change in size across generations. For both mass and wing, there were positive correlations between overwinter selection and the long-term trend in body size measured in the spring (Fig. 3c–d; mass: r = 0.30, p = 0.0122, n = 70 species; wing: r = 0.39, p = 0.0015, n = 63). In other words, species experiencing the strongest negative selection on size showed decreasing trends in size over the 46 year study period, whereas species undergoing positive overwinter selection showed increasing size. The correlation for wing remained

Table 1. Mixed-effects linear models on log-transformed mass of resident birds during summer and winter and migrants in spring and autumn. Estimates are variance components (for random effects, multiplied times 10 000) and coefficients (fixed effects, multiplied times 100). Long-term decline in size is reflected by significant negative effects of year in all four seasons. Test statistics are likelihood-ratio statistics (DF = 1) for random effects and type III F-ratios (denominator DF = number of species−1) for fixed effects.

		Summer residents			Winter residents			Spring migrants			Autumn migrants		
Source of variation		Estimate	Test stat.	p	Estimate	Test stat.	p	Estimate	Test stat.	p	Estimate	Test stat.	p
Random effects variance components													
species		5393.00	340.4	0.0000	5862.00	224.5	0.0000	4762.00	291.1	0.0000	3976.00	290.4	0.0000
species × year		0.0030	49.9	0.0000	0.0311	1047.6	0.0000	0.0012	421.3	0.0000	0.0012	653.6	0.0000
species × sex		35.87	3592	0.0000	3.94	790.4	0.0000	34.82	26006.7	0.0000	16.87	10390.3	0.0000
species × fat score		1.93	51.2	0.0000	4.33	2175.1	0.0000	1.63	1523.1	0.0000	2.58	9046.9	0.0000
species × time of day		0.0167	7.8	0.0052	0.0464	141.1	0.0000	0.0214	161.8	0.0000	0.0135	278.3	0.0000
species × date of passage		–	–	–	–	–	–	0.0217	3051.7	0.0000	0.0078	7441.3	0.0000
Fixed effects parameter estimates													
year		−0.040	8.55	0.0049	−0.080	9.82	0.0045	−0.028	145.11	0.0000	−0.059	224.74	0.0000
sex	female	1.828	2.61	0.0805	−2.794	26.25	0.0000	−2.002	8.83	0.0004	−1.526	16.93	0.0000
	male	3.842				2.527			2.956			4.128	
	unknown	0			0			0			0		
fat score		3.541	166.36	0.0000	4.048	85.53	0.0000	4.600	922.60	0.0000	4.774	642.90	0.0000
time of day		0.233	42.49	0.0000	0.440	60.33	0.0000	0.318	235.47	0.0000	0.281	302.85	0.0000
date of passage		–	–	–	–	–	–	0.008	0.20	0.6575	0.054	26.58	0.0000
breeding range	local	–	–	–	51.900	2.83	0.1049	47.880	9.63	0.0026	30.070	4.19	0.0442
	northern		–			0			0			0	
migration distance	short	58.000	9.45	0.0032	–	–	–	44.200	8.13	0.0055	33.280	4.93	0.0295
	long	0						0			0		
year × breeding range	local	–	–	–	0.125	2.75	0.1098	0.024	6.19	0.0149	0.015	2.83	0.0967
	northern	–			0			0			0		
year × migration dist.	short	0.017	0.65	0.4233	–	–	–	0.000	0.00	0.9830	0.022	5.79	0.0186
	long	0			–				0			0	
No. of individuals			17 738			40 022			125 879			283 453	
No. of species			61			26			83			75	

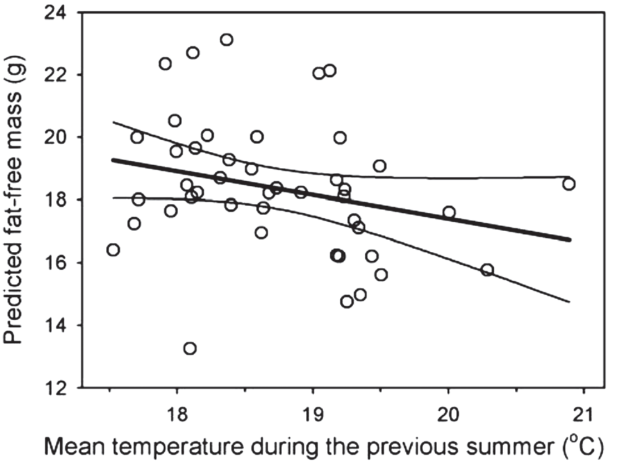

Figure 2. The fat-free body mass of local breeding birds at PNR declined with mean regional temperature during the preceding summer. The regression (heavy line) was estimated from the average mass predicted for each year by the mixed-effects linear model described in the text; the 95% CI (narrow curves) was based on the values shown in the figure.

significant even without two species that underwent especially strong selection for long wings (Fig. 3d; r = 0.31, p = 0.0165). The correlation for mass was not significant in the absence of the single outlier (Fig. 3c). The two outlying species, red-winged blackbird *Agelaius phoeniceus* for both mass and wing chord, and yellow-breasted chat *Icteria virens* for wing, do not appear unusual in terms of sample size or ecology.

Discussion

This study documents widespread declines in body size, measured by fat-free mass and wing chord length, of resident and migrant birds at Powdermill Nature Reserve (PNR), a bird-banding station in southwestern Pennsylvania, USA. There was little indication that smaller size was a consequence of birds experiencing deteriorating conditions within their breeding or wintering ranges, because population trends estimated from the Breeding Bird Survey and Christmas Bird Count were mostly unrelated to body size trends at PNR. This means that species with declining populations were not those that had smaller body sizes. Instead, we discovered that body size of breeding adults was negatively related in part to the mean regional temperature during the current and preceding summers, suggesting that warm temperatures either induce plasticity in size or cause differential survival with respect to size. One observation consistent with an evolved response to warming is that a measure of the strength of natural selection acting on size during the non-breeding season was associated with the long-term change in size, at least for wing chord. In spite of these several lines of evidence, our study cannot identify the mechanisms causing birds to become smaller in recent decades.

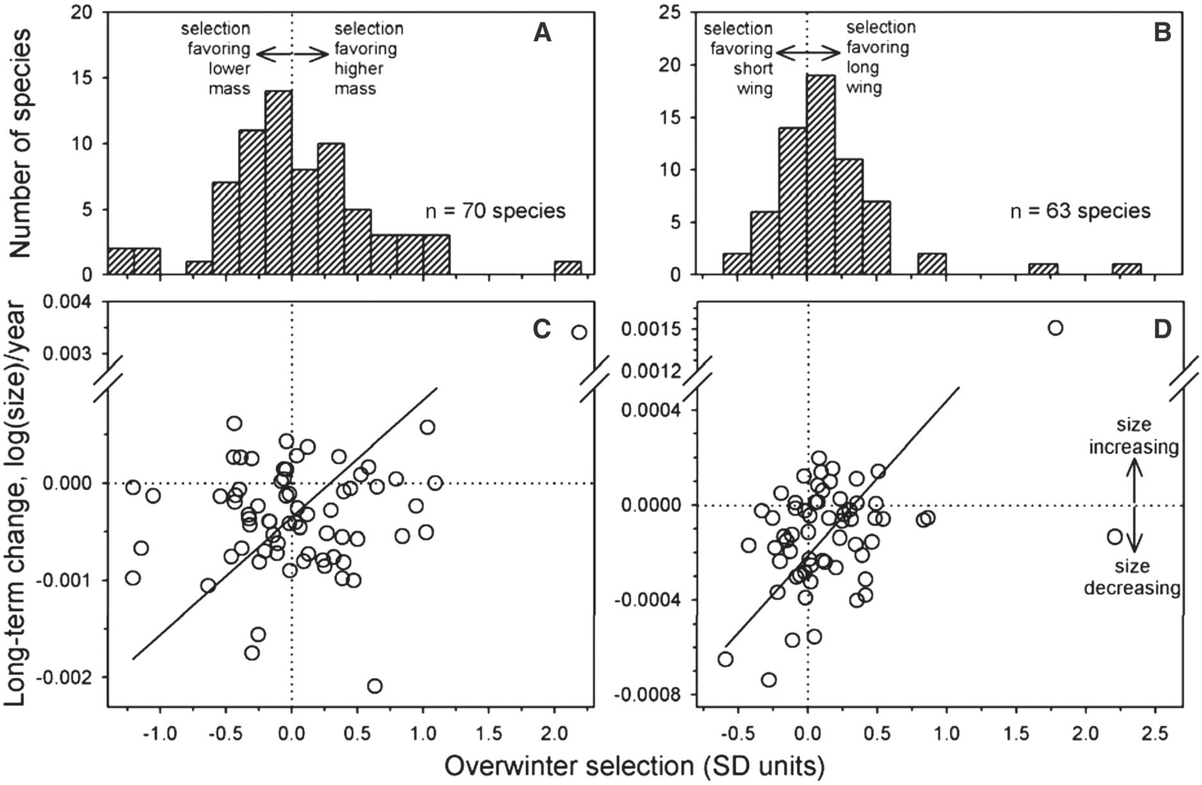

Figure 3. Frequency distributions of selection coefficients acting over the winter on fat-free mass (A) and wing chord (B), and correlations between overwinter selection and the long-term change in mass (C) and wing (D) measured during spring migration. Selection coefficients are the change in size over the winter expressed in units of SD in autumn, and long-term changes are estimated from mixed-effects models in Table 1 and Supplementary material Appendix 2. Dotted lines represent the situation of no selection or no long-term change in size, and solid lines are major axis regressions. Note axis breaks in panels (C) and (D).

Table 2. Population trends from the North American Breeding Bird Survey (BBS, 1966−2007) and the Christmas Bird Count (CBC, 1961−2007), and the correlations between these trends and long-term changes in body size at PNR between 1961 and 2006. BBS trends for southern species came from 124 routes located within the Allegheny Plateau region; trends for northern species came from 400 routes within the northern spruce−hardwoods and closed boreal forest regions. In (B) and (C), entries are correlation coefficients (above) and sample size (below). Some species common to both northern and southern BBS regions were included in both analyses; the CBC analysis includes only short-distance migrants. Only one correlation was significant at $p < 0.05$ (*), giving little indication that species with declining population density are becoming smaller at PNR during migration.

	Breeding Bird Survey trend		
	Southern species	Northern species	Christmas Bird Count trend
(A) Population trends			
mean (% per year)	−0.780	−0.865	−0.379
SD	2.51	4.14	2.23
no. of species	55	51	34
(B) Correlations with changes in body mass			
summer residents	−0.191 47	0.247 22	−0.191 19
winter residents	−0.591 11	0.446 11	−0.121 15
spring migrants	−0.075 55	0.029 49	−0.047 33
autumn migrants	−0.028 46	0.163 51	−0.428* 30
(C) Correlations with changes in wing chord			
summer residents	−0.033 47	−0.025 22	0.174 19
winter residents	−0.198 11	−0.073 11	−0.356 15
spring migrants	−0.135 55	−0.052 49	−0.110 33
autumn migrants	0.133 46	0.103 51	0.315 30

The decline in size of migrants at PNR occurred concurrently with a period of global and regional climate warming (Hansen et al. 2006, Van Buskirk et al. 2009). Many earlier studies of long term change in phenology or morphology have assigned causal influence to climate change simply because of the temporal association between phenotypic change and warmer temperatures (Parmesan 2006). The observed phenotypic changes for most species in our sample are in agreement with predictions derived from Bergmann's rule, as discussed in the Introduction (Millien et al. 2006). Although the absence of a well accepted causal connection between small body size and warm ambient temperature is somewhat unsettling, the ubiquity of Bergmann's rule across so many taxa makes the prediction relatively secure that declining body sizes should predominate under climate change (Ashton 2002, Millien et al. 2006). The conclusion that warming temperatures underlie our results was also supported by a negative correlation between body sizes of breeding residents and local temperatures in the current and preceding year.

The observed declines in body size cannot have resulted only from shifts in geographic distributions over the past few decades. A northward change in distribution might create an apparent decline in size because we would then sample an increasing number of individuals from the southern portion of the species' distribution. Because many of these species have larger body sizes at high latitude, consistent with Bergmann's rule (Ashton 2002), PNR would detect an apparent decline in size even when no change has occurred at the level of the entire distribution. This explanation is plausible for summer and winter resident birds. However, the fact that we observed strong declines in mass and wing for species that breed entirely to the north of PNR argues against this explanation. For these birds, the banding station potentially samples individuals from the entire latitudinal extent of the breeding range, indicating that individuals within populations are indeed smaller than they were several decades ago.

We argue that overwinter changes in mass and wing chord reflect, at least in part, natural selection acting on body size, and that our results are therefore consistent with an adaptive (genetic or purely phenotypic) response to climate change. Both of these statements require careful evaluation. Change in size between a cohort of individuals sampled in autumn and the following spring could be affected by three processes: feather wear, changing composition of the sampled population, and differential mortality over the winter with respect to size. In the case of wing, most species in our sample showed increasing size over the winter, which strongly implicates the third mechanism (selection) because the first two would act in the opposite direction or in no consistent direction. Feather wear in songbirds causes measureable shortening of the primaries between molts (Van Balen 1967, Norman 1983, Francis and Wood 1989). The composition of migrants sampled at PNR could differ between seasons because some species follow different migratory pathways in spring and autumn (Nisbet 1970, Rappole 1995, p. 85, Ruegg and Smith 2002). If sub-populations of these species differ in body size, birds measured in spring could be either larger or smaller than those examined the previous autumn. This situation would introduce error to our estimate of selection differentials, but would not create a consistent upward or downward bias in overwinter change across all species. Therefore, the fact that wing was on average larger in spring than in autumn suggests selection against small individuals or juveniles during winter, which is known to occur in some birds (Lahti et al. 1998, Conroy et al. 2002). The fact that the net direction of overwinter selection was positive (wing) or neutral (mass), while the observed phenotypic change over 46 years was negative, can be explained by countervailing selection on size acting early in life or during other phases of the annual cycle.

Species with the strongest negative size trends over the decades appear to be responding to conditions that favor small size, because there were positive correlations between long-term trends in size and selection on size, especially for wing chord (Fig. 3). The long-term trends could arise from phenotypic plasticity or genetic change. Plasticity is possible because environmental factors that generate directional selection are known to simultaneously induce adaptive phenotypic plasticity in the same direction as that favored by selection (Stearns 1989, Van Buskirk et al. 1997). Arguing against this interpretation in our study is the fact that selection was measured during a different phase of the life cycle from that during which body size is determined, especially in the case of wing chord. Plasticity in size can be induced by conditions during the nestling and rearing stages and during the annual prebasic molt in late summer (Pehrsson 1987, Searcy et al. 2004), whereas selection was measured over the winter between autumn and spring migrations. Given that body size is relatively heritable in birds (Boag 1983, Teplitsky et al. 2009), an evolved response to current selection is possible. In summary, although our data cannot identify mechanisms underlying long-term change, they do extend the observation of a phenotypic response noted in previous studies by indicating that the direction of change is adaptive (Parmesan 2006, Gienapp et al. 2008). Of course, studies of invertebrates regularly document genetic responses to environmental change, although most examples concern molecular markers with unknown phenotypic consequences (Hoffmann and Willi 2008).

Our results provide insight into the highly variable examples of climate-induced changes in vertebrate body size mentioned in the Introduction (Yom-Tov 2001, Guillemain et al. 2005, Yom-Tov et al. 2006a, 2006b, 2008, Monahan 2008, Teplitsky et al. 2008, Meiri et al. 2009). We too observed extensive heterogeneity among species in long-term change at PNR, and this implies that a study of one or a few species might support nearly any conclusion. To some extent, each species experiences slightly different ecological conditions, which in turn can modify or reverse the general tendency to evolve reduced body size in line with expectations based on Bergmann's rule. Previous studies suggest that variation among birds in recent size changes, and in the strength of Bergman's rule itself, are not easily explained by the ecology of individual species (Yom-Tov 2001, Ashton 2002, Yom-Tov et al. 2006b). In this context, it is important that we discovered variability in response to climate related to the type of species. Long-distance migrants showed stronger declines than short-distance migrants, especially in wing chord, and species with northern breeding distributions tended toward stronger declines than local breeders (Table 1, Supplementary material Appendix 2). These results are not consistent with the expectation that sedentary species should adhere more strictly to Bergmann's rule than migrants (Rensch 1936, Zink and Remsen 1986, Ashton 2002), but they do encourage hope that generalities will emerge to help predict future impacts of environmental change.

Debate continues about the capacity of organisms to evolve beneficial responses to climate change (Blows and Hoffmann 2005, Davis et al. 2005). This study, together with many previous studies (Parmesan 2006, Charmantier et al. 2008, Van Buskirk et al. 2009), offer compelling evidence that climate change has already produced observable adaptive shifts in morphology, behavior, and phenology of a great many species. The open question remains whether these shifts involve only phenotypic plasticity, or whether an evolved response to contemporary natural selection is also underway. Of course, we have long known that evolved changes are an inevitable consequence of almost any human activity that modifies the environment and thereby influences the selective regime experienced by organisms. Classic examples include adaptation to urbanization and contaminated soils (Bradshaw and Jain 1966, Partecke and Gwinner 2007). Similar responses to climate change may be on-going and widespread; whether they will prove to be adequate remains to be seen. Particularly salient and sobering, however, should current trends continue unabated, is the immense biological scope and geographic scale of changes that are taking place compared with the limited information and resources we presently have for measuring, understanding and mitigating those changes.

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Supplementary material (available online as Appendix O18349 at <www.oikos.ekol.lu.se/appendix>). Appendix 1–2.