

# Avian body size changes and climate change: warming or increasing variability?

RAE E. GOODMAN\*, GRETCHEN LEBUHN\*, NATHANIEL E. SEAVY†, THOMAS GARDALI† and JILL D. BLUSO-DEMERS‡

\*San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132, USA, †PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, USA, ‡San Francisco Bay Bird Observatory, 524 Valley Way, Milpitas, CA 95035, USA

## Abstract

There has been a growing interest in whether established ecogeographical patterns, such as Bergmann's rule, explain changes in animal morphology related to climate change. Bergmann's rule has often been used to predict that body size will decrease as the climate warms, but the predictions about how body size will change are critically dependent on the mechanistic explanation behind the rule. To investigate change in avian body size in western North America, we used two long-term banding data sets from central California, USA; the data spanned 40 years (1971–2010) at one site and 27 years (1983–2009) at the other. We found that wing length of birds captured at both sites has been steadily increasing at a rate of 0.024–0.084% per year. Although changes in body mass were not always significant, when they were, the trend was positive and the magnitudes of significant trends were similar to those for wing length (0.040–0.112% per year). There was no clear difference between the rates of change of long-distance vs. short-distance migrants or between birds that bred locally compared to those that bred to the north of the sites. Previous studies from other regions of the world have documented decreases in avian body size and have used Bergmann's rule and increases in mean temperature to explain these shifts. Because our results do not support this pattern, we propose that rather than responding to increasing mean temperatures, avian body size in central California may be influenced by changing climatic variability or changes in primary productivity. More information on regional variation in the rates of avian body size change will be needed to test these hypotheses.

**Keywords:** Bergmann's Rule, body mass, California, climatic variability, ecogeographic rules, ecotypic variation, energy reserves, morphology, wing length

Received 16 December 2010; revised version received 1 July 2011 and accepted 12 July 2011

## Introduction

There is mounting evidence that birds and other wildlife are responding to changes in climate in a variety of ways, including changes in phenology (Crick, 2004; Macmynowski *et al.*, 2007; Vegvari *et al.*, 2010), geographical distributions (Tingley *et al.*, 2009; Thomas, 2010), and population declines (Miller-Rushing *et al.*, 2008; Jiguet *et al.*, 2010). In addition, species of birds and mammals are exhibiting changes in body size that are linked to climate change (Yom-Tov *et al.*, 2006; Van Buskirk *et al.*, 2010; Gardner *et al.*, 2011). Recently, there has been a growing interest in whether established patterns of geographical variation in body size, such as Bergmann's rule, may explain changes in animal morphology that will occur as a result of climate change (Yom-Tov *et al.*, 2006; Gardner *et al.*, 2009; Van Buskirk *et al.*, 2010).

Bergmann's rule states that across species, body mass is positively associated with latitude (Bergmann, 1847;

Blackburn *et al.*, 1999). The rule has also been used to explain within-species variation in body mass (Ashton, 2002). Predictions about how body size will change as a result of climate change depend on the mechanistic explanation behind Bergmann's rule, of which there are several (Watt *et al.*, 2010; Meiri, 2011). One mechanism used to explain climate-related variation in body size under Bergmann's rule is that heat conservation associated with larger body sizes provides a thermoregulatory benefit in cooler climates. Using this mechanism, researchers have predicted that within a species, body sizes will decrease as the climate warms (Yom-Tov *et al.*, 2006; Salewski *et al.*, 2010; Van Buskirk *et al.*, 2010).

Alternatively, Bergmann's rule may be driven by fasting endurance (Ashton, 2002). Bumpus (1899) initially pointed out that severe weather events can exert significant selection pressure on bird body size. Further studies have shown that severe weather events, including cold snaps and storms, can exert directional selection pressure on birds, favoring heavier body mass (Jaramillo & Rising, 1995) and larger size (Brown & Brown, 1998; Acquarone *et al.*, 2004). Larger size may

Correspondence: Rae Goodman, tel. + 909 816 5606, fax + 415 405 0305, e-mail: rae.goodman@gmail.com

confer greater fasting endurance and cold-weather survival, due to increased energy stores (Murphy, 1985).

If the climate becomes more variable, it has been predicted that birds may need increased energy storage for fasting endurance to survive extreme weather events (Newton, 2007). Easterling *et al.* (2011) highlighted instances of extreme events underlying long-term changes in body size and suggested that many seemingly gradual shifts over recent decades may be driven by punctuated weather extremes. If Bergmann's rule is driven by climate variability and fasting endurance, then body sizes are predicted to increase within a species as the climate becomes more variable.

Finally, global shifts in climate may be affecting body size through broad changes in food availability. Yom-Tov & Geffen (2011) propose that food availability (driven by primary productivity) is the mechanism underlying Bergmann's rule and recent changes in body sizes. The direction of productivity change in response to climate change may vary regionally. In warm climates, higher temperatures may speed evaporative water loss, thereby decreasing productivity, while in water-starved or cool environments, increased precipitation and heat may increase productivity (Yom-Tov & Geffen, 2011). Under this mechanism, changes in body sizes would depend on the effect that climate change has on regional primary productivity.

Among birds, researchers have documented variation in the magnitude and direction of morphological changes (Gardner *et al.*, 2011). Results are similarly varied on whether the observed changes in body size appear to be linked to selection (Van Buskirk *et al.*, 2010) or phenotypic plasticity (Husby *et al.*, 2011). For North American birds, Van Buskirk *et al.* (2010) reported decreases in wing length and fat-free mass in Pennsylvania passerines in the last 40 years; changes in avian body size in other regions of North America have not been described. To investigate change in avian body size in western North America, document the effects of climate change on vertebrates, and test the above predictions to provide insight into the mechanism underlying Bergmann's rule, we analyzed changes in avian body mass and wing length among multiple-species at two long-term banding stations in central California, USA. We examined whether birds were decreasing in size, as predicted by a thermoregulatory explanation of Bergmann's rule, or increasing, as a possible response to climate variability or food availability changes.

## Methods

To examine morphological changes in passerine birds, we examined data from two long-term banding programs in

central California, USA: PRBO Conservation Science's Palomarin Field Station and San Francisco Bay Bird Observatory's Coyote Creek Field Station.

## Study sites

The Palomarin Field Station (Palomarin; 37°56'N, 122°45'W) is located on the central California coast, north of the town of Bolinas, in Marin County, California, USA, in the southern end of the Point Reyes National Seashore. Local vegetation consists of undisturbed and disturbed coastal scrub, second-growth Douglas-fir forest (*Pseudotsuga menziesii*), and mixed evergreen forest. See Johnson & Geupel (1996) and Jennings *et al.* (2009) for further descriptions of the site. In the past four decades, Palomarin has undergone significant successional change, from fallow fields to coastal scrub to conifer forest (Chase *et al.*, 2005). As a result of these changes in vegetation, there have also been predictable changes in bird community composition, with an increase in conifer-associated species (Chase *et al.*, 2005).

Coyote Creek Field Station (37°26'N, 121°55'W) is located at the southern end of the San Francisco Bay (approximately 110 km from Palomarin). Except for a strip of riparian habitat directly adjacent to Coyote Creek, the site was previously a pear orchard. The orchard was removed just prior to the beginning of the banding program in 1982, and much of the site was restored with riparian vegetation in 1987 and 1993. The restored sites have undergone significant vegetative growth since the initial plantings (Jaramillo *et al.*, 2003). Following the restoration and subsequent maturation of the vegetation, bird abundance has increased (Jaramillo *et al.*, 2003).

## Field methods

Data from Palomarin were available for 1971 through 2010. PRBO biologists have conducted mist-netting year round, generally 6–7 days per week in May through November and 3–4 days per week in December through April. Since 1979, all 20 nets were typically open for 6 h each day, weather permitting, beginning 15 min after sunrise. In earlier years, efforts were less standardized, and nets were sometimes open longer.

At Palomarin, birds were captured in 20 12-meter nylon mist nets, all within 200 m of each other. Of the 20 nets, 14 were located at 8 locations in the mixed evergreen forest, and the other 6 nets were located in coastal scrub habitat. At six net locations in the forest, the nets were double-stacked, one on top of the other. Larger mesh nets (36 mm) were used in the scrub habitat and smaller mesh nets (30 mm) were used in the evergreen forest (Ballard *et al.*, 2003; Jennings *et al.*, 2009). Nets were closed during rainy or windy conditions. The capture and handling of birds followed standardized protocols for mist-netting (Ralph *et al.*, 1993). Netting was conducted by interns who were intensively trained to ensure consistency in data collection.

Each bird captured was identified to species, aged (if possible), sexed (if possible), and given a unique, numbered US-FWS or USGS federal metal band (or the band number was noted, for recaptures). Un-flattened wing chord (wing length)

was measured to the nearest millimeter. Mass was measured to the nearest 0.1 g; a Pesola spring scale was used in earlier years, and more recently, an electronic scale was used. Body fat was rated using a 0–3 rating scale. Data on breeding condition, molt status, and feather condition were recorded. Birds were released immediately after processing (Jennings *et al.*, 2009).

Data from Coyote Creek Field Station were available beginning in December 1982. We used year-round data from 1983 to 2009. The study site consisted of 48 net locations in riparian habitat; 36 of these net locations were established in 1987 or earlier, and the remaining net locations were established by 1995. Capture, handling, and banding procedures were the same as those at Palomarin, except as noted herein. Standard banding hours were established in 1987. Net opening time was averaged for the month, so on any given day, opening time may be 20–60 min after sunrise. Nets were all 30 mm mesh, and nets were operated for 5 h, weather permitting. Year-round, weekly mist-netting operations were spread out over 3 days such that one-third of all nets were opened during each of three trapping days. Weight was measured with an electronic balance.

### Study species

Using only new captures of after-hatch-year birds, we divided captures by season to examine different patterns for wintering, breeding, and migratory birds. Spring was defined as 1 April–15 May, summer as 1 June–31 July, fall as 15 August–15 November, and winter was defined as 1 December–29 February. We used the same approach to selecting species for analysis that was employed by Van Buskirk *et al.* (2010): within each season, species were selected for analysis if at least one individual was captured in at least seven different years, with earliest and latest captures spanning a period of at least 25 years. This yielded a total of 14 735 individuals at Palomarin (summer: 5509 captures of 41 species; winter: 2846 captures of 26 species; spring: 4544 captures of 45 species; fall: 1836 captures of 35 species). These species represent an ecologically diverse sample of the birds banded at Palomarin in terms of size, migration distance, breeding distribution, nesting location, and feeding ecology (Goodman, 2010).

At Coyote Creek, we again used only new captures of after-hatch-year birds and divided those captures by season (using the same dates described for Palomarin). However, because of the shorter length of the study period, we selected species for which there was at least one capture in at least 7 years, with the earliest and latest capture spanning a period of at least 20 years. Selecting the species in this way yielded 18 052 individuals (summer: 2112 captures of 23 species; winter: 4333 captures of 20 species; spring: 8442 captures of 38 species; fall: 3165 captures of 26 species.) As at Palomarin, the resulting species assemblage is ecologically diverse (Goodman, 2010).

We followed Van Buskirk *et al.* (2010) in classifying the breeding range and migration distance for each species. Breeding range was categorized as either local (for species that nest in or nearby the two study areas) or northern (for species that breed only farther north or, in a few cases, at higher eleva-

tions). For migration distance, we categorized species as either long distance, if they wintered in Central or South America, or short distance, if they were year-round residents or generally wintered in the southern United States. A list of species and their migration distance and breeding range classifications used in this study is presented in Appendix S1.

### Analysis

Following Van Buskirk *et al.* (2010), we used linear mixed-models to estimate temporal trends in body size and wing length controlling for the effects of sex, migration distance, breeding range, fat score, time of day, and date of passage. For all analyses, we log-transformed body mass and wing length. We included species (random intercept) and the interaction between species and year (random slope) in all models with a structure that assumed that random slopes and intercepts were not correlated.

For body mass of summer residents, our full model included fixed effects for year, sex, fat score, time of day, migration distance, and migration distance by year interaction. For body mass of winter residents, we used the same model, except that migration distance was replaced by breeding range. For spring and autumn migrants, our full model for body mass included fixed effects for year, sex, fat score, time of day, date of passage, migration distance, and breeding range.

For wing length for summer residents, our full model included fixed effects for year, sex, migration distance, and the year by migration distance interaction. For wing length of winter residents, we used the same model as for summer residents, except that migration distance was replaced by breeding range. For wing length of spring and autumn migrants, our full model included fixed effects for year, sex, migration distance, and breeding range.

All analyses were performed separately for the Palomarin and Coyote Creek datasets. All statistical analyses were performed with R software (R Development Core Team, 2009). We used the nlme package (Pinheiro *et al.*, 2010) which allowed us to fit species (random intercept) and the species by year interaction (random slope) in a model with fixed and random effects. We specified no correlation between the random intercept and slope terms. We evaluated the significance of each parameter using the Wald-test *P*-values and 95% confidence intervals for each parameter estimate. In our initial models, we included the interactions between year and migration distance and breeding range. If these interactions were significant ( $P < 0.1$ ), we included them in the final model structure; if they were nonsignificant, we refit the models excluding these interaction terms. In three cases, these models failed to converge and provide reliable estimates of the random effects. In these cases, we excluded these data sets from the analysis.

## Results

### Wing length

Generalizing across species, wing length increased significantly at Palomarin and at Coyote Creek in all

**Table 1** Parameter estimates from mixed-effects linear models on log-transformed wing length of birds at (a) Palomarin Field Station and (b) Coyote Creek Field Station. Estimates are coefficients for fixed effects, multiplied times 100. The significant positive effect of year indicates a long-term increase in wing length. *P*-values were generated using Wald-tests and approximate confidence intervals were generated from the restricted maximum likelihood fit. If the interactive effects between year and migration distance and breeding range were not significant ( $P < 0.10$ ), they were excluded from the model

Source of variation	Summer captures			Winter captures			Spring captures			Autumn captures		
	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>
<b>(a) Palomarin</b>												
Year	0.051	0.041 to 0.061	<0.001	0.039	0.014 to 0.064	0.0021	0.025	0.007 to 0.004	0.0070	Model did not converge		
Sex												
Female	-2.172	-2.549 to -1.884	<0.0001	-0.811	-1.383 to -0.239	0.0055	-1.706	-2.021 to -1.392	<0.0001			
Male	0.641	0.338 to 0.994	<0.0001	2.370	1.792 to 2.948	<0.0001	1.588	0.013 to 1.895	<0.0001			
Unknown	0			0			0					
Breeding range												
Northern	-			17.416	-21.498 to 56.330	0.3648	-12.677	-42.129 to 16.776	0.3900			
Local	-			0			0					
Migration distance												
Short	-27.227	-3.798 to 19.628	0.7447	-			2.376	-22.468 to 27.222	0.8478			
Long	0			-								
Breeding × Year												
Migration × Year							0.026	0.007 to 0.051	ns			
<b>(b) Coyote Creek</b>												
Year	0.057	0.023 to 0.091	0.0010	0.056	0.031 to 0.081	<0.0001	0.058	0.038 to 0.079	<0.0001	0.084	0.055 to 0.113	<0.0001
Sex												
Female	-2.303	-2.879 to -1.727	<0.0001	-1.351	-1.750 to -0.951	<0.0001	-1.600	-1.960 to -1.238	<0.0001	-0.870	-1.621 to -0.118	0.0234
Male	1.181	0.574 to 1.789	0.0001	1.941	1.556 to 2.326	<0.0001	2.864	2.515 to 3.213	<0.0001	2.383	1.622 to 3.145	<0.0001
Unknown	0			0			0			0		
Breeding range												
Northern	-			-3.009	-34.362 to 28.343	0.8425	-15.789	-37.692 to 6.115	0.4346	0.607	-19.671 to 20.886	0.4343
Local	-			0			0			0		

Table 1 (continued)

Source of variation	Summer captures			Winter captures			Spring captures			Autumn captures		
	Estimate	95% CI	P	Estimate	95% CI	P	Estimate	95% CI	P	Estimate	95% CI	P
Migration distance												
Short	2.363	-26.407 to 31.133	0.8660	-	-	-	7.612	-12.018 to 27.241	0.1523	8.041	-12.861 to 28.944	0.9511
Long	0			-	-	-	0			0		
Breeding × Year			ns			ns						ns
Migration × Year			ns			ns						ns

seasons for which the model converged (Table 1; Fig. 1). The only significant interaction was at Palomarin in the spring: the rate of increase in short-distance migrants was greater than for long-distance migrants (Table 1; Fig. 1). At Palomarin, the magnitude of this increase ranged from 0.024% per year (long-distance migrants in the spring) to 0.051% per year (all species in the summer; Fig. 1). The model failed to converge for the fall captures at Palomarin (Table 1). At Coyote Creek, magnitude of the increase in wing length ranged from 0.056% per year (all species in the winter) to 0.084% per year (all species in the fall, Fig. 1).

Although we treated species as a random effect and random effect estimates are not designed to make comparisons between grouping variables, the estimate of the random slope for each species does provide information about the heterogeneity among species. At both Palomarin and Coyote Creek the estimated slopes for nearly all species were positive (Appendix S1).

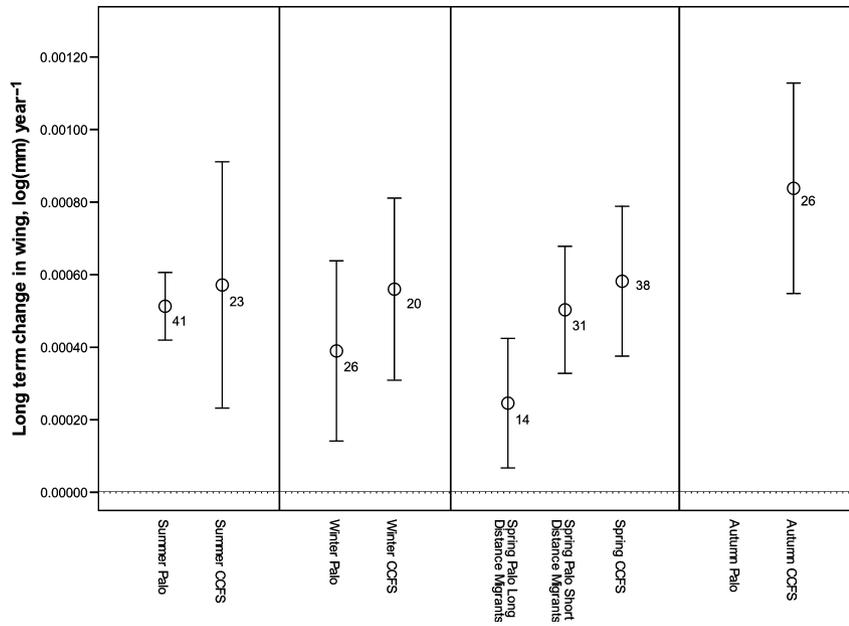
*Body mass*

Changes in fat-free body mass were significant at Palomarin and Coyote Creek in some but not all seasons (Table 1; Fig. 2). At Palomarin, body size was significantly increasing in summer (0.040% per year) but not in the winter or fall (model for spring captures did not converge). However, the estimates for winter (0.068%) and fall (0.031%) were positive (Fig. 2). At Coyote Creek, changes in body mass were significant for summer and spring but not winter (the model for fall captures did not converge). In spring, there was a significant interaction with migration distance; the body mass of long-distance migrants increased over the study period, whereas the body mass of short-distance migrants decreased slightly (Fig. 2). At Coyote Creek, the magnitude of the changes ranged from -0.030% (short-distance migrants in spring) to 0.112% (all birds in summer; Fig. 2).

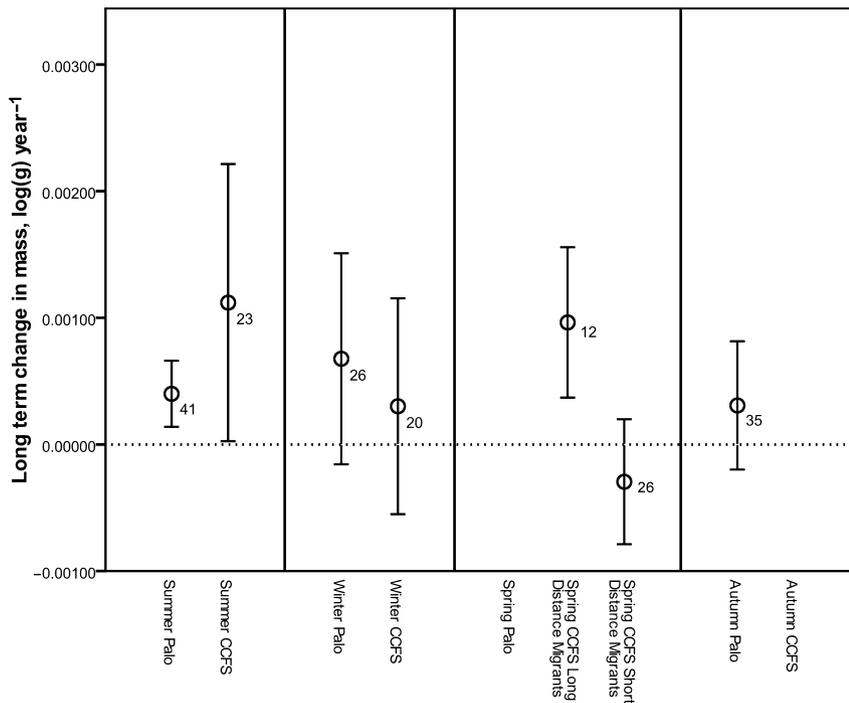
The random effects estimates of the slopes for individual species suggested that changes in body mass were more variable than changes in wing length. For example, at Palomarin, 41 of 41 species captured in the summer had increasing slopes for body mass, 22 of 24 captured in the winter had increasing slopes, and 29 of 35 captured in the fall were with increasing slopes (Appendix S1).

**Discussion**

At two independent sites on the west coast of California, we found evidence that wing length has increased across a wide variety of passerine species over the last 27–40 years. We also found evidence of increases in



**Fig. 1** Mean annual change in log-transformed wing length of birds captured at Palomarin Field Station (Palo; 1971–2010) and Coyote Creek Field Station (CCFS; 1983–2009). The bars indicate the 95% confidence intervals. The numbers next to the points indicate the number of species. Wing length increased significantly at Palomarin Field Station and at Coyote Creek Field Station in all seasons for which the models converged. The estimate for autumn captures at Palomarin is missing because the model did not converge.



**Fig. 2** Mean annual change in fat-free mass of birds captured at Palomarin Field Station (Palo; 1971–2010) and Coyote Creek Field Station (CCFS; 1983–2009). The bars indicate the 95% confidence intervals. The numbers next to the points indicate the number of species. Fat-free mass increased significantly at Palomarin Field Station in summer and at Coyote Creek Field Station in summer and spring. The estimates for spring captures at Palomarin and autumn captures at Coyote Creek are missing because the model did not converge.

body mass over this time period, although these changes were not significant for all groups. We suspect that trends in body mass are more difficult to detect than trends in wing length, because even after controlling for fat levels and time of day, body mass is probably still more dynamic than wing length. We interpret our results as evidence for increasing body size across a wide range of bird species that occur in central California. These results contrast with other studies that have documented decreasing avian body size (Yom-Tov, 2001; Yom-Tov *et al.*, 2006; Van Buskirk *et al.*, 2010).

In the only other North American study of avian body size, Van Buskirk *et al.* (2010) reported decreases in passerine body mass and wing length from banding data collected in Pennsylvania, USA. Although the direction of morphological change differed between these two studies, there were also some striking similarities. First, Van Buskirk *et al.* (2010) reported changes in body mass and wing length that ranged from  $-0.08\%$  to  $+0.02\%$  per year. In our study, the changes in body mass and wing length ranged from  $-0.03\%$  to  $+0.11\%$  per year. Thus, the general magnitude of the changes, although in different directions, was similar in both studies. Second, our estimates for other parameters were very similar to those reported by Van Buskirk *et al.* (2010). For example, we found that for every 1 level increase in fat score, body mass increased by 1.2–4.3% (Table 2), whereas their estimates covered a similar range of 3.5–4.8% (Van Buskirk *et al.*, 2010). Similarly, our effect for time of day in the body mass models ranged from 0.18% to 0.51% (Table 2), similar to the estimates of 0.23–0.44% reported by Van Buskirk *et al.* (2010).

While variation may exist between methodologies or researchers, it is unlikely that our observed trends could result from these errors. For example, at Palomarin, body mass (measured with a spring scale in early years and an electronic scale in later years) and wing length (measured in the same way the entire study period) changed similarly over time, suggesting that the change in method used to measure body mass was not responsible for the pattern we found. Furthermore, the agreement in the body mass from Palomarin and Coyote Creek (where body mass has always been measured with an electronic scale) suggests that direction bias resulting from the change in methods at Palomarin is unlikely. At both Palomarin and Coyote Creek, banding has been conducted by many different researchers over the course of the study, however, the emphasis on training and standardization makes temporal drift in both wing length and body mass measurements unlikely. Furthermore, if such a shift did occur, it seems unlikely that it would have occurred with a similar magnitude at these two, independently operated banding stations.

Given that these changes are widespread across many species at two sites in central California, we suggest climate change may play a role. Mean temperatures are increasing at similar rates across North America (Jones *et al.*, 1999; Hansen *et al.*, 2010). At the Palomarin Field Station, mean temperatures have been increasing in all seasons in recent decades, with strong increases from 1979 until the 1990s followed by a slight decline (K. Dybala, unpublished data). During this same time period, the number of days below  $0^{\circ}\text{C}$  has been declining (K. Dybala, unpublished data). Therefore, if changes in body size represented a response to thermoregulation associated with increasing mean temperatures, we would expect that body sizes would have changed in a similar manner in Pennsylvania and California. The disparity between the body size change in Pennsylvania (decreasing; Van Buskirk *et al.*, 2010) and California (increasing; this study) suggests that the explanation is more complicated.

Beyond warmer temperatures, the consequences of climate change include changes in precipitation and severe weather activity (Rind *et al.*, 1989; Stouffer & Wetherald, 2007; Min *et al.*, 2011). The global climate is becoming more variable (Alexander *et al.*, 2006; Tebaldi *et al.*, 2006). Spatially explicit analyses of climate variability show that both California and Pennsylvania are experiencing changes in variability, but the nature of these changes varies depending on what parameter is examined (Kunkel *et al.*, 1999; Alexander *et al.*, 2006; Pryor *et al.*, 2009). Trends in extreme temperatures and precipitation patterns vary across the country (Kunkel *et al.*, 1999; Alexander *et al.*, 2006; Pryor *et al.*, 2009). If body size is influenced by climate variability rather than mean temperatures, then these regional differences in variability could result in different changes in body size across North America.

Alternatively, changes in climate could produce changes in primary productivity and food availability that explain changes in avian body size (Yom-Tov & Geffen, 2011). This hypothesis could potentially explain why this study found increasing body sizes, whereas other studies have predominantly found decreases. Warming temperatures have been found to increase productivity when paired with increased precipitation (Seo, 2011; Wu *et al.*, 2011) but to decrease productivity when precipitation is not increased (De Boeck *et al.*, 2008). Increases in productivity have been found to be stronger in cooler climates (Rustad *et al.*, 2001) and in more arid systems (Weltzin *et al.*, 2003). Different biomes have been shown to respond differently to climate change, with chaparral areas showing increased productivity while most other biomes experience productivity decreases (Seo, 2011). These patterns suggest that central California, with its cooler, drier summers, and

**Table 2** Parameter estimates from mixed-effects linear models on log-transformed body mass of birds at (a) Palomarin Field Station and (b) Coyote Creek Field Station. Estimates are coefficients for fixed effects, multiplied times 100. Fat score was included in all models, so results reflect changes in fat-free mass. A significant positive effect of year indicates a long-term increase in mass. *P*-values were generated using Wald-tests and approximate confidence intervals were generated from the restricted maximum likelihood fit. If the interactive effect between year and migration distance and breeding range were not significant ( $P < 0.10$ ), they were excluded from the model

Source of variation	Summer captures			Winter captures			Spring captures			Autumn captures		
	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>	Estimate	95% CI	<i>P</i>
<b>(a) Palomarin</b>												
Year	0.040	0.014 to 0.066	0.0027	0.068	-0.157 to 0.151	<0.1115	Models did not converge			0.031	-0.020 to 0.081	0.2329
Sex												
Female	0.293	-0.030 to 0.887	0.3339	-2.327	-3.701 to -0.950	0.0009				-2.032	-3.654 to -0.409	0.0141
Male	0.421	-0.204 to 1.046	0.1867	3.018	1.629 to 4.407	<0.0001				2.946	1.260 to 4.631	0.0006
Unknown	0			0						0		
Fat score	1.201	0.838 to 1.565	<0.0001	1.961	1.308 to 2.614	<0.0001				4.300	3.583 to 5.018	<0.0001
Time of day	0.185	0.080 to 0.289	0.0005	0.347	0.180 to 0.514	<0.0001				0.442	0.199 to 0.685	0.0004
Date of passage	-			-						0.058	0.025 to 0.091	0.0005
Breeding range												
Northern	-			30.614	-73.058 to 134.287	0.5479				25.322	-45.147 to 95.791	0.4695
Local	-			0						0		
Migration distance												
Short	40.242	-17.838 to 98.326	0.1690	-						50.203	-20.267 to 120.673	0.1565
Long	0			-						0		
Breeding × Year	-			-		ns						ns
Migration × Year	-		ns	-								ns
<b>(b) Coyote Creek</b>												
Year	0.112	0.026 to 0.221	0.0449	0.022	-0.038 to 0.083	0.4659	0.0964	0.037 to 0.156	0.0015	Models did not converge		
Sex												
Female	-0.062	-1.207 to 1.083	0.9155	-0.964	-1.772 to -0.156	0.0194	-1.075	-1.875 to -0.276	0.0084			
Male	2.328	1.122 to 3.535	0.0002	2.415	1.635 to 3.195	<0.0001	4.216	3.443 to 4.989	<0.0001			
Unknown	0			0			0					

Table 2 (continued)

Source of variation	Summer captures			Winter captures			Spring captures			Autumn captures		
	Estimate	95% CI	P	Estimate	95% CI	P	Estimate	95% CI	P	Estimate	95% CI	P
Fat score	2.411	1.852 to 2.971	<0.0001	1.317	0.981 to 1.761	<0.0001	4.033	3.805 to 4.261	<0.0001			
Time of day	0.390	0.173 to 0.607	0.0004	0.499	0.332 to 0.665	<0.0001	0.509	0.384 to 0.634	<0.0001			
Date of passage	-			-			0.009	-0.010 to 0.028	0.3569			
Breeding range												
Northern	-			7.505	-80.665 to 95.675	0.8601	-33.152	-91.985 to 25.680	0.2604			
Local	-						0					
Migration distance												
Short	40.597	-344.418 to 115.634	0.2732	-			46.463	-6.263 to 99.190	0.0823			
Long	0			-								
Breeding × Year	-			-								ns
Migration × Year	-		ns	-			-0.126	-0.201 to -0.050	0.0011			

abundant chaparral ecosystems, may show stronger increases in productivity in response to climate change, compared to areas such as Pennsylvania. This hypothesis could potentially explain why body sizes are increasing in California but decreasing in other parts of the world.

Our results show that a large assemblage of avian species are increasing in size and demonstrate that, while body size changes may be a pervasive response to climate change, sizes are not universally decreasing. Global climate change provides the largest possible, albeit unreplicated, experiment with which to test mechanistic explanations for broad patterns such as Bergmann's rule. Our results suggest that a response to mean temperatures is not the sole or primary mechanism behind Bergmann's rule. Other factors, such as climate variability or climate-related patterns in primary productivity, are likely to play a role in shifting morphology.

## Acknowledgements

We thank the staff, interns, and volunteers of PRBO and SFBBO who worked to collect these data. We thank Phil Nott and Ed Connor for their input and ideas. Thanks are due to Fran James, John Wiens, Ed Connor, and Diana Humple for early reviews of the manuscript. We also thank C. J. Ralph, D. F. DeSante, G. R. Geupel, L. R. Mewaldt, M. Rigney, members and board of directors of PRBO and SFBBO, Chevron Corporation, the Bernard Osher Foundation, Jiji Foundation, Gordon and Betty Moore Foundation, the Kimball Foundation, the Karen A. & Kevin W. Kennedy Foundation, Mrs Marilyn M. Strand, the Schulz Donor Advised Fund, Don and Louise Johnston, the late Dorothy Hunt, the National Park Service Inventory and Monitoring Program, the Santa Clara Valley Water District, and the City of San Jose. The research was supported by the National Science Foundation grants (DBI-0533918) and (DUE-0728279). This is PRBO Contribution number 1818.

## References

Acquarone C, Cucco M, Malacarne G, Silvano F (2004) Temporary shift of body size in hooded crows *Corvus corone cornix* of NW Italy. *Folia Zoologica*, **53**, 379–384.

Alexander LV, Zhang X, Peterson TC *et al.* (2006) Global observed changes in daily climate extremes of temperature and precipitation. *Journal of Geophysical Research-Atmospheres*, **111**, 1–22.

Ashton KG (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11**, 505–523.

Ballard G, Geupel GR, Nur N, Gardali T (2003) Long term declines and decadal patterns in population trends of songbirds in Western North America, 1979–1999. *Condor*, **105**, 737–755.

Bergmann C (1847) Ueber die verhältnisse der warmeconomie der thiere zu ihrer grosse. *Göttinger studien*, **3**, 595–708.

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.

Brown CR, Brown MB (1998) Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution*, **52**, 1461–1475.

Bumpus HC (1899) Biology Lectures. *Marine Biology Lab Woods Hole*, **11**, 209.

Chase M, Holmes A, Gardali T, Ballard G, Geupel G, Nur N (2005) Two decades of change in a coastal scrub community: songbird responses to plant succession. In: *Bird Conservation Implementation and Integration in the Americas: Proceedings of the*

*Third International Partners in Flight Conference, US Department of Agriculture, Forest Service General Technical Report PSW-191* (eds Ralph CJ, Rich T), pp. 613–616. US Department of Agriculture, Forest Service, Washington, DC.

Crick HQP (2004) The impact of climate change on birds. *Ibis*, **146**, 48–65.

De Boeck HJ, Lemmens C, Zavalloni C *et al.* (2008) Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences*, **5**, 585–594.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2011) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Gardner JL, Heinsohn R, Joseph L (2009) Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3845–3852.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third universal response to warming? *Trends in Ecology and Evolution*, **26**, 285–291.

Goodman R (2010) Changes in bird body size and mass in northern California: morphological responses to climate change. Masters Thesis, San Francisco State University, San Francisco.

Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. *Reviews of Geophysics*, **48**, 29.

Husby A, Hille S, Visser ME (2011) Testing mechanisms of Bergmann's rule: phenotypic but no genetic decline in body size in three passerine bird populations. *The American Naturalist*, **178**, 202–213.

Jaramillo AP, Rising JD (1995) Intense natural selection in a population of cliff swallows. *Kansas Ornithological Society Bulletin*, **46**, 21.

Jaramillo A, Hudson SE, Strong CM (2003) Coyote Creek Field Station Ten Year Report: 1987–1996. Final Report Prepared for Santa Clara Valley Water District, San Jose, CA. San Francisco Bay Bird Observatory, Milpitas, CA.

Jennings S, Gardali T, Seavy NE, Geupel GR (2009) Effects of mist netting on reproductive performance of wrentits and song sparrows in central coastal California. *Condor*, **111**, 488–496.

Jiguet F, Gregory RD, Devictor V, Green RE, Vorisek P, Van Strien A, Couvet D (2010) Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology*, **16**, 497–505.

Johnson MD, Geupel GR (1996) The importance of productivity to the dynamics of a swainson's thrush population. *Condor*, **98**, 133–141.

Jones PD, New M, Parker DE, Martin S, Rigor IG (1999) Surface air temperature and its changes over the past 150 years. *Reviews of Geophysics*, **37**, 173–199.

Kunkel KE, Andsager K, Easterling DR (1999) Long-term trends in extreme precipitation events over the conterminous United States and Canada. *Journal of Climate*, **12**, 2515–2527.

Macmynowski DP, Root TL, Ballard G, Geupel GR (2007) Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate. *Global Change Biology*, **13**, 2239–2251.

Meiri S (2011) Bergmann's rule – what's in a name? *Global Ecology and Biogeography*, **20**, 203–207.

Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P (2008) Bird migration times, climate change, and changing population sizes. *Global Change Biology*, **14**, 1959–1972.

Min SK, Zhang X, Zwiens FW, Heger GC (2011) Human contribution to more-intense precipitation extremes. *Nature*, **470**, 378–381.

Murphy EC (1985) Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. *Evolution*, **39**, 1327–1334.

Newton I (2007) Weather-related mass-mortality events in migrants. *Ibis*, **149**, 453–467.

Pinheiro J, Bates D, DebRoy S, Sarkar S, R Core team (2010) *nlme: linear and nonlinear mixed effects models. R package version 3.1-97*.

Pryor SC, Howe JA, Kunkel KE (2009) How spatially coherent and statistically robust are temporal changes in extreme precipitation in the contiguous USA? *International Journal of Climatology*, **29**, 31–45.

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org> (accessed 21 September 2011).

Ralph CJ, Geupel GR, Pyle P, Martin TE, DeSante DF (1993) Handbook of field methods for monitoring landbirds. *US Department of Agriculture, Forest Service General Technical Report PSW-144*. US Department of Agriculture, Forest Service, Washington, DC.

Rustad LE, Campbell JL, Marion GM *et al.*, GCTE-News (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.

- Rind D, Goldberg R, Ruedy R (1989) Change in climate variability in the 21st century. *Climatic Change*, **14**, 5–37.
- Salewski V, Hochachka WM, Fiedler W (2010) Global warming and Bergmann's rule: do central European passerines adjust their body size to rising temperatures? *Oecologia*, **162**, 247–260.
- Seo SN (2011) The impacts of climate change on Australia and New Zealand: a Gross Cell Product analysis by land cover. *Australian Journal of Agricultural and Resource Economics*, **55**, 220–238.
- Stouffer RJ, Wetherald RT (2007) Changes of variability in response to increasing greenhouse gases. Part I: Temperature. *Journal of Climate*, **20**, 5455–5467.
- Tebaldi C, Hayhoe K, Arblaster JM, Meehl GA (2006) Going to the extremes. *Climatic Change*, **79**, 185–211.
- Thomas CD (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.
- Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19637–19643.
- Van Buskirk J, Mulvihill RS, Leberman RC (2010) Declining body sizes in North American birds associated with climate change. *Oikos*, **119**, 1047–1055.
- Vegvari Z, Bokony V, Barta Z, Kovacs G (2010) Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biology*, **16**, 1–11.
- Watt C, Mitchell S, Salewski V (2010) Bergmann's rule; a concept cluster? *Oikos*, **119**, 89–100.
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927–942.
- Yom-Tov Y (2001) Global warming and body mass decline in Israeli passerine birds. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 947–952.
- Yom-Tov Y, Geffen E (2011) Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biological Reviews*, **86**, 531–541.
- Yom-Tov Y, Yom-Tov S, Wright J, Thorne CJR, Du Feu R (2006) Recent changes in body weight and wing length among some British passerine birds. *Oikos*, **112**, 91–101.

### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Species used for analysis for Palomarin Field Station and Coyote Creek Field Station. Each species is classified by migration distance and breeding range, with 'local' referring to the study site; these classifications were incorporated into the model. Numbers listed for each species are the number of individual captures included in the analysis; the change in log-transformed wing length per year; and the change in log-transformed mass per year.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.