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Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines

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Intraspecific latitudinal clines in the body size of terrestrial vertebrates, where members of the same species are larger at higher latitudes, are widely interpreted as evidence for natural selection and adaptation to local climate. These clines are predicted to shift in response to climate change. We used museum specimens to measure changes in the body size of eight passerine bird species from south-eastern Australia over approximately the last 100 years. Four species showed significant decreases in body size (1.8–3.6% of wing length) and a shift in latitudinal cline over that period, and a meta-analysis demonstrated a consistent trend across all eight species. Southern high-latitude populations now display the body sizes typical of more northern populations pre-1950, equivalent to a 7° shift in latitude. Using ptilochronology, we found no evidence that these morphological changes were a plastic response to changes in nutrition, a likely non-genetic mechanism for the pattern observed. Our results demonstrate a generalized response by eight avian species to some major environmental change over the last 100 years or so, probably global warming.

Keywords: climate change; adaptation; phenotypic plasticity; Bergmann's Rule; ptilochronology; meta-analysis

1. INTRODUCTION

Global mean surface temperatures have risen by 0.6°C since the late nineteenth century and by 0.2–0.3° over the last 40 years, and the increase is largely attributed to an anthropogenic increase in atmospheric greenhouse gases (Jones *et al.* 2001). Evidence is accumulating that these recent climatic and atmospheric changes are having wide-ranging effects on taxonomically diverse organisms (Hughes 2000; Parmesan and Yohe 2003; Parmesan 2006). Such effects include poleward and altitudinal shifts in the distribution of species, physiological changes affecting processes such as respiration and photosynthesis, changes in phenology (potentially leading to a mismatch in the timing of life cycles of interacting species, e.g. predator–prey cycles) and adaptation via microevolutionary changes *in situ* in species with short generation times and rapid population growth rates (Hughes 2000; Parmesan & Yohe 2003; Parmesan 2006).

A number of recent studies have reported correlative evidence for a decline in the body size of birds and mammals in response to global warming (Yom-Tov 2001; Schmidt & Jensen 2005; Yom-Tov & Yom-Tov 2006; Yom-Tov *et al.* 2006; Teplitsky *et al.* 2008; Meiri *et al.* 2009). Such responses are often interpreted as microevolutionary changes in the context of Bergmann's Rule (Bergmann 1847), which was originally proposed to explain geographical variation in the body size of endotherms. It predicts a mean increase in body size with increasing latitude

as an adaptive, thermoregulatory response to colder environments. This is driven by the relationship between surface area and volume: larger individuals have proportionally smaller surface areas and lose less heat compared to smaller individuals, and they have a consequent improvement in energy efficiency. Bergmann's Rule is thought to be an adaptive response involving changes in genes that code for body size, and a recent phylogenetic analysis of global patterns of avian body size supports this view. Geographic patterns are likely to be driven by adaptation, although a range of other factors also influence temperature–size relationships (Olson *et al.* 2009).

A within-population decrease in body size may, however, be a plastic response to changes in a range of environmental factors. These include inter- and intraspecific competition (Brown & Wilson 1956; Dayan & Simberloff 1998), predation pressure (Gosler *et al.* 1995; Gentle & Gosler 2001), the prevalence of parasites (Poulin 2007) and changes in nutrition (Blem 1990). Of these, the most widely recognized mechanism is a change in food availability or food quality that affects nutrition. Rather than an adaptive, genetically based response to global warming, nutrition-mediated declines in body size would represent a plastic response to a degrading environment. This is a plausible explanation for observed temporal declines in body size given evidence that habitat quality is decreasing as a result of anthropogenic habitat fragmentation and degradation, processes that are global in their extent (Groombridge 1992).

Disassociating microevolutionary (genetic) responses from phenotypic plasticity (non-genetic) as mechanisms

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in explaining responses to global warming is important. There are limits to the degree of change that can be achieved via plasticity compared with adaptation, and this is significant in the context of rapid environmental change, like global warming (DeWitt *et al.* 1998). Although plasticity can evolve under selection it is unlikely to provide long-term solutions to continued directional change, and the faster the change the sooner a species will reach the limit of its ability to maintain fitness (Nussey *et al.* 2005). Despite this, distinguishing between adaptation and plasticity has proved difficult, with direct evidence for genetic responses to global warming rare (Gienapp *et al.* 2008). In birds in particular, the genetic basis of many morphological traits, including body size, is largely unknown, so direct evidence is hard to obtain. Alternatively, genetic responses may be too slow to detect using current methods (Postma 2006), or warming so recent that evolutionary change is lagging (Gienapp *et al.* 2008).

In Australia, mean surface temperatures have risen by 0.7° since the early 1900s and most change has occurred post-1950 (Collins 2000; Nicholls 2003). However, no study has investigated phenotypic responses to global warming in Australian birds. Because the genes that influence body size in natural populations of birds are unknown, we took alternative approaches to test for effects of climate change. First, we tested for temporal changes in the body size of eight insectivorous bird species from south-east Australia over the last century. Second, because body size could be influenced by latitude we tested for the presence of latitudinal clines in body size. Third, we tested for temporal changes in clines as a predicted response to global warming. Finally, using ptilochronology we tested a likely non-genetic mechanism for temporal changes in body size: whether changes in body size are the result of changes in nutrition associated with a degrading environment. Ptilochronology is a widely used technique to assess nutritional status in birds and involves measurement of the width of daily growth bars on feathers to provide an index of the availability of nutrients during the period of growth (Grubb 2006).

2. MATERIAL AND METHODS

(a) *Species and study area*

We examined museum skins housed at the Australian National Wildlife Collection (ANWC) and the Australian Museum, collected over a period of approximately 140 years between 1860 and 2001 (table 1). We selected only adults from localities spanning 18° of latitude (-20 to -38° S) collected in south-eastern Australia from Victoria to Queensland. Where a species is represented by more than one subspecies we selected a single subspecies for examination, as subspecies may differ in morphology.

The eight species were selected on the basis that they were well represented in collections, and growth bars were readily visible. All are sedentary small- to medium-sized insectivores, a group that is known to be declining worldwide (Sekercioglu *et al.* 2004). Among passerines, insectivores are particularly vulnerable to habitat fragmentation and there is evidence that reduced nutrition may be a contributing factor in south-east Australia (Zannette *et al.* 2000) and elsewhere (Burke & Nol 1998; Stratford & Stouffer 2001; Doherty &

Grubb 2003; Zannette *et al.* 2003; Suorsa *et al.* 2004). Five of the eight species are listed as threatened and declining across their ranges, while three are widespread and secure (table 1).

(b) *Measurement of body size*

We measured the length of the flattened wing chord from the carpal joint to the tip of the longest primary (to an accuracy of 0.5 mm) using a butted ruler. Among passerines, wing length is the best single linear predictor of body mass, and accordingly may be used as an index for body size (Gosler *et al.* 1998).

We also recorded the sex of the specimen, the location (latitude, distance to coast and altitude) at which it was collected and the year of collection. We used distance to coast instead of longitude as a measure of geographic location because individuals at the same longitude may experience very different temperatures depending on direct distance to the coast. This is highly variable in south-eastern Australia because of the shape of the coastline.

(c) *Nutritional condition and ptilochronology*

We used ptilochronology as a relative measure of nutritional condition, following the method of Grubb (2006). The rate of feather growth affects the width of the resulting growth bar, with narrower width representing slower growth, which occurs when food is limited. For museum skins of these species, growth bar width represents condition within 12 months of the date of collection (i.e. the previous annual moult). The causes and time sequence for the formation of growth bars have been studied in captive birds and via manipulation of food supply in the wild (reviewed in Grubb 2006). Ptilochronology has most recently been adopted by conservation biologists for use as an indicator of habitat quality in fragmented landscapes (Stratford & Stouffer 2001; Doherty & Grubb 2003).

We measured the width of growth bars on a single tail feather—in most species this was the outermost left (T6) as it was easiest to access *in situ* without causing damage to the skin. We slid an index card between the feather of interest and the adjacent one, pushing the card upward until it touched the body tissue. We used a fine pin to puncture the card at the feather's tip and then at the start of each pair of growth bars, starting about one-third along the length of the feather from the distal end. We recorded as many consecutive growth bars as were visible. Using digital callipers we measured the distance between pinpricks marking the first and last growth bars and calculated average width by dividing by the number of bars, with a minimum of three bars measured for inclusion in analyses. We also measured the total length of the feather. Larger birds tend to have wider growth bars so it is necessary to control for intraspecific differences in body size (Grubb 2006). To achieve this, we used the residuals from a regression of mean growth bar width on feather length (residual condition), following the method of Eeva *et al.* (1998). All feather and body measurements were conducted by the same person (J.L.G.) to avoid bias.

(d) *Statistical analyses*

We used generalised linear models (GLM) with normal distributions and identity link functions to test for a temporal decline in body size, using separate models for each species. We fitted wing chord (index of body size) as the response variable and tested whether year of collection, latitude,

Table 1. Number of individuals, weight and conservation status of each species examined, mean wing length (\pm s.e.) and the temporal change in body size (percentage difference) of individuals collected before and after 1950. T, threatened; S, secure.

species	N	weight (g)	status	wing length (mm)		% change
				before 1950	after 1950	
Climacteridae						
brown treecreeper, <i>Climacteris picummus</i>	78	28–37	T	93.50 \pm 0.96	91.48 \pm 0.31	–2.16
Pomatostomidae						
grey-crowned babbler, <i>Pomatostomus temporalis</i>	71	63–79	T	117.48 \pm 0.53	114.91 \pm 0.51	–2.19
Petroicidae						
hooded robin, <i>Melanodryas cucullata</i>	62	20–25	T	97.91 \pm 0.73	95.60 \pm 0.61	–2.35
jacky winter, <i>Microeca fascians</i>	87	15–18	T	90.00 \pm 0.59	88.37 \pm 0.25	–1.81
Acanthizidae						
speckled warbler, <i>Pyrholaemus sagittatus</i>	59	11–15	T	62.72 \pm 0.81	62.81 \pm 0.42	0.24
yellow-rumped thornbill, <i>Acanthiza chrysorrhoa</i>	60	8–10	S	61.21 \pm 0.69	59.35 \pm 0.39	–3.04
white-browed scrubwren, <i>Sericornis frontalis</i>	80	11–15	S	56.29 \pm 0.44	56.74 \pm 0.32	0.80
Maluridae						
variegated fairy-wren, <i>Malurus lamberti</i>	50	7–11	S	49.66 \pm 0.72	47.85 \pm 0.55	–3.64

distance to coast, altitude, sex or residual condition affected body size. We had no *a priori* reason to assume that temporal declines in body size would be linear in nature, as shown elsewhere (Nevoux *et al.* 2008), so we treated year of collection as a categorical variable: skins collected before 1950 and those after 1950. This is an appropriate division, because the rate of warming in Australia has increased since 1950. All analyses were carried out in GENSTAT 9.2 (Payne *et al.* 2006). We fitted full models with all explanatory variables and two specific two-way interaction terms of interest: year of collection \times latitude, and year of collection \times residual condition. We did not fit all possible two-way interactions because of the increased potential for type I statistical errors when many terms are fitted (Mundry & Nunn 2009). We sequentially removed non-significant interaction terms, followed by non-significant main effects, until only significant terms remained. We removed the terms in varying order to confirm the consistency of effects in the final models. We also tested the effect of removing non-significant terms together as recommended by Mundry & Nunn (2009). Residual plots and normal probability plots were used to check for deviations from normality among residuals.

Note that our models have limited power to detect an effect of nutrition on body size *per se*, because we effectively controlled for body size by regressing growth bar width against feather length (see above). However, our models are able to detect changes in residual condition (unexplained by body size) over time in a residual condition \times year of collection interaction, and therefore nutrition was included in the above models.

To further explore whether levels of nutrition had changed over time, we ran additional models that tested for effects on growth bar width itself, and in particular whether the width of growth bars differed before and after 1950. We fitted growth bar width as the response and used wing length as a

covariate to control for body size, following the method of Grubb (2006). These models also included the terms year of collection, latitude, distance to coast, altitude and sex.

We performed a meta-analysis on the coefficients of models containing multiple terms to test whether the effect sizes of the important predictor variables on body size varied across species. We calculated mean effect sizes weighted by sampling variance using METAWIN 2.0 (Rosenthal *et al.* 2000). We used Pearson's correlation coefficient r as a measure of the relationship between body size and each of the three variables year, latitude and nutrition. We transformed F statistics into a correlation coefficient using the formulae for transformations given by Rosenthal (1991, p. 19). These Pearson correlation coefficients were subsequently transformed by means of Fisher's transformation to Z_r values on which all subsequent analyses were performed. The weighting factor in meta-analysis is the inverse of the effect size variance. Hence studies where the effect size is known with greater certainty receive a larger weighting. The asymptotic variance in Fisher's transformation of r is $V = 1/(n - 3)$. We therefore adjusted the mean weighted effect size at the species level using $n - 3$ as the adjustment factor (Rosenthal 1991, pp. 27–28). We subsequently calculated an estimate of heterogeneity in effect sizes using the formula provided by Rosenthal (1991, pp. 73–74). We report the mean effect size and 95 per cent confidence intervals calculated using a bias-corrected bootstrap approach (1000 replicates), as well as heterogeneity (Q), assuming Q follows a chi-squared distribution with d.f. = number of species – 1.

3. RESULTS

(a) Temporal declines in body size

Our results based on measurement of 517 museum skins of eight insectivorous species from south-eastern Australia

show that a temporal decline in body size has occurred over approximately the last 100 years (table 1). The magnitude of the decline ranged from 1.8 to 3.6 per cent of wing length, which is an index of body size (table 1). Four of the eight species showed significant reductions in wing length, whereas a further two species showed non-significant trends in this direction (table 2). Our meta-analysis confirmed the generality of the decrease in body size by showing that variation across species was no more than expected by chance once sample size was considered. The weighted average effect size for the relationship between body size and year was $r = 0.275$ (95% CI 0.185–0.397) and there was no significant heterogeneity in effect size among species ($Q = 6.957$, d.f. = 7, $p = 0.434$).

(b) Nutrition

There was no evidence that the temporal decline in body size was due to changes in nutrition associated with a degrading environment. We found no significant differences between residual condition (index of nutrition) for specimens collected before and after 1950 ($0.056 \leq p \leq 0.910$) and there was no effect of residual condition in any of the statistical models explaining body size in the eight species (table 2). Our meta-analysis confirmed the generality of this result by showing that the relationship between residual condition and body size was weak but similar across species (weighted average effect size $r = 0.074$, 95 per cent CI 0.042–0.107; heterogeneity in effect size $Q = 0.714$, d.f. = 7, $p = 0.998$). Our additional models examining possible effects on growth bar width, controlling for body size (wing length), showed no difference in growth bar width before and after 1950 (year: $0.068 \leq p \leq 0.920$), and there was no significant effect of latitude ($0.065 \leq p \leq 0.910$), distance to coast ($0.110 \leq p \leq 0.965$), altitude ($0.078 \leq p \leq 0.840$) or sex ($0.059 \leq p \leq 0.715$) for any of the eight species.

(c) Latitudinal clines in body size

In individual analyses, four of the eight species showed clinal variation in body size associated with latitude, with size increasing in southern populations as predicted by Bergmann's Rule, and one species showed a non-significant trend in this direction (figure 1). Our meta-analysis again confirmed the generality of this result by showing no difference in effect sizes across species for the relationship between body size and latitude once sample size was considered (weighted average effect size $r = 0.251$, 95 per cent CI 0.153–0.327; heterogeneity in effect size among species $Q = 6.529$, d.f. = 7, $p = 0.480$).

Because of the effect of body size declines in the post-1950 sample, latitudinal clines have shifted: southern populations of four species now display the body sizes typical of more northern populations pre-1950, with the magnitude of the shift equivalent to approximately 7° in latitude (figure 1). The change in intercept but not slope of regression lines suggests a universal, rather than localized, effect across latitudes (figure 1).

4. DISCUSSION

Our individual analyses of trends in eight species, combined in a meta-analysis, demonstrate a temporal decline in the body size of insectivorous passerine bird species from south-east Australia over the last 100 years or so. The magnitude of the decline ranged from 1.8 to 3.6 per cent of wing length, which is an index of body size. We found no evidence that the decline in body size was due to changes in nutrition associated with a degrading environment, a plausible non-genetic mechanism for the pattern observed. Four of the eight species showed classic latitudinal clines with body size increasing in southerly populations, presumably as a physiological response to colder climates as predicted by Bergmann's Rule. Owing to the effect of body size declines in the post-1950 sample, however, latitudinal clines have shifted; southern populations now display the body sizes typical of more northern populations pre-1950, with the magnitude of the shift equivalent to approximately 7° in latitude.

Geographical clines are widely interpreted as evidence for natural selection and adaptation to environmental variables, particularly to climate (Endler 1986; Olson *et al.* 2009). These are predicted to shift with climate change (Huey *et al.* 2000; Umina *et al.* 2005; Meiri *et al.* 2009), which is consistent with our results. Despite variation in the body size of the species studied (approx. 10–79 g), all species shown to decrease in size showed an equivalent 7° shift in latitudinal clines. Such a universal response suggests that a general phenomenon, like temperature, underlies temporal size declines. In comparison, phenotypic responses such as those due to changes in nutrition would be likely to affect species differently and lead to more variable responses in body size across latitudes. Declines in body size could be driven by other adaptive mechanisms (Olson *et al.* 2009) or result from plastic responses to other environmental changes, but we know of no factor, apart from the increased temperatures associated with global warming, that would show such universal expression across latitudes.

Other than nutrition, most other hypotheses suggested to account for changes in body size relate to local effects rather than broad-scale changes across multiple species. These include predation pressure (Gosler *et al.* 1995), inter- and intra-specific competition (Brown & Wilson 1956; Grant & Grant 2006), and the distribution and abundance of parasites (Poulin 2007). Species richness and resource availability have also been shown to correlate with body-size patterns secondarily to temperature (Olson *et al.* 2009), but will again have variable effects within and between species across latitudes because they involve (unidentified) community-level processes. In contrast to the variable direction of change predicted by these hypotheses, our data show consistent directional change across multiple species, suggesting a single, broad-scale mechanism driving temporal patterns.

Correlation between rising temperatures due to global warming and body-mass changes in birds have been reported from Israel (Yom-Tov 2001), Denmark (Schmidt & Jensen 2005; Yom-Tov & Yom-Tov 2006), Britain (Yom-Tov *et al.* 2006) and New Zealand (Teplitsky *et al.* 2008), and these trends have been interpreted as microevolutionary responses to global

Table 2. Results of generalized linear models (GLMs) examining the effects of year, nutrition, latitude, sex, altitude and distance to coast on body size (wing length) of eight passerine species. Year = year of collection, before 1950 and after 1950. Values that are significant or show a trend are in bold type. Mean growth bar width was used as an index of nutritional condition; to control for differences in body size within species we used the residuals from a regression of growth bar width on the length of the tail feather from which growth bars were measured (residual condition). Neither two-way interaction term (see text) significantly improved any of the models ($0.110 \leq p \leq 0.920$). Parameter estimates \pm s.e. (change in intercept for factors (year, sex) and slope for continuous variables (latitude, distance to coast, altitude)) for all highlighted (significant or near-significant) effects listed in the table are as follows: grey-crowned babbler, year 3.45 ± 0.88 , sex 1.87 ± 0.83 , latitude 0.33 ± 0.19 ; jacky winter, year 1.53 ± 0.66 , sex 1.93 ± 0.05 , latitude 0.13 ± 0.07 ; hooded robin, year 3.59 ± 0.92 , sex 5.15 ± 1.0 , latitude 0.49 ± 0.21 ; brown treecreeper, year 1.03 ± 0.63 , sex 2.12 ± 0.57 , latitude 0.22 ± 0.08 , altitude 0.01 ± 0.003 ; white-browed scrubwren, sex 3.11 ± 0.44 , latitude 0.23 ± 0.01 , distance to coast 1.44 ± 0.438 ; variegated fairy-wren, year 1.08 ± 0.70 ; yellow-rumped thornbill, year 2.08 ± 0.654 ; speckled warbler, sex 2.07 ± 0.61 , altitude 0.002 ± 0.001 .

species	model terms																	
	year			nutrition			latitude			sex			altitude			distance to coast		
	d.f.	F	p	d.f.	F	p	d.f.	F	p	d.f.	F	p	d.f.	F	p	d.f.	F	p
grey-crowned babbler	1,42	13.73	< 0.001	1,39	0.23	0.635	1,37	3.32	0.075	1,37	4.26	0.046	1,40	0.27	0.606	1,41	0.02	0.903
jacky winter	1,63	8.02	0.006	1,56	0.02	0.878	1,61	7.27	< 0.009	1,61	19.68	< 0.001	1,57	0.52	0.472	1,58	0.77	0.384
hooded robin	1,50	11.21	0.002	1,47	0.24	0.625	1,52	5.36	< 0.001	1,52	19.32	< 0.001	1,48	0.01	0.924	1,49	0.0	0.968
brown treecreeper	1,60	3.08	0.080	1,53	0.37	0.546	1,55	7.8	0.004	1,55	9.22	0.004	1,54	19.25	0.001	1,52	0.01	0.921
white-browed scrubwren	1,62	0.39	0.537	1,63	1.51	0.224	1,61	5.37	0.024	1,61	54.89	< 0.001	1,64	0.04	0.884	1,65	3.49	0.066
variegated fairy-wren	1,32	2.01	0.056	1,33	0.29	0.594	1,31	2.57	0.117	1,31	1.98	0.170	1,34	0.07	0.799	1,35	0.0	0.952
yellow-rumped thornbill	1,38	3.91	0.003	1,38	0.03	0.873	1,36	0.0	0.65	1,36	0.21	0.649	1,39	0.80	0.378	1,38	2.21	0.147
speckled warbler	1,41	0.14	0.711	1,42	0.09	0.767	1,45	0.0	0.961	1,40	10.03	0.003	1,43	4.19	0.047	1,44	0.0	0.998

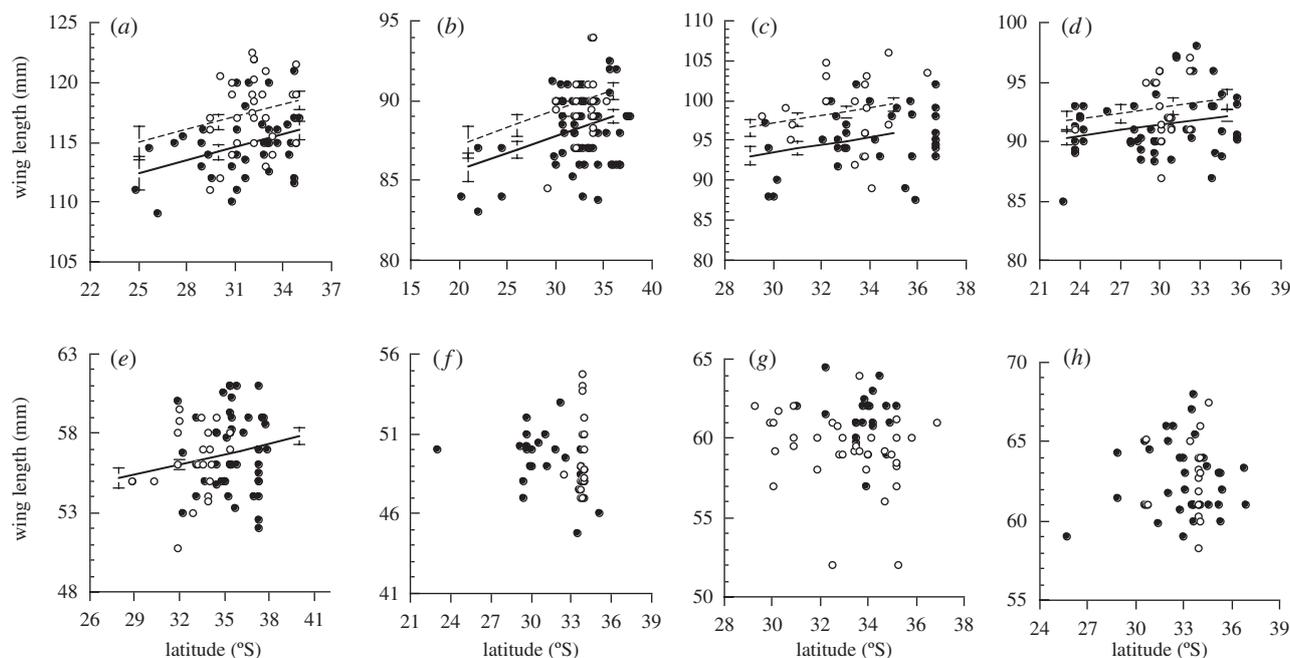


Figure 1. Change in latitudinal patterns of body size (wing length) for eight species between the late 1800s and 1950 (open circles), and between 1950 and 2001 (filled circles). (a) Grey-crowned babbler; (b) jacky winter; (c) hooded robin; (d) brown treecreeper; (e) white-browed scrubwren; (f) variegated fairy-wren; (g) yellow-rumped thornbill; (h) speckled warbler. Linear regressions examined association between body size and latitude, with a significant effect of latitude for four species (jacky winter, hooded robin, brown treecreeper, white-browed scrubwren) and a non-significant trend for one (grey-crowned babbler). Solid and dashed lines represent regression model predictions for wing length before 1950 and after 1950, respectively; the single line for white-browed scrubwren represents all data (no year effect). See table 2 for statistics.

warming or changes in nutrition associated with diet or habitat quality. Despite these assumptions, no study has identified the specific mechanisms underlying temporal trends and only one has attempted to distinguish between adaptation and phenotypic plasticity. Teplitsky *et al.* (2008) concluded that the body-size decline in red-billed gulls (*Larus novaehollandiae*) was more likely to be due to phenotypic plasticity driven by changes in environmental conditions because they found no evidence for genetic change using an animal model approach.

Similarly, no studies have yet demonstrated a genetic basis for temporal trends in avian body size in response to global warming, although there is strong evidence for adaptation to global warming in insects (reviewed in Gienapp *et al.* 2008). Umina *et al.* (2005) demonstrated a rapid shift in the clinal pattern of allele frequencies associated with temperature in *Drosophila melanogaster* in south-eastern Australia. Southern high-latitude populations of *Drosophila* now have the genetic constitution that more northern populations had 20 years ago, a pattern consistent with global warming. For *Drosophila*, this change is equivalent to a 4–7° shift in latitude. Although our data do not allow as robust estimation of the time frame in which change has occurred, we document remarkably similar shifts in latitudinal clines, both in the parallel nature of clinal change and the extent of the shift (approx. 7°).

Similar temporal responses to climatic variables, unrelated to global warming, have previously been demonstrated in birds. For example, the body size of house sparrows (*Passer domesticus*) correlated with local

temperatures and seasonality within 100 years of their introduction to new latitudes, consistent with latitudinal change driving adaptation (Johnston & Selander 1971; Baker 1980), although direct evidence for genetic change has not been demonstrated in this case (Reznick & Ghalambor 2001). Rapid adaptive evolution of body size (wing length) and bill morphology in response to drought has, however, been convincingly demonstrated in a Darwin's Galápagos finch species *Geospiza fortis* (Grant & Grant 1995).

Our study is important because it shows a generalized response to some major environmental change over the last 100 years, probably global warming. We show that phenotypic plasticity in the form of nutritional stress is unlikely to account for observed declines in body size, yet the extent of latitudinal shift in size is remarkably similar to the latitudinal shift in allele frequencies shown by *Drosophila* in south-eastern Australia. Given that these changes in *Drosophila* are an adaptive response to global warming, we suggest that adaptation may also underlie avian responses. Further studies are required to establish the precise mechanism.

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