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RESEARCH ARTICLE

# Clinal variation in avian body size is better explained by summer maximum temperatures during development than by cold winter temperatures

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## ABSTRACT

Across many taxa, clinal variation in body size has been observed to follow Bergmann's rule, which predicts larger body size in colder climates. For more than a century, this pattern has typically been ascribed to selection for large body size in cold winter climates. Here, in spatially distributed observational data from 30 populations of House Sparrow (*Passer domesticus*) introduced into Australia and New Zealand, we show that this relationship appears to be explained by a negative relationship with high temperatures during the breeding season. Our results suggest that higher temperatures during the breeding season could reduce body size through developmental plasticity, which should be considered in combination with or as an alternative to selection. Our findings would predict that a hotter climate during breeding could drive significant changes in morphology among populations (and potentially within populations as well, if climate varies temporally across a breeding season). This idea, and our support for it, could account for much of the variation in body size that drives the well-observed patterns first described by Bergmann, and that are still largely attributed to selection on adult body size during cold winters. Understanding the mechanisms behind any climate-dependent developmental plasticity could prove useful for understanding how endotherms may be affected by climate change in the future.

*Keywords:* Bergmann's rule, phenotypic plasticity, morphology, *Passer domesticus*

## La variación clinal en el tamaño corporal es mejor explicada por las temperaturas máximas de verano durante el desarrollo y no por las temperaturas frías de invierno

## RESUMEN

A través de muchos taxa, se ha observado que la variación clinal en el tamaño corporal sigue la regla de Bergmann, que predice tamaños corporales más grandes en climas más fríos. Por más de un siglo, este patrón ha sido típicamente atribuido a la selección de un tamaño corporal grande en climas de inviernos fríos. Aquí, usando datos observacionales espacialmente distribuidos provenientes de 30 poblaciones de *Passer domesticus* introducidos en Australia y Nueva Zelanda, mostramos que esta relación parece estar explicada por una relación negativa con las altas temperaturas durante la estación reproductiva. Nuestros resultados sugieren que las mayores temperaturas durante la estación reproductiva podrían reducir el tamaño corporal a través de la plasticidad del crecimiento, la cual debería ser considerada en combinación o como una alternativa a la selección. Nuestros hallazgos predecirían que un clima más cálido durante la cría podría inducir cambios significativos en la morfología entre poblacionales (y potencialmente también al interior de las poblaciones si el clima varía temporalmente a lo largo de una estación reproductiva). Esta idea, y nuestro apoyo a ella, podría explicar mucha de la variación en el tamaño corporal que determina los patrones largamente observados descriptos originalmente por Bergmann y que son aún atribuidos principalmente a la selección del tamaño corporal del adulto durante los inviernos fríos. Entender los mecanismos detrás de cualquier plasticidad del desarrollo que dependan del clima podría resultar útil para entender como los endotermos pueden verse afectados por el cambio climático en el futuro.

*Palabras clave:* morfología, *Passer domesticus*, plasticidad fenotípica, regla de Bergmann

## INTRODUCTION

For over 100 years since the publication of Bergmann's rule in 1847 (Bergmann 1847), a clinal pattern of animals having larger body sizes in colder climates has been observed in a majority of the hundreds of species that have been examined (Mayr 1956, James 1970, Ashton et al. 2000, Ashton 2002, Meiri and Dayan 2003, Millien et al. 2006, Clauss et al. 2013, Teplitsky and Millien 2014). To date, most studies still cite Bergmann's original explanation that larger body size is favored by natural selection in colder climates because of the thermoregulatory benefits of a smaller volume to surface area ratio (Briscoe et al. 2015, Cardilini et al. 2016, Salewski and Watt 2017). A classic example of clinal variation in avian body size has previously been demonstrated in North American populations of the introduced House Sparrow (*Passer domesticus*; Johnston and Selander 1964, 1973, Murphy 1985). If winter temperatures are the selective force responsible for this clinal variation, as predicted by Bergmann's rule, then variation in body size between populations should be best explained by winter minimum temperatures. However, in hotter climates, smaller body size can also be advantageous to an individual's ability to thermoregulate by dissipating heat (Partridge and Coyne 1997), even though the benefits of minor changes in body size within species have been questioned for more than 40 yr (Scholander 1955, McNab 1971).

Understanding the mechanisms that create the morphological differentiation described by Bergmann's rule has gained fresh impetus as part of the study of the effects of a changing climate on animal populations (Gardner et al. 2011). Indeed, declining body size in a number of avian species has been linked to increasing temperatures consistent with climate change (Gardner et al. 2009, Van Buskirk et al. 2010), and it has been suggested that higher temperatures during development may act as an influence on plasticity in growth (Merilä and Hendry 2014). The idea that clines in body size are a result of phenotypic plasticity in morphology that is mediated by the effects of high temperatures on growth is now gaining traction (Teplitsky et al. 2008, Van Buskirk et al. 2010, Yom-Tov and Geffen 2011). In hot climates, nests can potentially act to buffer ambient conditions, but they can still get very hot. Recent work found that Zebra Finch (*Taeniopygia guttata*) nests in the Australian desert were typically several degrees warmer than ambient conditions and that internal nest temperatures occasionally exceeded 50°C (Griffith et al. 2016). Nest microclimates may therefore be a significant determinant of variation in developmental plasticity and may have the capacity to affect development and growth. Indeed, it has recently been found observationally in a wild population and experimentally in a captive population of the Zebra Finch that higher temperatures during develop-

ment lead to reduced fledgling and adult body size (Andrew et al. 2017).

If temperature during development is indeed important, then, at the population level, summer maximum temperatures will be a better predictor of mean body size across locations than winter minimum temperatures. As with the House Sparrows studied in North America (Johnston and Selander 1964, 1971, Murphy 1985), the species was deliberately introduced into Australia and New Zealand in the mid-19<sup>th</sup> century from founders taken from north-western Europe (Andrew and Griffith 2016). Over the next century, House Sparrows expanded their range to occupy most of the urban areas across both the North and South islands of New Zealand and the eastern half of Australia (Andrew and Griffith 2016), and today are found in a range of climates that are far more variable and extreme than those in the area from which they were sourced. The House Sparrow populations in Australia and New Zealand therefore provide an opportunity to assess the extent to which a species may respond to a changing climate in a relatively short period of time (~160 yr at most, and <50 yr for the populations at the extreme edge of their range in Australia; Andrew and Griffith 2016). Here, we use these populations of a sedentary avian species (Anderson 2006) to test the extent to which clinal variation in body size is related to both winter minimum and summer maximum temperatures. This will provide new insight into the extent to which body size is a response to the climate experienced during development rather than a response to selection over the winter.

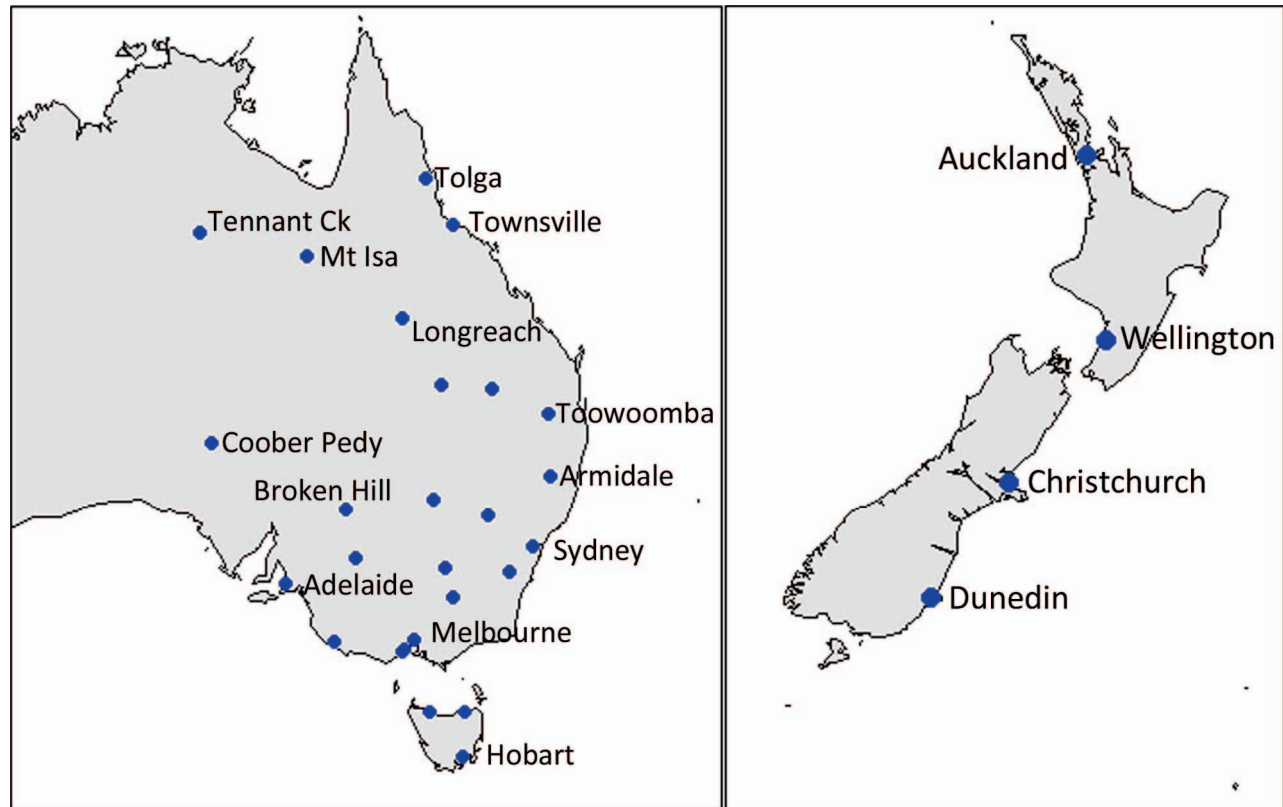
## METHODS

### Sampling

Adult House Sparrows were sampled at 26 locations across Australia (Figure 1, Appendix Table 4), with ~40 birds measured in each location ( $n$  males = 636,  $n$  females = 512). Measurements were taken from birds in Australia from April to September, 2014, and in March, 2015. Measurements were taken from birds in New Zealand in 4 locations (Appendix Table 4;  $n$  males = 511,  $n$  females = 242) between June and August, 2005, as part of earlier work. New Zealand House Sparrow measurements were collected by a separate team from Otago University (Dunedin, New Zealand). Birds were captured using mist nets and placed in bird bags until they were measured. Birds were not held for more than 30 min and were released as soon as possible after they had been measured and banded in accordance with the local bird banding authority.

### Measurements

We determined the age and sex of captured birds by plumage and bill color. All juvenile birds were removed



**FIGURE 1.** Map of House Sparrow sampling sites where we tested the extent to which clinal variation in body size was related to winter minimum and summer maximum temperatures. The map plots 26 sampling sites in Australia (there are 3 points near Melbourne) and 4 in New Zealand. Not all sampling sites are labeled; for a full list see Appendix Table 4.

from the morphological analyses. We recorded the tarsus length and body mass of all individuals sampled in Australia and New Zealand. Tarsus length was measured for the right leg, from the bottom of the tarsus with the toes bent forward to the ankle joint. Body mass was measured to the nearest 0.1 g using a Pesola spring scale (Pesola, Schindellegi, Switzerland).

All House Sparrows sampled in Australia were measured by 1 of 2 measurers (S. C. Griffith and M. Awasthy), and some birds were measured by both investigators to test the consistency of tarsus measurements (the regression between tarsus length measurements was significant:  $R^2 = 0.89$ ,  $t = 20.20$ ,  $P < 0.001$ ). In New Zealand, all measurements were taken by a single investigator (K. Ludwig, a research associate of S. Nakagawa). We used tarsus length and mass as surrogate measures of body size primarily because tarsus length is the most widely applied measure of skeletal size in passerine birds and body mass relates to overall size as well as being indicative of condition in passerine birds. Therefore, the 2 metrics provided 2 different surrogate measures of body size.

### Geographic and Climatic Data

Latitude, longitude, and date of collection were recorded for each sampling site. We used the geographic coordinates to extract the average daily Maximum Temperature of Warmest Month (BIO5), the average daily Minimum Temperature of Coldest Month (BIO6), and average Temperature Seasonality (BIO4 = standard deviation  $\times$  100) from WorldClim Global Climate Data (Hijmans et al. 2005), which uses climatic data averaged over 30 yr from 1970 to 2000. The average daily Maximum Temperature of the Warmest Month (hereafter, 'summer maximum') was our measure of high temperatures during the breeding season to look for a relationship between the average maximum temperature during the breeding season and body size. Average daily Minimum Temperature of Coldest Month (hereafter, 'winter minimum') was used as a measure of winter extremes to test for a relationship due to the selection pressure of cold conditions.

To test for a relationship between variation in temperature during the breeding season and variation in body size within populations, we looked at the change in mean maximum temperature across the breeding season. In our

study locations, the House Sparrow breeding season typically occurs from September to December (Duursma et al. 2017). Using the weather stations closest to our 26 Australian sampling sites, we took the difference in mean maximum temperatures between December and September (Australian Bureau of Meteorology; <http://www.bom.gov.au>). Data for New Zealand was sourced from the National Institute of Water and Atmospheric Research (NIWA; <https://www.niwa.co.nz/education-and-training/schools/resources/climate>). The close proximities of the relevant government weather stations to the sampling sites (mean distance = 10.7 km, range = 0.2–34.1 km; see [Supplemental Material Data S3](#)) meant that WorldClim and weather station data were highly correlated (e.g., using data for the hottest month from both sources: Pearson's correlation coefficient = 0.98,  $n = 30$ ,  $P < 0.001$ ; using data for the coldest month: Pearson's correlation coefficient = 0.96,  $n = 30$ ,  $P < 0.001$ ). A second measure of climatic variability in Australia used daily maximum temperatures from the 3 breeding seasons (September to December) prior to sampling (2011–2013). Daily maximum temperatures for these 360 days were downloaded from the Australian Water Availability Project (Jones et al. 2009, <http://www.bom.gov.au/jsp/awap/>). Temperature variability for this period was calculated, using the same method as for body size, by adding the log of sample standard deviation to sample variance (Nakagawa et al. 2015). Temperature variability was found to be highly correlated with breeding season range in Australia (estimate = 0.11,  $t_{24} = 6.17$ ,  $P < 0.001$ ,  $R^2 = 0.61$ ).

### Data Analysis

All statistical analyses were conducted using R 3.3.1 (R Core Team 2017). All R code and data used are provided as [Supplemental Material](#) ([Supplemental Material Data](#), [Supplemental Material R Code](#)). The individual body size measurements for mass and tarsus length showed a normal distribution. We calculated the mean body size (mass and tarsus length) and variability for each sample population. Variability was calculated by adding the log of the sample standard deviation to the sample variance; this method was chosen because it produces variability that is linearly related to the mean (Nakagawa et al. 2015). If temperature during development affects mass or tarsus length, then we would expect higher variability in body size in locations where the climate shows a higher degree of variation in temperature during the breeding season. For the mean and variability data, linear models were fitted using the standard `lm` function in R. Males and females were analyzed separately as well as combined. Summer maximum and winter minimum were used as fixed effects in models for mean size. Summer maximum and temperature range across the breeding season were used as fixed effects in size variability models. To account for

differences in sample sizes, all linear models included weights (sample weight =  $2(n - 1)$ ). All linear models using variability included the log of the mean size as a predictor to account for any relationship between mean body size and variability.

Linear mixed models (LMM) were used for fitting individual measurements from all 1,901 birds. For these models, sample population was used as a random factor. LMMs were fitted using the R package `lme4` (Bates et al. 2015). For the LMMs,  $P$ -values and degrees of freedom were calculated with the R package `lmerTest` (Kuznetsova et al. 2016). Summer maximum, winter minimum, and sex were included as fixed effects in the LMMs. Interclass correlation coefficients (ICC) were also calculated for the random effect of sample population to describe how much variation was partitioned between populations (Nakagawa and Schielzeth 2010). The interclass correlation coefficient (ICC),  $R^2$ , and narrow sense heritability ( $h^2$ ) all estimate the proportion of the variance in the response variable that is explained by factors in the model (Nakagawa and Schielzeth 2013). Because ICC is a proportion, it can be compared between similar models (such as our LMMs) that share the same fixed and random effects. To calculate the proportion of variance explained by random factors, the residual variance and the variance explained by fixed effects (known as marginal  $R^2$ ) need to be included. As a result, the total variance explained by the model, that is the conditional  $R^2$  (Nakagawa and Schielzeth 2013), can also be calculated. We report the marginal (fixed effects) and conditional (total model)  $R^2$  for both mass and tarsus length models.

To compare the predictive power of the individual fixed effects, we used semipartial correlations for all of our main models (Schielzeth 2010). Semipartial correlations (hereafter, 'semipartial  $r$ ') scale the response and predictor variables so the mean is 0 and the standard deviation is 1. This scaling results in estimates that are able to be related to estimates of other response variables within and between models. However, all  $P$ -values and  $t$ -values remain unchanged due to scaling. Scaling also allows for binary variables, such as sex, to be coded as  $-1$  and  $1$ , which allows these binary factors to be directly compared with continuous variables (Schielzeth 2010). We chose summer maximum and winter minimum as our 2 bioclimatic variables because they were the most relevant to our hypotheses and because summer maximum was highly correlated with other bioclimatic variables such as latitude and seasonality, but not winter minimum (Appendix Table 5).

## RESULTS

Using the mean mass and tarsus length measurements of sampled House Sparrow populations, we found that

**TABLE 1.** Results from multiple linear regression models using House Sparrow mean body mass in relation to temperature variables. Mean body mass was calculated for 30 sampling locations across Australia and New Zealand (Appendix Table 4) and for males and females separately. Significant effects are in bold font. Summer maximum temperature (Summer max) had a significant negative relationship in all 3 models. Winter minimum temperature (Winter min) was not a significant predictor in any of the 3 models.

	Semipartial <i>r</i>	SE	<i>t</i>	df	<i>P</i>
Male mass					
Intercept	-0.092	0.116	-0.790	27	0.44
Summer max	-0.549	0.120	<b>-4.562</b>	27	< <b>0.001</b>
Winter min	-0.191	0.132	-1.450	27	0.16
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = <b>0.529</b> ; <i>R</i> <sup>2</sup> = <b>0.561</b>				
Female mass					
Intercept	-0.061	0.121	-0.504	27	0.62
Summer max	-0.728	0.129	<b>-5.644</b>	27	< <b>0.001</b>
Winter min	0.069	0.135	0.509	27	0.62
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = <b>0.530</b> ; <i>R</i> <sup>2</sup> = <b>0.562</b>				
All birds mass					
Intercept	-0.043	0.119	-0.365	27	0.72
Summer max	-0.686	0.124	<b>-5.513</b>	27	< <b>0.001</b>
Winter min	-0.087	0.134	-0.646	27	0.52
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = <b>0.567</b> ; <i>R</i> <sup>2</sup> = <b>0.597</b>				

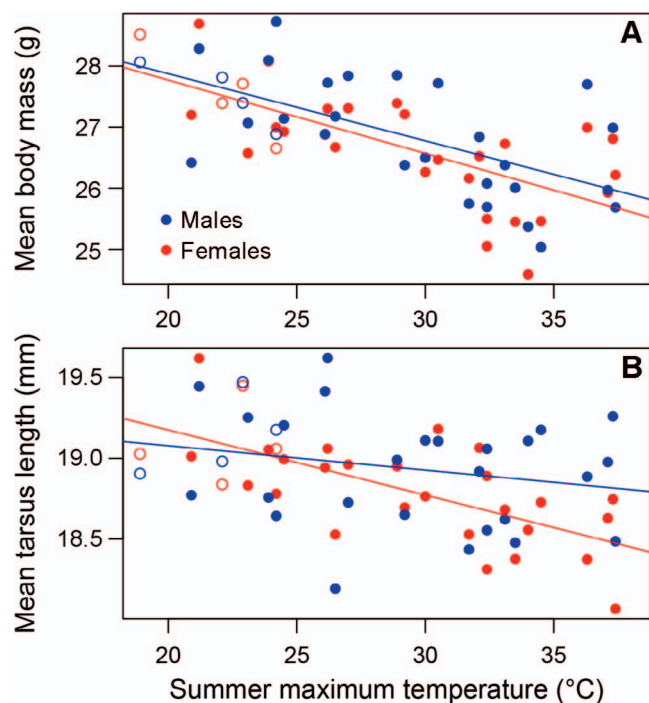
summer maximum was a better predictor of body size than winter minimum (Tables 1 and 2). The relationship between mean body size and summer maximum temperature was strongly negative for both males and females, as was the relationship between female mean tarsus length and summer maximum temperature (Figure 2). All relationships of mean body mass and mean tarsus length with winter minimum temperature were nonsignificant (Appendix Figure 4). Likewise, at the individual level, where both summer maximum and winter minimum were used as fixed effects in linear mixed models (LMMs), summer maximum was a substantially better predictor of body mass than winter minimum temperature (semipartial  $r = -0.34$  vs. semipartial  $r = -0.01$ ; Table 3). For tarsus

length, the fixed effect of summer maximum temperature was a stronger predictor than winter minimum temperature, but the effects were similar (semipartial  $r = -0.13$  vs. semipartial  $r = -0.10$ ; Table 3). The random factor of location explained a similar amount of variance in both body mass and tarsus length (11% and 9%, respectively; Table 3).

We would expect populations breeding across a relatively long breeding period (September–December in our study region) to encounter a wide range of ambient temperatures. In locations with a broader range of temperatures, we would expect individuals to experience a wider range of temperatures during development, resulting in greater variation in body size in these

**TABLE 2.** Results from multiple linear regression models using House Sparrow mean tarsus length in relation to temperature variables. Mean tarsus length was calculated for 30 sampling locations across Australia and New Zealand (Appendix Table 4) and for males and females separately. Significant effects are in bold font. Summer maximum temperature (Summer max) was significantly negatively related to tarsus length for females and all birds combined; however, the same negative trend was not significant for males. Winter minimum temperature (Winter min) was not a significant predictor in any of the 3 models.

	Semipartial <i>r</i>	SE	<i>t</i>	df	<i>P</i>
Male tarsus length					
Intercept	0.230	0.172	1.335	27	0.19
Summer max	-0.301	0.178	-1.693	27	0.10
Winter min	-0.063	0.195	-0.321	27	0.75
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = 0.069; <i>R</i> <sup>2</sup> = 0.133				
Female tarsus length					
Intercept	0.118	0.148	0.801	27	0.43
Summer max	-0.560	0.158	<b>-3.543</b>	27	<b>0.001</b>
Winter min	-0.100	0.166	-0.601	27	0.55
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = <b>0.337</b> ; <i>R</i> <sup>2</sup> = <b>0.383</b>				
All birds tarsus length					
Intercept	0.197	0.171	1.154	27	0.26
Summer max	-0.460	0.179	<b>-2.568</b>	27	<b>0.02</b>
Winter min	-0.082	0.193	-0.426	27	0.67
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = <b>0.196</b> ; <i>R</i> <sup>2</sup> = <b>0.252</b>				



**FIGURE 2.** Mean (A) body mass and (B) tarsus length of House Sparrow populations in relation to summer maximum temperature. Males and females are plotted separately, with males represented by blue circles and females by red circles. The 26 Australian sample sites are plotted as filled circles and the 4 New Zealand sites as open circles. Male and female body mass and female tarsus length were significantly negatively related to summer maximum temperature (Tables 1 and 2).

populations that experience the greatest temperature ranges across the breeding season. We did not find any significant relationships between temperature range and variability in mass or tarsus length (Appendix Tables 6 and 7). However, the variability of body mass in our sample populations was positively related to summer maximum temperature; this positive relationship was also significant for females but not for males when they were analyzed separately (Figure 3, Appendix Table 6). For tarsus length, there was a nonsignificant positive relationship between summer maximum and tarsus variability for males, females, and both sexes combined (Figure 3, Appendix Table 7). There was no strong linear relationship between the temperature range across the breeding season and summer maximum temperature, indicating that these 2 variables were not conflated in this case (estimate = 0.18,  $t_{28} = 2.63$ ,  $P = 0.01$ ,  $R^2 = 0.20$ ).

## DISCUSSION

Our observational work on the House Sparrow populations introduced into Australia and New Zealand essentially replicates the earlier work done in North America

(Johnston and Selander 1964, 1973) and Europe (Murphy 1985) that revealed latitudinal clines in body size in this species. As with most other similar studies across animal taxa, in these earlier studies the clinal variation in body size was attributed to the selective effects of cold weather during the winter (Johnston and Fleischer 1981, Fleischer and Johnston 1984). However, there have been suggestions that a similar pattern may also be driven by constraints affected by the climate experienced during development (Van Buskirk et al. 2010, Gardner et al. 2011, Cunningham et al. 2013). We found support for this idea through our observation that summer maximum temperatures better predicted body size variation than winter minimum temperatures. As all variables were scaled, we were able to use the semipartial  $r$  values from our models to identify summer maximum as a stronger predictor than winter minimum temperature. This observational finding, from House Sparrow populations introduced into the range of climates found in Australia and New Zealand ~150 yr ago (Andrew and Griffith 2016), supports the hypothesis that excessive environmental heat during development may affect growth (Van Buskirk et al. 2010, Gardner et al. 2011, Burness et al. 2013, Andrew et al. 2017). We also explored this hypothesis by looking at the relationship between variability in body size within populations and climatic variability. We did not find any significant relationships between temperature range across the breeding season and variation in mass or tarsus length (Appendix Tables 6 and 7). However, we found the expected positive relationship between summer maximum temperature and body size traits, although it was not always significant (Appendix Tables 6 and 7). The nonsignificant results could have been due to low statistical power (only 30 populations) or a weaker effect on skeletal measurements (tarsus length) than mass. The relationship between summer maximum temperature and variability in body size could have been due to warmer climates being more likely to exceed possible ‘threshold temperatures’ that significantly affect development. The analysis of body size variability promises to be a useful avenue for future studies to explore, especially those with large numbers of sample populations, to test whether this result can be replicated. Only a small portion of the variation in body size observed in this study was explained by temperature; in addition to this, a meaningful portion (~10%) of the variation in tarsus length and mass was partitioned between locations by the random factor of location. These differences between populations could have been linked to genetic differentiation (due to selection or drift) or to other environmental factors not included in the model, such as the time of year that birds were measured. It is also important to note that, in many contexts, temperature may not directly affect body size because of adaptations for mitigating the effects of

**TABLE 3.** Results from linear mixed models (LMMs) examining individual House Sparrow body mass and tarsus length measurements in relation to temperature. These LMMs used the measurements from 30 House Sparrow populations across Australia and New Zealand ( $n = 1,901$  individuals) and included sampling location as a random factor. Significant effects are in bold font. Body mass had a significant negative relationship with summer maximum temperature (Summer max) but not winter minimum temperature (Winter min). Males were heavier than females, but the difference between the sexes was only marginally significant. Tarsus length decreased with increasing summer maximum temperature. Males had longer tarsi than females, but the semipartial correlation value was low, indicating a small size difference between the sexes.

Body mass					
Fixed effects	Semipartial $r$	SE	$t$	df	$P$
Intercept	0.010	0.068	0.140	25.2	
Summer max	-0.339	0.071	<b>-4.804</b>	25.5	<b>&lt;0.001</b>
Winter min	-0.007	0.066	-0.102	25.8	0.92
Sex	0.043	0.021	<b>1.998</b>	1,885.0	<b>0.05</b>
Variance components					
	Variance	SD	$n$	ICC	Conditional $R^2$
Marginal $R^2$	0.120			0.116	
Location	0.111	0.334	30	0.107	
Residual	0.804	0.897	1,901		0.223
Tarsus length					
Fixed effects	Semipartial $r$	SE	$t$	df	$P$
Intercept	-0.085	0.064	-1.334	26.9	
Summer max	-0.134	0.066	<b>-2.037</b>	27.3	<b>0.05</b>
Winter min	-0.103	0.061	-1.675	27.8	0.11
Sex	0.076	0.022	<b>3.423</b>	1,888.5	<b>&lt;0.001</b>
Variance components					
	Variance	SD	$n$	ICC	Conditional $R^2$
Marginal $R^2$	0.046			0.046	
Location	0.093	0.306	30	0.093	
Residual	0.867	0.931	1,901		0.138

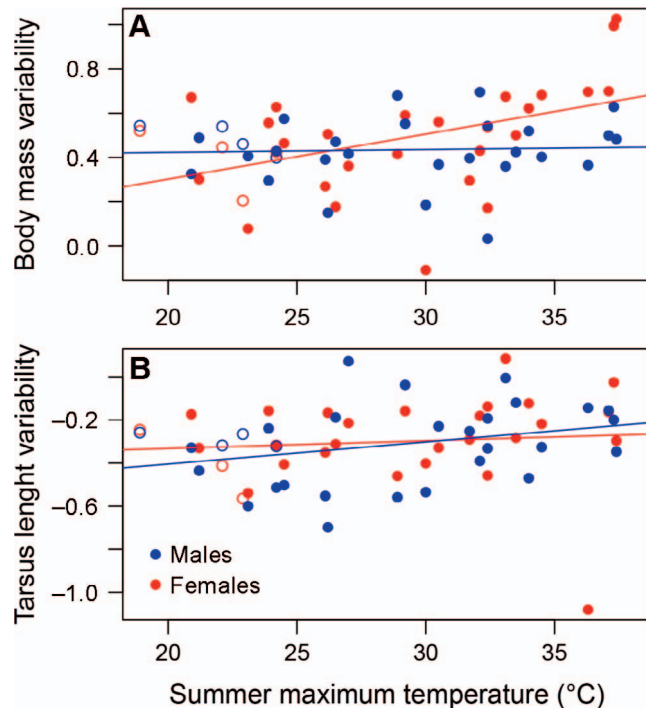
temperature, such as behavioral adaptations that reduce the exposure of developing offspring to high temperatures.

Summer temperatures explained variation in both tarsus length and mass, having a larger effect on mass. A comparison of the 3 locations that had the hottest summer maximum temperatures with the 3 locations that had the coolest summer maximums revealed that sparrows in the hottest locations were ~6% lighter and had tarsi that were ~2% smaller than sparrows in the coolest locations. The greater magnitude of the effect of summer temperatures on mass than the skeletal measure of tarsus length is consistent with earlier studies that showed greater plasticity and lower heritability of body mass (Alatalo et al. 1990, Jensen et al. 2003). Similarly, a study on North American migratory birds (249 species migrating during all 4 seasons) found that increases in summer temperature caused a larger percentage decline in mass (0.34% per degree Celsius) than wing chord length (0.09% per degree Celsius; Van Buskirk et al. 2010). By comparison, in the House Sparrow populations studied here, mass declined by 0.33% and tarsus length declined by 0.11% per degree

Celsius. Although observational, the findings that we report here are similar to those from a recent study of the Zebra Finch, in which the temperature during development in an observational study in the field (fledglings were ~8% lighter in hot vs. cold breeding attempts by the same pair), and in an experimental study in the laboratory (mass was 5% lower in the high temperature treatment), caused similar decreases in body size (Andrew et al. 2017).

Our findings regarding the House Sparrow populations in Australia and New Zealand are consistent with Bergmann's rule, but not the widely cited mechanism that cold temperatures select for large adults. Future studies should explore the mechanistic link between the climate experienced during development and the body size attained. Temperatures experienced during development could also be relevant to another ecogeographical rule, that of larger extremities relative to core size in warmer climates, as predicted by Allen's rule (Allen 1877, Symonds and Tattersall 2010). For example, a large proportion of the variation in the bill surface area (82–89%) among species





**FIGURE 3.** Variability in (A) body mass and (B) tarsus length of House Sparrow populations in relation to summer maximum temperature. Males and females are plotted separately, with males represented by blue circles and females by red circles. The 26 Australian sample sites are plotted as filled circles and the 4 New Zealand sites as open circles. There was a significant positive relationship between variability in body mass and summer maximum temperature for females, but not for males. There was also a significant positive relationship for all birds combined (Appendix Table 6). There were no significant relationships between variability in tarsus length and summer maximum temperature (Appendix Table 7).

of North American tidal salt marsh sparrows is explained by summer temperature (Greenberg et al. 2012). Possible mechanisms for determining plasticity in morphological development include physiological constraints (Gardner et al. 2009), constraints on parental provisioning (Cunningham et al. 2013), and parental effects (Mariette and Buchanan 2016). We believe that our study of the House Sparrow and recent experimental work on the Zebra Finch (Andrew et al. 2017) lead to the prediction that increasing summer temperatures at a given site will drive down the average body size of that population, consistent with the effect reported by Gardner et al. (2009). However, while our data could suggest that this decline in body size might simply be the result of developmental plasticity, our data also do not exclude the possibility that selection may contribute to a change in body size over time. For example, the effect that we describe here may be accounted for, wholly or partly, by higher reproductive success or differential survival of smaller adults in hotter locations.

Both of these possible scenarios remain to be tested in the House Sparrow. However, in a recent study of the Zebra Finch, the same pairs produced offspring of different sizes in the laboratory when breeding in cool vs. hot experimental temperatures (Andrew et al. 2017), which certainly suggests that developmental plasticity can contribute to the size differences observed across climates. Yet, even in Zebra Finches, which are highly adapted to breeding in a very hot climate (Griffith et al. 2016), the question remains regarding the extent to which size differences can be attributed to selection on the genes underlying body size and/or developmental plasticity. Our study highlights the fact that, when addressing the possible selective response of body size to a changing climate (Gardner et al. 2011), we should be considering not only selection on adults during the cold of winter, but also selection on both adults and offspring during the breeding season and the hot extremes of the summer climate.

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**APPENDIX TABLE 4.** Summary of sampled House Sparrow populations in Australia (Aus) and New Zealand (NZ) used to test the extent to which clinal variation in body size was related to winter minimum and summer maximum temperatures. Shown are sampling locations, sample sizes, and climatic variables (Summer max = mean maximum temperature of the hottest month; Winter min = mean minimum temperature of the coldest month). Sample populations are ordered from north to south within country.

Sample population	Country	Latitude	Longitude	Total birds	Number of females	Number of males	Summer max (°C)	Winter min (°C)
Tolga	Aus	−17.2145	145.4795	41	19	22	29.2	10.9
Townsville	Aus	−19.3191	146.8238	44	18	26	31.7	13.1
Tennant Ck	Aus	−19.6567	134.1924	39	12	27	37.4	11.1
Mt Isa	Aus	−20.7296	139.5025	104	49	55	37.1	8.3
Longreach	Aus	−23.4358	144.2554	43	13	30	37.3	7.0
Charleville	Aus	−26.4030	146.2511	47	22	25	34.5	3.9
Roma	Aus	−26.5617	148.7910	42	18	24	34.0	3.7
Toowoomba	Aus	−27.7218	151.6318	42	14	28	30.0	3.5
Coober Pedy	Aus	−29.0063	134.7480	18	11	7	36.3	5.9
Armidale	Aus	−30.5161	151.6735	47	21	26	26.1	0.0
Cobar	Aus	−31.4923	145.8299	42	12	30	33.5	4.6
Broken Hill	Aus	−31.9464	141.4654	43	17	26	32.4	4.1
Dubbo	Aus	−32.2214	148.6262	39	17	22	32.1	2.8
Sydney	Aus	−33.6197	150.8163	53	22	31	28.9	3.7
Wentworth	Aus	−34.1048	141.9166	25	11	14	33.1	4.4
Leeton	Aus	−34.5619	146.4154	49	20	29	32.4	3.3
Goulburn	Aus	−34.7633	149.6993	46	23	23	27.0	0.5
Adelaide	Aus	−35.2324	138.4888	30	18	12	26.5	7.5
Albury	Aus	−35.8373	146.8022	69	37	32	30.5	2.5
Melbourne	Aus	−37.7888	144.9149	43	20	23	26.2	5.5
Mt Gambier	Aus	−37.8565	140.8481	37	30	7	24.2	5.4
Geelong	Aus	−38.1783	144.3715	39	16	23	24.5	5.6
Torquay	Aus	−38.3170	144.2990	34	13	21	23.9	5.6
Wynyard	Aus	−40.9719	145.6532	44	20	24	21.2	4.6
Bridport	Aus	−41.0001	147.3875	43	22	21	23.1	4.3
Hobart	Aus	−42.9358	147.3513	45	17	28	20.9	3.3
Auckland	NZ	−36.8649	174.7757	210	72	138	24.2	6.9
Wellington	NZ	−40.6229	175.2877	257	71	186	22.9	4.9
Christchurch	NZ	−43.5318	172.6269	205	77	128	22.1	1.9
Dunedin	NZ	−45.8764	170.4957	81	22	59	18.9	1.7

**APPENDIX TABLE 5.** Relationship between latitude and summer maximum and winter minimum temperature at our sampling sites in Australia and New Zealand. Latitude had a significant negative relationship with both summer and winter temperature. The highest  $t$ -value and most significant relationship was for summer maximum temperature. However, there was no significant relationship between summer and winter temperature for our 30 sampling locations (estimate = 0.634,  $t_{28} = 1.951$ ,  $P = 0.06$ ,  $R^2 = 0.120$ ). The summer maximum temperature (of the hottest month) had a positive relationship with seasonality, which is a metric of climatic variability (estimate = 0.038,  $t_{28} = 6.505$ ,  $P < 0.001$ ,  $R^2 = 0.602$ ). There was a weaker relationship between breeding season temperature range and summer maximum temperature (estimate = 0.177,  $t_{28} = 2.631$ ,  $P = 0.01$ ,  $R^2 = 0.198$ ).

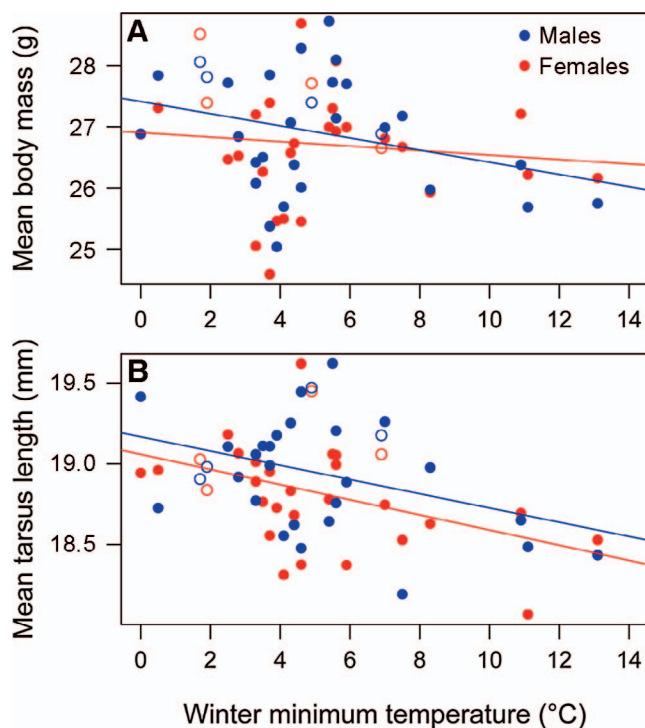
	Estimate	SE	$t$	df	$P$
Intercept	65.353	3.632	17.993	27	
Summer max	-0.956	0.132	<b>-7.221</b>	27	<b>&lt;0.001</b>
Winter min	-0.985	0.243	<b>-4.059</b>	27	<b>&lt;0.001</b>
Multiple $R^2$	Adjusted $R^2 = 0.789$ ; $R^2 = 0.773$				

**APPENDIX TABLE 6.** Results from multiple linear regression models using variability in House Sparrow body mass per population (see Appendix Table 4) in relation to temperature in Australia and New Zealand. We found a significant positive relationship between body mass variability and summer maximum temperature (Summer max) for female birds and all birds combined. The positive slope for summer maximum temperature for male birds was not significant. A positive slope shows that in warmer climates there is more variability in body mass at the population level. There was no significant effect of temperature range (Temp range) across the breeding season.

	Semipartial $r$	SE	$t$	df	$P$
Male mass variability					
Intercept	0.097	0.168	0.577	26	0.57
Summer max	0.398	0.262	1.515	26	0.14
Temp range	-0.313	0.209	-1.498	26	0.15
Mean mass	0.456	0.270	1.691	26	0.10
Multiple $R^2$	Adjusted $R^2 = 0.040$ ; $R^2 = 0.140$				
Female mass variability					
Intercept	0.009	0.146	0.064	26	0.95
Summer max	0.640	0.221	<b>2.902</b>	26	<b>0.007</b>
Temp range	-0.015	0.172	-0.086	26	0.93
Mean mass	0.305	0.236	1.296	26	0.21
Multiple $R^2$	Adjusted $R^2 = 0.200$ ; $R^2 = 0.283$				
All birds mass variability					
Intercept	0.070	0.156	0.447	26	0.66
Summer max	0.646	0.249	<b>2.594</b>	26	<b>0.02</b>
Temp range	-0.126	0.185	-0.681	26	0.50
Mean mass	0.456	0.248	1.837	26	0.08
Multiple $R^2$	Adjusted $R^2 = 0.117$ ; $R^2 = 0.209$				

**APPENDIX TABLE 7.** Results from multiple linear regression models using variability in House Sparrow tarsus length per population (see Appendix Table 4) in relation to temperature in Australia and New Zealand. There was no significant relationship in any of the 3 models between temperature and variability in tarsus length. There was a consistent, nonsignificant, positive slope for summer maximum temperature (a significant positive slope would have meant that in warmer climates there was more variability in tarsus length at a population level).

	Semipartial <i>r</i>	SE	<i>t</i>	df	<i>P</i>
Male tarsus variability					
Intercept	0.177	0.151	1.169	26	0.25
Summer max	0.020	0.166	0.123	26	0.90
Temp range	0.045	0.179	0.249	26	0.81
Mean tarsus	-0.321	0.163	-1.970	26	0.06
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = 0.069; <i>R</i> <sup>2</sup> = 0.165				
Female tarsus variability					
Intercept	-0.042	0.156	-0.270	26	0.79
Summer max	0.267	0.216	1.232	26	0.23
Temp range	0.032	0.180	0.176	26	0.86
Mean tarsus	-0.010	0.203	-0.050	26	0.96
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = 0.018; <i>R</i> <sup>2</sup> = 0.120				
All birds tarsus variability					
Intercept	0.085	0.154	0.552	26	0.59
Summer max	0.246	0.185	1.331	26	0.20
Temp range	0.054	0.179	0.299	26	0.77
Mean tarsus	-0.135	0.168	-0.800	26	0.43
Multiple <i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup> = 0.099; <i>R</i> <sup>2</sup> = 0.193				



**APPENDIX FIGURE 4.** Mean (A) body mass and (B) tarsus length of House Sparrow populations in Australia and New Zealand in relation to winter minimum temperature. The relationship between body mass and winter minimum temperature was much weaker than the relationship with summer maximum temperature (see Table 1). Similarly, the relationship between tarsus length and winter minimum temperature was weaker than the relationship with summer maximum temperature (see Table 2). No relationships with winter minimum temperature were significant in multiple linear regressions (Tables 1 and 2). Males and females are plotted separately, with males represented by blue circles and females by red circles. The 4 New Zealand populations are shown with open circles and the 26 Australian populations are plotted as filled circles.