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Australian songbird body size tracks climate variation: 82 species over 50 years

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Title: Australian songbird body size tracks climate variation: 82 species over 50 years

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41 **Abstract**

42 Observed variation in the body size responses of endotherms to climate change may be
43 explained by two hypotheses: size increases with climate variability (*The starvation*
44 *resistance hypothesis*); size shrinks as mean temperatures rise (*The heat exchange*
45 *hypothesis*). Across 82 Australian passerine species over 50 years, shrinking was associated
46 with annual mean temperature rise exceeding 0.012°C driven by rising winter temperatures
47 for arid and temperate zone species. We propose *the warming winters hypothesis* to explain
48 this response. However, where average summer temperatures exceeded 34°C, species
49 experiencing annual rise over 0.0116°C tended toward increasing size. Results suggest a
50 broad-scale physiological response to changing climate, with size trends likely reflecting the
51 relative strength of selection pressures across a climatic regime. Critically, a given amount of
52 temperature change will have varying effects on phenotype depending on the season in which
53 it occurs, masking the generality of size patterns associated with temperature change. Rather
54 than phenotypic plasticity, and assuming body size is heritable, results suggest selective loss
55 or gain of particular phenotypes could generate evolutionary change, but may be difficult to
56 detect with current warming rates.

57

58 **Introduction**

59 Animal body size is predicted to decline in response to climate warming, in line with the
60 global pattern of size variation known as Bergmann's Rule: smaller bodies tend to be
61 associated with warmer, lower latitude climates and larger bodies with cooler higher latitudes
62 [1], although the mechanisms underlying variation in body size remain contentious [2]. This
63 relationship between body size and climate has also been observed across geological
64 timeframes with reductions in body size associated with warming climates over millenia
65 [3,4]. The nature and scale of these patterns have given rise to the prediction of pervasive

reduction in body size as the climate warms [4,5]. Because body size directly affects energy and water requirements for thermoregulation, and rates of energy uptake and expenditure [6,7,8], changes in body size have implications for thermal biology and energetics with consequences for individual fitness and thus population dynamics.

Despite the prediction of declining body size, studies have reported considerable variation in climate-related size trends over the last 50-100 years. While some species have declined in size, others have increased or shown no change over time [reviews: 9-12]. Two hypotheses have been advanced to explain this variation in endotherms. The heat exchange hypothesis [sensu 13] suggests that smaller body sizes will be favoured in a gradually warming climate because smaller bodies are more efficient at dissipating heat; this explanation relates to a mechanistic link with thermoregulation, either in relation to increased capacity for heat dissipation [14] or a reduction in the need for heat conservation [15].

The starvation resistance hypothesis (also known as the fasting endurance hypothesis) suggests that unpredictable environments should favour larger-bodied individuals because larger size increases resistance to starvation via capacity to carry more body reserves [8,16]. Energy stores increase with body size faster than does metabolic rate, so resistance to starvation will increase with increasing body size [17]. In the context of climate change, [18] suggested that observed increases in climate variability may reduce the predictability of resources, with potential to increase starvation risk, hence selecting for increasing body size with improved capacity to endure extreme events.

A special case of the starvation resistance hypothesis relates to the increase in frequency of heatwaves that is associated with a warming climate [19]; more frequent and extreme heatwaves are an important signature of current climatic variability [20]. Smaller individuals

exposed to heatwaves use disproportionately more energy and water to dissipate heat than larger individuals (due to their greater surface area to volume ratio), while having proportionately fewer reserves available [21,22]. Larger-bodied individuals are expected to be favoured in such events, particularly when environmental temperatures exceed body temperature and the only avenue for dissipating heat is via evaporative cooling [22, 23]. This hypothesis implies climate-related hard selection via size-dependent mortality; smaller individuals will be selected against in heatwaves leading to a mean increase in the body size of populations over time. When ambient temperatures regularly exceed body temperature, smaller body size ceases to be an advantage but becomes a liability.

Here, we test these hypotheses using a large dataset of body size measurements of 82 species of Australian birds from the Infraorder Meliphagides [*sensu* 24], formerly Meliphagoidea, a large and diverse radiation of Australasian passerines that include the honeyeaters, fairy-wrens, pardalotes, thornbills and allies [25] (Table S1). We characterised changes in body size for each species over the last ca 50 years (1958-2010), during a period of rapid climate change, using 12,029 museum specimens sampled from multiple populations across the distribution of each species (Fig. S1). We then calculated the change in annual mean temperature, annual mean monthly rainfall and annual mean maximum summer temperature in each species' distribution over the same 50-year period. We predicted that (1) body size will tend to decrease over time more in species that have experienced larger increases in mean ambient temperature over time (the heat exchange hypothesis); (2) body size will tend to increase over time in environments with higher summer maximum temperatures that regularly exceed body temperature (the starvation risk hypothesis).

Methods

Study Species

Our study focused on species from the Infraorder Meliphagides [*sensu* 24], formerly superfamily Meliphagoidea), the largest radiation of Australasian passerines, consisting of five families and some 276 species of which 145 are Australian; they comprise almost one third of Australia's passerines [25]. The group comprising honeyeaters, fairy-wrens, pardalotes, thornbills and allies, displays great diversity in life history, ecology and morphology, spanning a wide range of body sizes (6-260 g) and climatic regions (from desert to tropics), and together with their well-resolved phylogeny [25,26], they are an ideal group for investigating responses to environmental change.

Museum specimens

Specimens examined from the major museums in Australia were collected between 1960 and 2010 (Table S1). Specimen localities spanned about 35° of latitude (10 to 45° S). We sampled multiple populations across each species' range in Australia, including Tasmania (Fig. S1) in order to minimise effects of local factors that can affect body size, such as predation pressure and intraspecific competition. We aimed to quantify species-level responses to broad environmental change, testing overarching hypotheses for causes. For each species, we examined between 20 and 702 specimens (mean 146) (Table S1). We included 11 species with <50 individuals because, although sample sizes are small, these species are relatively well sampled for their small ranges (Table S1). Eight of the 11 species with the smallest sample sizes also have some of the smallest ranges, and so are relatively well-sampled (Table S1). The remaining 3 species (pied honeyeater, *Certhionyx variegatus*, black honeyeater *Sugomel niger*, striped honeyeater, *Plectorhyncha lanceolata*) occur in relatively large ranges. However, these species are nomadic and/or irruptive following good conditions so their core range/distribution is smaller than the range maps would indicate (Fig. S1). All

occur in the more extreme (and remote) arid environments which are difficult to sample but represent important species in the context of the questions we address.

Body size measurement

We measured the length of the flattened wing chord from the carpal joint to the tip of the longest primary, recording to 0.5mm using a butt-ended ruler, as a measure of structural body size. Each species was measured by a single observer. Among passerines, wing length is the best linear predictor of body mass, and accordingly may be used as an index of body size [27]. Some authors have used tarsus or culmen length as indices of body size because these traits are less variable across an individual's life. However, both are subject to Allen's Rule, which predicts a decrease in such traits with increasing latitude, opposite to Bergmann's Rule [28]. This is because in warmer climates appendages of endotherms that play a role in thermoregulation as a source of heat loss will be larger to allow for dissipation of heat loads [29]. Thus, as temperatures rise, increases in bill and tarsus length are predicted and have been demonstrated in several bird species [29, 30]. From the associated metadata we recorded the sex, year of collection and location (latitude, longitude) at which each specimen was collected. We estimated two additional parameters using Geographic Information Systems: altitude, estimated from the latitude and longitude from each specimen, and nearest direct line (orthodromic) distance to the coastline. 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 their position relative to the coast. We assigned an abrasion score of 1-12 based on month of capture, with 1 = new feathers assigned to birds captured in March and 12 = old, abraded feathers for captures in February. This is based on our knowledge of moult in Australian birds - most species moult Dec-March after breeding.

Data sets

(a) Body size

We measured 12,667 individuals of 93 species from the Infraorder Meliphagides [*sensu* 24], formerly superfamily Meliphagoidea) (Table S1). We excluded known juveniles and immatures based on skull ossification recorded during specimen preparation and available from the associated metadata, individuals for which there was no month of capture because abrasion score could not be estimated and 545 individuals for which no sex was recorded from gonads and the sexes were not dichromatic.

(b) Climate data

We extracted climate data for the distribution of each species. These data were generated using the ANUClimate 1.0 spatial model [31]. This model produces monthly Australian climate variables for the period January 1970 to December 2013 on a 0.01° longitude/latitude grid interpolated from Australian Bureau of Meteorology national point climate data. We collated monthly estimates of rain, minimum temperature and maximum temperature for the years 1970 to 2012 (one raster for each month x year x climate variable combination). We then extracted summary values for each raster from within each species range (we converted the species range to a raster and used this as a mask for zonal statistics on the climate rasters). These summary values were then tabulated to a .csv file for each species.

(c) Climate variables

We created climate variables as follows. Change in annual mean temperature: we calculated the mean temperature for each year for each species, based on mean temperature for each month, extracted for all cells in the distribution of each species. We then fitted annual mean temperature as a response variable and year as an explanatory variable fitting models for each

species separately to extract the rate of change over time (year estimate), for use in subsequent models. Models were fitted using the “lm” function in R. Mean monthly rainfall was calculated by averaging mean rainfall for each month. Mean summer maximum temperature was calculated by averaging mean maximum temperature for the hotter months in each year, December, January, February. For our post-hoc analysis we calculated the change in mean minimum winter temperature and change in mean maximum summer temperature using the same procedure as described above for estimating change in mean temperature. We defined winter as the months June, July, August and summer as December, January, February.

(d) *Climate zones*

We calculated the proportion of each species’ distribution that occurs in equatorial, arid or temperate climate zones using the Köppen-Geiger climate classification (K-G GIS layer, [32]). We classified species as arid/temperate if >70% of their distribution fell within arid or temperate or arid and temperate zones; tropical species were those with >70% of their distribution in the equatorial zone. Species that were widespread, occurring in both tropical and arid/temperate zones were excluded from our post-hoc analysis.

Statistical Analyses

The analysis of the data was done in several steps. First, we estimated temporal change in body size for each species. Then we used these species-specific rates of size change to test for associations between changing climate and body size.

(a) *Patterns of year-to-year variation*

We used generalized additive models to describe patterns of year-to-year variation in body

size, using separate models for each species. The response variable was the wing length of each specimen and the explanatory variables were the year of collection (with a smooth function), latitude, altitude, distance to the coastline, abrasion score and sex of each specimen. All the explanatory variables but the year of collection were centred before the analysis. The models were fitted using the ‘mgcv’ package [33] in R version 2.15.2 [34]. We assumed a normal distribution and identity link function and estimated the degree of smoothness of the year function using the Generalized Cross Validation with $\gamma = 1.4$ to avoid overfitting [33]. To avoid multicollinearity among the explanatory variables, we first estimated pair-wise Pearson’s correlation coefficients between the explanatory variables (Table S2) and confirmed that correlations were not high for any of the combinations ($|r| < 0.65$).

To account for model selection uncertainty, we adopted a multi-model inference approach based on AIC (Akaike Information Criterion) [35]. For each species, we first generated a candidate set of models with all possible parameter subsets, which were then fitted to the data and ranked by ΔAIC values (the difference between each model’s AIC and $\text{AIC}_{\min}$, the value of the “best” model). Models with $\Delta\text{AIC} < 2$ are usually considered to have substantial support [35]. We considered species to show important inter-annual variation in body size if they have a smoothed year term in, at least, one of the models with $\Delta\text{AIC} < 2$ (Fig S2). For the visual inspection of the estimated smoothed function, we used the result based on the model with the smallest AIC that included the smoothed year term.

(b) Rates of temporal size change

For species showing linear or near linear change in body size across time (effective degrees of freedom < 3 in the full model; edf shows the flexibility of the smoothed function) we

calculated the annual rate of size change. After removing 11 species with $\text{edf} > 3$, the final data set contained 82 species (Table S1). We fitted separate linear regression models for each species with body size (wing length) as the response variable and year as the explanatory variable, while controlling for sex, age, altitude, latitude and distance to coast when identified in the generalized additive models as important. Residual plots and normal probability plots were used to check for deviations from normality among residuals. All models were fitted using the `lm` function in R.

(c) *Comparative analysis*

We used Phylogenetic Generalised Least Squares (PGLS) to test for associations between climate and changes in body size over the last 50 years for 82 species of Meliphagides. This approach controls for the phylogenetic relatedness between species by applying a phylogenetic variance-covariance matrix to the linear regression [36]. The analysis was implemented through the R package, *caper* [37]. The phylogeny employed was taken from the maximum likelihood tree produced for the Meliphagides [25], with the tree made ultrametric using the `chronoPL` function in the *ape* package [38]. To account for model selection uncertainty, we adopted a multi-model inference approach based on AIC (Akaike Information Criterion) as described above.

We used the slope of the relationship between body size and year for each species (estimated as described above in ‘Rates of temporal size change’) as the response variable and fitted the climate variables (change in mean temperature, mean monthly rainfall, and mean summer maximum temperature, and 2 two-way interactions - change in mean temperature : mean summer maximum temperature, and change in mean temperature : mean monthly rainfall) as explanatory variables, controlling for phylogenetic relatedness. All variables were z -

standardised prior to analysis. Because the response variable comprised single point estimates of the relationship between body size and year without acknowledging the error in those estimates, we also conducted a second analysis where the response variable was a random value taken from the normal distribution with mean equal to the observed estimate, and standard deviation equal to the standard error around that estimate. The final model estimates here were the mean of the estimates derived from 1000 simulations.

(d) *Post-hoc analyses*

To test whether the declines in body size we observed (see results) were associated with rates of warming in winter versus summer, we undertook the following post-hoc analysis. We used the slope of the relationship between body size and year as the response variable and fitted climate variables (change in winter temperature, change in summer temperature, mean summer maximum temperature, mean winter minimum temperature) and two interactions (between mean winter temperature and mean change in winter temperature; and between mean summer temp and mean change in summer) as explanatory variables. We included only arid and temperate species, and controlled for phylogenetic relatedness as in the main analysis. As above, we also repeated the analyses using repeat simulations of the response variable. There were only 8 tropical species in our dataset, too few to detect an effect.

Results and Discussion

Annual mean temperature has increased over the last 50 years in 81 of the 82 species' distributions we considered (Fig. 1). In contrast, patterns of mean rainfall showed considerable variation across distributions with some showing increases in mean rainfall and others declines or no change (Fig. 1).

Change in mean temperature, rather than summer temperature or rainfall, showed the strongest association with estimates of body size changes across species, and was the only climate variable included in all top models (Table 1). Similar estimates to those in Table 1 were derived from 1000 model simulations where errors in the estimates of body size change were taken into account, providing strong support for this result (Table S3). Declines in body size start to be observed in cases where the rate of mean temperature change within a species' distribution exceeded 0.012°C per year (1.2°C per 100 years), consistent with the heat exchange hypothesis (Fig. 2). Given the diversity of species and habitats included in our analyses, the identification of a rate of temperature change beyond which declines in body size were observed suggests a broad-scale physiological response to changing climate.

Although there was no association between body size and mean maximum temperature *per se*, a shift in the extent and direction of size change was observed for species experiencing both high levels of warming and high summer temperatures (Table 1). Fig. 2b indicates that above about 34°C , no decreases in body size are predicted, regardless of amount of temperature change experienced (all of the model predictions > 0), and for species experiencing greater than 0.0116°C (the point at which the regression lines intersect in Fig 2c), body size may even increase in warmer climates (interaction $T_{\text{max}} \times T_{\text{mean}}$; Fig. 2; Table 1, Table S3). Increasing body size to increase body reserves as climate variability increases is consistent with the starvation resistance hypothesis in the context of heatwaves. Our result is unlikely to be an artefact of sampling because the species included in the analysis covered the entire range of these two variables: 67% of species (55/82 species) experienced $>0.0116^{\circ}\text{C}$ per year change, with 38 species experiencing mean maximum summer temperatures below 34°C and 17 species exceeding 34°C (Fig. 2). When environmental temperatures exceed body temperature (ca. 40°C) the only avenue for birds to

dissipate body heat is via evaporative cooling, with small bodied individuals particularly vulnerable to dehydration and mortality because of their disproportionately large surface areas [21,22]. Smaller individuals thus face twin costs under heatwave conditions: lower energy and water reserves, and disproportionately high rates of water loss. Accordingly, the benefit of smaller body size is plausibly outweighed by the costs of exposure to extreme temperatures during heatwaves.

Recent work by [39] examined evaporative cooling capacity and heat tolerance in 5 passerine species in Australia's arid zone, including two of the species in this study (yellow-plumed and spiny-cheeked honeyeaters). They confirmed the reliance of these species on evaporative heat loss via panting at high air temperatures, consistent with studies of other Australian passerines. When air temperatures exceeded 38°C rates of evaporative water loss (EWL) increased rapidly and linearly to 7-fold (670-860%) above basal rates [39]. Moreover, rates of EWL scaled negatively with body mass with smaller-bodied individuals more vulnerable to dehydration, consistent with our result. This work accords with recent studies showing that a body temperature of 45°C is the upper limit to physiological function in most birds [39]. In contrast, increase in metabolic rate associated with the onset of panting varied considerably among species, suggesting that dehydration rather than energy balance represents the greatest threat to species in heatwaves [23]. Thus, although our results are consistent with the starvation risk hypothesis, they also suggest the significance of maximizing resistance to dehydration in the face of increasing heatwaves.

Empirical studies of wild populations identify air temperatures in the mid-30s as potentially harmful, with individuals unable to maintain body condition following prolonged exposure to such temperatures, sometimes leading to size-dependent mortality [40,41]. In a population of

Australian white-plumed honeyeaters, *Ptilotula penicillata*, repeated exposure to daily maxima $>35^{\circ}\text{C}$ in a semi-arid region was associated with increases in mean body size over a time scale of decades, apparently via the loss of small individuals from the population [42]. This effect appeared to be mediated by size-dependent effects of weather on body condition; smaller individuals lost more mass when exposed to high temperatures and were less likely to survive to the following spring [41]. Our observed mean summer temperature threshold of about 34°C , at which no decrease in body size is predicted, is remarkably consistent with empirical studies that identify prolonged exposure to air temperatures $>35^{\circ}\text{C}$ as harmful, and is also consistent with hard selection because the observed change in avian body size aligns with known physiological tolerances associated with fitness [21,22, 23].

Although recent attention has mainly focused on spring and summer temperatures in mediating size changes under global warming, declining body size may also be associated with reduced selection pressures on small individuals experiencing warmer autumns and winters, leading to their higher survival. Winter is considered a challenging time, and can cause direct mortality via cold stress, reductions in immune function, or energetic constraints as a result of resource shortages [43,44]. Indeed, energetic costs of thermoregulation in winter during periods of low food availability can exceed those during the breeding season [43]. Moreover, winter mortality is often observed to be size-dependent with the smallest individuals suffering higher mortality, contributing in part to the widely accepted rule for positive viability selection on body size [45]. Accordingly, reduced selection pressures associated with warming winters may increase the survival of smaller individuals leading to an incremental decrease in mean body size over time; hence we propose “the warming winters hypothesis”. Because animals are acclimatized to local conditions and winter represents the harshest conditions in temperate environments, a release from selection

pressures associated with a given level of temperature rise (here 1.2°C/100 years) is likely to have similar effects across all populations, in this case favouring smaller individuals, regardless of the severity of winter conditions experienced.

By comparison, the decrease in body size we observed across species is less likely to relate to warming summers because the same rate of warming will have different effects on body size depending on the thermal tolerances of individual species and the summer conditions each experiences [7,21]. Only if rising temperatures push individuals beyond the upper bound of the thermoneutral zone (TNZ) - the range of air temperatures where no additional energy and water are specifically allocated to maintain homeostasis - will the adaptive significance of body size change. Because the location of the TNZ varies among species due to differences in body size and shape [7, 23] and phylogeny [46], a given degree of temperature change is likely to affect species differently. Indeed, our post-hoc analysis found that declining body size was associated with increasing winter, but not summer, temperatures for arid and temperate species in line with our warming winters hypothesis (Table 2, Table S4).

Analysis of long-term data sets of wild populations provide some of the strongest evidence that temporal declines in body size may be associated with a release from winter stress. In Soay sheep, *Ovis aries*, warmer winters have led to higher survival of smaller individuals, leading, in part, to a decline in body size over the last 30 years [47]. A similar pattern was observed in a much milder climate in Western Australia where winters do not generally involve sub-zero temperatures. Warmer winter conditions were associated with higher survival of smaller individuals in two small passerine species monitored over 39 years [48]. Although most evidence suggests that shifts in body size are climate related, density-dependent effects (e.g. competition for food) are also likely to be important and drive

complex size patterns. However, such effects are likely to be site specific so unlikely to account for the broad scale patterns observed.

In contrast to species in temperate climates, relaxation in selection pressure is unlikely to account for temporal declines in endotherm body size in the tropics which experience low seasonality and limited temperature range. As temperatures rise, selection pressures in the tropics are more likely associated with increasing costs of keeping cool, favouring smaller body sizes with increased capacity for heat dissipation. James [14] argued that selection for smaller body size is particularly strong in the tropics because high temperatures coincide with high humidity which reduces the gradient driving evaporation, thereby limiting heat loss. Smaller bodies with relatively larger surface areas are therefore advantageous [49]. In addition, the capacity for acclimatization is likely limited for tropical species because they experience narrow daily and seasonal temperature range [50], so a given increase in temperature is likely to impose greater costs on tropical compared with temperate species. Thus, although a warming climate might favour smaller body sizes in both the tropics and temperate regions, the underlying mechanisms may differ. Our dataset included only 8 tropical species, and so lacked the necessary power to test for an effect.

Overall, our study suggests that avian body size is indeed responsive to climate change [contra 12,51], and that climate-driven changes in body size are both temperature-related and founded in a physiological response to changing conditions. Temperature-related effects may account for global patterns of changing body size in the absence of extreme events, (both summer and winter), and regardless of rainfall patterns which have previously been suggested as important in driving selection [52] even though water availability differs between northern and southern hemispheres [53] and rainfall patterns are highly variable at regional scales

[54]. We found no evidence that rainfall directly underlies body size trends at the species level; rainfall and its interaction with mean temperature were included in the top model, but their effects were weak (Table 1). Nevertheless, rainfall can mediate responses to temperature, in both hot and cold conditions, as well as affect foraging behavior and food availability [55,56]. Rainfall is therefore likely to be integrally linked with climate-driven changes in physiology at the level of populations.

More broadly, the suggestion that changes in food availability driven by climate-related changes in primary production underlie observed temporal trends in body size across species [12, 52] seems unlikely on the basis of our results. With the exception of the relatively small alpine zone, primary productivity on the Australian continent is regulated and constrained by rainfall and plant water availability rather than temperature *per se* [54], and climate change impacts on rainfall regimes are varying greatly at regional scales [57]. Accordingly, body size trends we observed across species that inhabit different climatic zones and regions are unlikely to be associated primarily with rainfall-related variation in primary productivity. To further address this issue, we re-ran our main model replacing mean monthly rainfall with change in rainfall (estimated using the same method as for change in mean temperature). Models with rainfall change were a poorer fit to the data compared with the equivalent models using mean rainfall (best model with rainfall change included AIC: 235.0 versus 231.7 for best model with mean rainfall), and the top model did not include rainfall change, (and was the same as model 3 in Table 2), supporting our conclusion. Moreover, in the northern hemisphere, primary production is associated primarily with temperature not rainfall [58], so it seems unlikely that changing primary production underlies global trends in body size if the drivers of productivity differ between hemispheres.

Our findings have important implications. We provide strong evidence for changes in body size as a response to climate change, with multiple mechanisms likely to underlie species' responses. Temporal trends in body size are likely to reflect the relative strength of selection pressures at different times of the year and different phases of a climatic regime, including release from winter conditions as well as increased pressure from summer extremes [e.g. 59]. To date, most studies have focused on the negative consequences of extreme events but our results also highlight the potential importance of relaxation in winter conditions. Given the importance of temperature extremes in this context, birds might indeed be considered the 'canaries in the coalmine' because they are likely to be more responsive to changing climate than are mammals, being diurnal, with small body sizes, and limited in their capacity to store body reserves because of the demands of flight. This may explain, in part, the finding that mammals are less likely to show temporal size change than birds [12].

When analyzing size trends, studies should consider the rate of temperature change experienced, given that our results suggest that declines in body size are triggered only when increasing mean temperature exceeds 0.012°C per year. Studies that include climate variables as predictors often fit static measures, omitting rates of change, and critically ignore the season (window) in which the temperature change has occurred. A recent study by [60] concluded that there was no evidence that warmer mean temperatures are associated with selection for smaller body size. However, our results suggest that a given amount of (mean) temperature change will result in differing effects on phenotype depending on the season in which the temperature change occurs. For example, a given mean temperature change that occurs in winter might be associated with declining size, but not when it occurs in spring. Similarly, selection on body size associated with rising summer temperatures will only be detectable in species where the given increase in mean temperature occurs in summer, and

pushes the species beyond its TNZ thereby changing the selection pressure. Attempts to find associations between selection gradients for size and mean temperature change are therefore unlikely to succeed. This is especially the case where selection gradients are derived from differing, often short, timeframes [60], making it even more difficult to detect patterns.

We agree with [12] that more data are needed on how climatic factors shape selection pressures and the adaptive nature of temporal size trends in relation to climate change. Nevertheless, although most evidence to date suggests that shifts in body size are the result of phenotypic plasticity, our results raise the possibility that change in the composition of a population via the selective appearance or disappearance of particular phenotypes could generate evolutionary change, assuming body size is heritable [61]. However, detecting such shifts may be difficult if rising temperatures are only now reaching levels at which changes in selection pressures may occur, and the translation from effects on individuals to population-level changes in mean body size are likely to be incremental. This may account for difficulty thus far in detecting microevolutionary responses to climate change [62].

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Figure Legends

Fig. 1. Temporal trends in (a) body size (wing length) and (b) mean annual temperature and (c) mean summer maximum temperature and (d) mean monthly rainfall across 50 years (1970 – 2010) for 82 species of passerine bird in the Meliphagides. Each line represents a single species, and the order of species is the same in each panel. We calculated mean temperature, mean summer maximum temperature and mean monthly rainfall for each year for each species, based on values for each month, extracted for all cells in the distribution of each species. Solid green dots represent significant change in body size; green circles indicate trends.

Fig. 2. Association between the change in structural body size (wing length) and change in mean annual temperature, given mean maximum summer temperature for 82 species of passerine bird from Meliphagides [*sensu* 24], formerly superfamily Meliphagoidea). (a) 3D-representation of the phylogenetic generalised least squares model predicted relationship; (b) 2D-representation showing species data points, PGLS regression lines for the relationship between change in body size and mean summer maximum temperature showing species that experience different degrees of temperature change with PGLS model regression lines for 0, 0.004, 0.008, 0.012, 0.013, 0.014, 0.015 and 0.016 °C increase in mean temperature; (c) similar representation of relationship between change in body size and change in mean annual temperature showing species that experience different mean summer temperatures: model lines represent relationship at 18, 23, 28, 33 and 38 °C (colours as represented in legend).

Table 1. Top phylogenetic generalized least squares models ($\Delta AIC < 2$) predicting body size changes over time in 82 species of Meliphagides. Predictors are ΔT_{mean} : mean temperature change ($^{\circ}\text{C}$ / year), T_{max} : mean summer maximum temperature ($^{\circ}\text{C}$), Rain: mean monthly rainfall (mm), and all interaction terms. Response variable is the regression slope estimate of body size over time for the species. All variables were standardised and model estimates (with standard errors) are shown for each model (larger estimates are therefore larger effects). W_i = Akaike weight of the model. Parameter estimates in the models that were statistically significant (at $\alpha = 0.05$) are indicated in bold.

Model	ΔT_{mean}	T_{max}	Rain	$\Delta T_{\text{mean}}:T_{\text{max}}$	$\Delta T_{\text{mean}}:\text{Rain}$	R^2	ΔAIC	w_i
1	-0.904 (0.248)	-0.133 (0.154)	-0.338 (0.180)	0.548 (0.211)	0.317 (0.182)	0.149	0	0.254
3	-0.682 (0.217)	-0.229 (0.144)	-0.361 (0.181)	0.403 (0.198)		0.114	0.879	0.164
4	-0.169 (0.110)					0.029	1.729	0.107

Table 2. Top phylogenetic generalized least squares models ($\Delta AIC < 2$) predicting body size changes over time for 64 temperate and arid zone species of Meliphagides. Predictors are mean minimum winter temperature (T_{winter}), mean summer maximum temperature (T_{summer}), and the mean change over time ($^{\circ}\text{C} / \text{year}$) for both measures (ΔT_{winter} and ΔT_{summer} , for winter and summer temperatures respectively). Response variable is the regression slope estimate of body size over time for the species. All variables were standardized and model estimates (with standard errors) are shown for each model (larger estimates are therefore larger effects). W_i = Akaike weight of the model. All parameter estimates in the models that were statistically significant (at $\alpha = 0.05$) and are indicated in bold.

Model	T_{winter}	T_{summer}	ΔT_{winter}	ΔT_{summer}	R^2	ΔAIC	w_i
1	1.354 (0.535)	-1.803 (0.547)	-0.978 (0.340)	0.510 (0.292)	0.349	0	0.187
2	0.837 (0.469)	-1.294 (0.492)	-0.592 (0.277)		0.257	0.493	0.146
3					0	0.573	0.140
4		-0.540 (0.298)	-0.610 (0.298)		0.136	0.963	0.116
5			-0.178 (0.186)		0.032	1.911	0.072



