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Spatial variation in avian bill size is associated with temperature extremes in a major radiation of Australian passerines

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Abstract

Morphology is integral to body temperature regulation. Recent advances in understanding of thermal physiology suggest a role of the avian bill in thermoregulation. To explore the adaptive significance of bill size for thermoregulation we characterized relationships between bill size and climate extremes. Most previous studies have focussed on climate means, ignoring extremes, and do not reflect thermoregulatory costs experienced over shorter time scales. Using 79 species (9847 museum specimens), we explore how bill size variation is associated with temperature extremes in a large and diverse radiation of Australasian birds, Meliphagides. Overall, across the continent, bill size variation was associated with both climate extremes and means and was most strongly associated with winter temperatures. However, associations at the level of climate zones differed from continent-wide associations, were complex and non-linear, yet consistent with physiology and a thermoregulatory role for avian bills. We provide strong evidence that climate extremes have contributed to the evolution of bill morphology in relation to thermoregulation, and demonstrate the importance of including extremes to understand fine scale trait variation across space. Increasing frequency and intensity of climate extremes, a signature of climate change, may lead to changes in bill size, but this is yet to be tested.

Keywords: bill size; climate extremes; Meliphagides; thermoregulation

Introduction

Morphological traits are integral in regulating animal body temperature and for the maintenance of homeostasis, so greater understanding of climate-related changes in traits may provide insights into adaptation to climate change. Bill size and shape in birds has conventionally been considered in relation to diet and foraging strategies (Benkman 1993; Grant and Grant 2006; Gómez-Blanco et al. 2019) but recent advances in our understanding of thermal physiology suggest an additional role in thermoregulation (Tattersall et al. 2009; van de Ven et al. 2016; Tattersall et al. 2017; Tattersall et al. 2018; Janse van Vuuren et al. 2020). Bills are not inert structures but part of a larger network of cranial vasculature (Tattersall et al. 2017). In hot conditions, birds can increase blood flow to the highly vascularized and uninsulated bill to increase heat loss (Tattersall et al. 2017). Conversely, at low temperatures heat loss via the bill surface is regulated through vasoconstriction (Hagan and Heath 1980). The larger the bill the greater the heat exchange; so larger bills may be advantageous in hot conditions but can become a liability at low temperatures (Greenberg et al. 2012). In this context, bill morphology has direct significance for thermoregulatory function. This in turn may have contributed to the evolution of bill size and shape and may have implications for adaptation to climate change.

Like all endotherms, birds maintain their body temperature within a narrow thermal range (McNab 2001; McKechnie et al. 2017). Excess metabolic heat is dissipated via evaporative (both cutaneous and respiratory), radiative, convective or conductive mechanisms to maintain body temperature within safe limits (Whittow 1986; Cunningham et al. 2021). Recent studies have confirmed that a significant portion of body heat is released from the bill surface via radiation at high environmental temperatures, thereby reducing the need for evaporative cooling (Tattersall et al. 2009; van de Ven et al. 2016; Gómez-Blanco et al. 2019). In song sparrows, for example, nearly 10% of metabolic heat production can be released from the bill which accounts for only 2% of total body surface area (Greenberg et al. 2012). Toco toucans (*Ramphastos toco*) can release up to 60% of total body heat through the bill (Tattersall et al. 2009). In cold conditions, vasoconstriction can act to significantly limit heat loss from bills; in white Pekin ducks (*Anas platyrhynchos*), between 85 – 117% of total metabolic heat is released from vasodilated bill at 0°C, whereas only 18-25% is lost from a vasoconstricted bill (Hagan and Heath 1980).

Observed geographical patterns of bill size are mostly consistent with Allen's Rule (Allen 1877) - that the relative size of appendages (mammalian limbs and ears, avian bills and tarsi) change with latitude reflecting responses to variation in local climate (Ryding et al. 2021). Larger appendages, for a given body size, are typical of individuals in lower latitudes where climates are warmer, while smaller appendages are more likely to occur in the colder climates of higher latitudes, helping to conserve body heat by minimizing heat loss (Allen 1877; Wathen et al. 1971). A similar pattern is also observed across altitudinal gradients, with larger appendages at lower elevations typified by comparatively warmer environments (Laiolo and Rolando 2001; Bears et al. 2008). A study of 214 bird species across several continents showed a significant positive association between bill size and mean annual temperature, with larger bills found in warmer climates (Symonds and Tattersall 2010). The bill sizes of ten subspecies of tidal marsh sparrows in California, starlings (*Sturnus vulgaris*) and several species of parrots in Australia, were larger in environments with higher mean maximum summer temperature (Greenberg et al. 2012; Campbell-Tennant et al. 2015; Cardilini et al. 2016). This suggests that bill size patterns may have evolved to improve heat dissipation in warm periods of the year, rather than to conserve heat during cold periods. However, bill sizes of song sparrows (*Melospiza melodia*) in eastern North America, multiple

species of Meliphagides in Australia and Oriental magpies (*Pica serica*) in Mainland China showed significant associations with winter temperatures revealing that Allen's Rule patterns may be driven by cold winter temperatures (Danner and Greenberg 2015; Friedman et al. 2017; Fan et al. 2019). Thus, those aspects of temperature which underlie geographic patterns in bill size can vary.

There are limits to the effectiveness of any thermoregulatory strategy when climate extremes reach or exceed physiological thresholds, resulting in sub-lethal costs and even mortality. Most previous studies of the relationship between bill size and climate have focused on mean annual or seasonal temperatures, ignoring temperature extremes and interacting effects of other climate variables. Mean values for temperature do not reflect thermoregulatory costs that may be experienced by an individual over a shorter time scale as a result of exposure to temperature extremes. For example, a mean maximum summer temperature of 30°C may be characterized by daily maxima between 28°C and 32°C or maxima as low as 25°C and as high as 40°C or above. Thermoregulatory costs in these two instances will differ. When environmental temperatures exceed body temperature (~40°C), the bill will absorb heat from the environment rather than dissipate it and thus large bills may be maladaptive in climates where summer temperatures regularly exceed body temperature (Dawson 1982). For example, although relative bill size in song sparrows increased monotonically with ambient temperature across their range, bill size decreased in size in parts of their range where average summer temperatures exceeded body temperature, above about 36°C (Greenberg and Danner 2012). Thus, we predict non-linear responses to increasing exposure to high temperature extremes if heat exchange strongly underlies bill size variation across space.

Temperature will also interact with other climate variables to influence thermoregulatory costs. Humidity has a strong influence on evaporative heat loss: in conditions of high humidity the efficiency of evaporative cooling is substantially reduced (Gerson et al. 2014), favouring radiative and convective heat loss via the bill. In sociable weavers *Philetairus socius*, for example, high humidity inhibited rates of evaporative water loss by up to 36% at 48°C (Gerson et al. 2014). Accordingly, larger bills may be a particularly important adaptation in humid environments, because the efficiency of radiative heat loss is unaffected by humidity (Greenberg et al. 2012). Aridity may also increase the cost of evaporative cooling, as its prolonged use may lead to lethal dehydration if body water pools are not replenished via drinking or from dietary sources (Dawson 1982). Larger bills may also therefore be favoured in hot, arid environments where water availability is limited in summer, thereby improving water conservation (Greenberg and Danner 2012). At the cold end of the temperature scale, feathers that insulate from extremes of cold may become less effective in wet environments where rainfall is high as the thermal resistance of wet plumage is compromised (Lustick and Adams 1977, Webb & King 1984), potentially favouring smaller bills that reduce heat loss. This increase in thermoregulatory costs will be additive, leading to disproportionately small bills, not a reversal in bill size as is predicted for extreme heat.

To identify the significance of thermoregulatory mechanisms as drivers of bill size variation, we thus argue that it is necessary to clarify associations between bill size and climate extremes associated with physiological performance and fitness. A recent study highlighted the importance of temperature extremes in survival patterns for two bird communities based on over 37 years of monitoring in semi-arid Australia. The study showed that survival probability declined strongly with increasing exposure to days with thermal maxima >38°C or minima <0°C (Gardner et al. 2022). Thus, we expect strong selection on bill size in its role for thermal physiology.

Here, we explore how bill size variation is associated with temperature extremes and how interactions among climate variables influence bill size patterns in a large and diverse radiation of Australasian birds, the Meliphagides. We first describe geographical patterns of bill size in multiple species at a continental scale, then investigate whether spatial patterns are likely to be shaped by the role of the bill in thermoregulation by studying bill size associations with high and low temperature extremes. We used morphological data from 9847 individual museum specimens of 79 species, sampled across the entire geographic ranges of each species, along with the location-specific geographic and climate data to test the following predictions:

1. Relative bill size will decline with increasing exposure to cold extremes to facilitate heat retention.

2. Relative bill size will vary non-linearly with hot extremes, specifically:

Larger bills will be associated with an increase in the frequency of hot extremes. However, in climates where environmental temperature regularly exceeds body temperature, selection pressure acting on bill size will be reversed, favouring smaller bills to reduce heat gain from the environment. Hence, we predict a non-linear response to extreme high temperatures.

3. The effects of extreme temperatures will vary with humidity and rainfall, specifically:

(a) Smaller bills will be found in cold environments with high winter rainfall to compensate for additional heat loss due to reduced thermal resistance of wet plumage.

(b) Larger bills will be found in hot environments with higher humidity to compensate for the reduced effectiveness of evaporative cooling, and also in hot environments with lower rainfall to mitigate the effects of water loss associated with evaporative cooling. These effects will be greatest where ambient temperature does not regularly exceed body temperature.

Methods

Study system

We used 79 species from the infraorder Meliphagides, the largest radiation of Australian passerines (formerly Meliphagoidea), to assess bill size patterns across geographic space and to test for associations between bill size and climate across the Australian continent (Table S1). The clade shows a diversity of habits and dietary types, with the majority of species in this study being nectarivores and insectivores (see supplementary material for details). In addition to their diversity, the species-level phylogeny for the Meliphagides radiation is well-resolved (Marki et al. 2017).

Data collection

Bird data

We measured bill dimensions (length, width and depth) of 9847 specimens of Meliphagides collected between 1956 and 2015 (see supplementary material). Bill length was measured from the feathering at base of the upper mandible to the bill tip (Subasinghe et al. 2021). Bill width was measured from the posterior edge of the nares on one side of the bill to the same

on the other side and bill depth from the posterior edge of the nares (Gardner et al. 2016). From these three measurements we estimated bill surface area using the formula for lateral surface area of a cone (Greenberg et al. 2012; see Subasinghe et al. 2021 for details).

We compiled measurements for the flattened wing chord from the carpal joint to the tip of the longest primary feather, and associated metadata (sex, capture date and capture location [latitude, longitude]) for each specimen from Gardner et al. (2019). We collated feeding guild information from the literature, classifying species based on their primary source of food (nectarivore or insectivore). We defined the climate zone from each individual's capture location, as tropical, temperate or arid using the Koppen-Geiger climate classification (Köppen 1936, Hijmans et al. 2005, Kriticos et al. 2012) (Fig. S1).

Climate data

We extracted location-specific climate data for the 72 months prior to the capture date of each bird following Gardner et al. (2016), at a resolution of 5 km² from the Australian Bureau of Meteorology's daily gridded spatial climate data sets (<http://www.bom.gov.au/climate/austmaps/metadata-daily-temperature.shtml>; <http://www.bom.gov.au/climate/austmaps/metadata-daily-rainfall.shtml>), to obtain information on the weather experienced by each individual during five preceding seasons of summer/ winter/ wet/ dry as required. Climate variables included the number of days of thermal maxima ($\geq 35^{\circ}\text{C}$, $\geq 40^{\circ}\text{C}$) and thermal minima ($< 5^{\circ}\text{C}$, $< 0^{\circ}\text{C}$), mean summer daily maximum temperature, mean winter daily minimum temperature, total rainfall and mean vapour pressure. From the monthly data, we calculated the total number of days with maxima $\geq 35^{\circ}\text{C}$ and $\geq 40^{\circ}\text{C}$ for each summer (December, January and February) and the number of days of minima $< 5^{\circ}\text{C}$ and $< 0^{\circ}\text{C}$ for each winter (June, July and August). For each summer, we calculated mean maximum temperature by averaging the mean maximum temperatures of December, January and February; mean minimum temperature for each winter by averaging mean minimum temperatures of June, July and August. Likewise, we calculated mean total rainfall and mean vapour pressure for both summer and winter seasons from monthly data.

Although most of Australia experiences four seasons, the tropical north has only two seasons; wet (November to March) and dry (April to October), so we used these periods to calculate the number of days of thermal maxima and minima. Mean total rainfall and mean vapour pressure were calculated for both wet and dry seasons.

Geographic data

In addition to latitude and longitude, we also collated data for elevation and minimum distance to the coast (GEODATA 9sec DEM; Geoscience Australia (2008). as these variables can influence local climate variation. We also gathered data on IBRA7 (the classification of Australian ecoregions known as bioregions – Thackway and Cresswell 1995), corresponding to capture locations, which define 89 geographically distinct regions based on similarity in climate, geology, landforms, and vegetation (SEWPaC 2012).

Statistical analysis

Data analysis was carried out in a series of steps. First, we analysed patterns of bill size across geographic space. Then we tested for associations between bill size and climate at two scales: first at a continental level, and then within each climate zone separately (tropical, arid, temperate). Finally, we incorporated phylogenetic information to estimate the extent to which

differences among species were phylogenetically determined, first of bill size itself and then species' responses to climatic variation (i.e. the degree to which phylogeny predicts the relationship between bill size and temperature extremes). All analyses were carried out using a Bayesian Markov chain Monte Carlo phylogenetically controlled generalized linear mixed model approach, using the package *MCMCglmm* v.2.27 (Hadfield 2019) in R version 4.0.3. The global Phylogeny of Birds website (www.birdtree.org) was used to download data required to construct phylogeny (Jetz et al. 2012). We downloaded 1000 trees with the “Hackett backbone” (Hackett et al. 2008) and calculated a 50% majority-rule consensus phylogeny using *consensus* function of the *ape* package in R (Paradis and Schliep 2019).

Bill size patterns across geographic space

We described broad scale geographic patterns of bill size across Meliphagides by fitting a model [m1], with bill size as the response variable and geographic variables (i.e. latitude, longitude, elevation, minimum distance to coast) as explanatory variables, while controlling for structural body size (using wing length as the proxy), feeding guild, sex, season and year of capture as fixed effects, and IBRA region and species as random effects. The year of capture was also included as a random effect, but as a categorical variable (or factor) to control for any effect due to repeated sampling and differences in sample sizes between collection years. The relatedness matrix was included for the random effect, species, using the argument *ginverse* in *MCMCglmm*. Season of collection was included as a control variable, as there could be variations in bill size due to differences in the rate of bill wear caused by seasonal differences in foraging behaviour (Matthysen 1989; Gosler 1987). As some species show sexual dimorphism in bill size, usually smaller in females, we included sex as a covariate. Bill size and structural body size were log transformed to achieve normality. Both the response and explanatory variables as well as all continuous control variables except the year of capture were *z*-standardized before fitting the model. The year of capture was centred on its mean (1985).

Three distinctly different environments are found along the latitudinal gradient within Australia; humid tropics at northern most latitudes, hot and dry arid zone at mid latitudes and cold temperate zone at southern most latitudes. Bill size might therefore not change linearly with latitude due to differences in thermoregulatory costs between climate zones. Hence, to further explore the pattern with latitude, we fitted a separate model [m2] including a quadratic term of standardized absolute latitude as an explanatory variable (see supplementary material for [m1, m2]). We ran the models with 13000 iterations using weakly informative priors, with a burn-in of 3000 and thinning interval of 10. We applied default broad Gaussian priors for fixed effects and inverse-Wishart priors, with parameters $V=1$ and $\nu=0.002$, for random effects.

Testing associations with climate

After describing geographic patterns, we investigated the importance of including climate extremes in models and the nature of the relationship between bill size and climate extremes. We started by looking at associations at the continent scale. We fitted a model [m3] using *MCMCglmm* as described earlier and model selection to identify the most parsimonious model (referred to as the best model) based on Akaike information criterion corrected for small sample sizes (AICc) using *MuMIn* package v 1.43.17 (Bartoń 2020) (see supplementary material for [m3]).

We included all climate variables i.e. days $\geq 35^{\circ}\text{C}$, $\geq 40^{\circ}\text{C}$, $< 5^{\circ}\text{C}$, $< 0^{\circ}\text{C}$, mean maximum summer temperature, mean minimum winter temperature, mean summer vapour pressure, total summer rainfall, total winter rainfall in the model, along with the quadratic terms for; days $\geq 35^{\circ}\text{C}$, $\geq 40^{\circ}\text{C}$, $< 5^{\circ}\text{C}$, $< 0^{\circ}\text{C}$ (i.e. to account for the likelihood that bill size might increase up to a certain level of exposure to hot extremes and decrease at very high exposures to minimize heat gain), mean maximum summer temperature, mean minimum winter temperature, and mean summer vapour pressure as well as the interactions between; mean summer vapour pressure with days $\geq 35^{\circ}\text{C}$, $\geq 40^{\circ}\text{C}$ and mean maximum summer temperature, total summer rainfall with days $\geq 35^{\circ}\text{C}$, $\geq 40^{\circ}\text{C}$ and mean maximum summer temperature, and total winter rainfall with days $< 5^{\circ}\text{C}$, $< 0^{\circ}\text{C}$ and mean minimum winter temperature in global model (see model m3).

When performing model selection for m3, the subsets with more than one clearly autocorrelated variable to describe extremes of a particular season were excluded (i.e. models with both days $\geq 35^{\circ}\text{C}$ and $\geq 40^{\circ}\text{C}$ or the days $< 5^{\circ}\text{C}$ and $< 0^{\circ}\text{C}$ were excluded). Note that the subsets with hot extremes (days $\geq 35^{\circ}\text{C}$ or $\geq 40^{\circ}\text{C}$) also included (i.e. controlled for) mean maximum summer and the subsets with cold extremes (days $< 5^{\circ}\text{C}$ or $< 0^{\circ}\text{C}$) were controlled for mean minimum winter temperature. This was done to disentangle whether the correlation between bill size and temperature is being driven by the mean seasonal temperature maxima/minima rather than number of extreme days *per se* (Dormann et al. 2013; Graham 2003; Morrissey and Ruxton 2018). All climate variables were z-standardized prior to analysis. Other than climate variables, we included all control variables in m1 and m2.

Following analyses of continental-wide associations between bill size and climate, we ran separate analyses for each climate zone. Here, we created model subsets for m3 separately for each climate zone to identify any specific climate conditions that might underlie size patterns.

Testing the effect of phylogeny and species variation in bill size response

We quantified the degree of phylogenetic signal in bill size independent of body size and climate across Meliphagides, or in other words how much variation in bill size is explained by shared ancestry (Housworth et al. 2004). For this we constructed a model, adding all fixed and random terms including the climate variables contained in the best model from the continental wide analysis (See Table 2), with two additional random terms to describe species effect; *species.phylo* capturing the variance due to the phylogenetic relationship (equivalent to Pagel's λ) and *species.non-phylo* accounting the species specific contributions that are not related to phylogeny (including sampling error) (Housworth et al. 2004; Hadfield and Nakagawa 2010). We also tested if there were differences among species in how they responded to climate extremes within each climate zone (see supplementary material for details).

Results

Bill size (surface area) of Meliphagides ranged between 18.11 mm^2 in the weebill *Smicrornis brevirostris* and 508.18 mm^2 in the blue-faced honeyeater *Entomyzon cyanotis*. Males of Meliphagides had significantly larger bills, relative to body size, than females (Table 1), and individuals captured during winter had relatively smaller bills than in other seasons (Table 1). The latter confirmed a seasonal effect on bill size associated with bill wear, as indicated in

previous studies (Greenberg et al, 2013). Feeding guild, however, showed no significant association with relative bill size (Table 1).

Bill size patterns across geographic space

Our analysis, controlling for phylogeny, showed a significant relationship between latitude and relative bill size across species of Meliphagides (Table 1). Bill size was larger on average in Meliphagides in the tropical north of the continent compared to the temperate south which is characterized by colder climates, a spatial pattern conforming to Allen's rule. A decrease in AICc value (from -9727.019 to -9730.772; Table 1) with the inclusion of a quadratic term for latitude indicated that the relationship with latitude is non-linear; bill size decreased strongly before levelling off at southernmost latitudes (Fig. 1a). Bill size variation across latitude did not differ significantly between feeding guilds (guild \times latitude interaction; Table 1). There were significant negative associations with elevation and minimum distance to coast (Fig. 1b, c; Table 1).

Associations between bill size and climate at a continent level

The best model of the subset of 26,113 models generated in the continent-wide analysis indicated that bill size variation was best explained by the frequency of days $<5^{\circ}\text{C}$, mean minimum winter temperature and mean maximum summer temperature with an AICc of -9765.50 (Table S2). The best model with no climate extremes ranked 126 with an AICc of -9757.30. In the best model that included extremes, mean minimum winter temperature showed a strong positive association with relative bill size, with the largest effect size of any predictor after wing length (Fig. 2, Table 2). The effect sizes of the unexpected positive association between bill size and days $<5^{\circ}\text{C}$ and the negative association with mean maximum summer temperature were relatively lower (Fig. 2, Table 2).

Bill size associations in each climate zone

Climatic variation

There was considerable variation in the climatic conditions in the different climate zones (Fig. S2). Tropical populations experienced high humidity (mean = $32.31 \text{ hPa} \pm 2.46 \text{ SD}$) and high rainfall (mean monthly total rainfall = $199.59 \text{ mm} \pm 63.92 \text{ SD}$) during the wet season which co-occurred with high frequencies of days $\geq 35^{\circ}\text{C}$.

Arid populations also experienced high frequencies of days $\geq 35^{\circ}\text{C}$ in summer, including severe extremes (days $\geq 40^{\circ}\text{C}$), but in low rainfall conditions (mean monthly total rainfall = $60.80 \pm 63.36 \text{ SD}$) (Fig. S2). Most populations across the temperate zone experienced low humidity (mean = $24.85 \pm 4.37 \text{ SD}$) and rainfall (mean monthly total rainfall = $95.45 \text{ mm} \pm 77.99 \text{ SD}$) in summer, and fewer hot extremes than populations in either the tropical or arid zones. Exposure to cold conditions $<5^{\circ}\text{C}$ during winter was common across both temperate and arid zones.

Associations with climate extremes

Bill size variation was best explained when extremes were included in the model, except in the tropical zone, as indicated by the poorer AICc value of the best model without extremes (temperate zone: ΔAICc of model without extremes = 13.11; arid zone: ΔAICc of model without extremes = 0.62; tropical zone: ΔAICc of model *with* extremes = 1.63)

Relative bill size in the arid zone was associated with the frequency of cold extremes $<5^{\circ}\text{C}$, whereas in temperate regions hot extremes $\geq 35^{\circ}\text{C}$ were important (Table 3). Further, the effect of temperature extremes on bill size was mediated by humidity and rainfall. The parameter estimates for the best model of each of the three climate zone analyses and associated credible intervals are given in Table 3. All models with $\Delta\text{AICc} \leq 2$ for all climate zone analyses are shown in Table S3 – S5.

Arid zone: We found no strong evidence for direct linear or non-linear associations between relative bill size and the frequency of hot extremes, days $\geq 35^{\circ}\text{C}$ (or $\geq 40^{\circ}\text{C}$ Table S3), as neither the linear nor quadratic terms were included in the best model (Table 3). Similarly, summer humidity was not included in best model (Table 3). The relationship between bill size and the frequency of exposure to daily minima $<5^{\circ}\text{C}$, however, was significant and this association was mediated by winter rainfall: bill size declined with increasing exposure to days $<5^{\circ}\text{C}$, but only in high rainfall conditions (Table 3, days $<5^{\circ}\text{C}$ x winter rainfall interaction; Fig. 3a, b). The association between bill size and mean minimum winter temperature was also significant with slightly smaller effect sizes (Table 3). This relationship was also mediated by winter rainfall (Table 3, mean minimum winter temperature x winter rainfall interaction) with a strong reduction in bill size in warmer winters as rainfall increased (Fig. S3a, b).

Temperate zone: There were no associations between relative bill size and exposure to cold extremes $<5^{\circ}\text{C}$ (or 0°C Table S4) as these variables were not included in the best model (Table 3). By contrast, relative bill size increased with increasing summer humidity (mean summer vapour pressure) up to a point, then decreased. This relationship was mediated by temperature extremes in summer (summer vapour pressure \times days $\geq 35^{\circ}\text{C}$ interaction, Table 3, Fig. 3c, d), such that at low humidity, bill size increased with increasing exposure to days $\geq 35^{\circ}\text{C}$. As humidity increased, there was a switch toward smaller bill size with increasing exposure to days $\geq 35^{\circ}\text{C}$.

The association between bill size and mean summer maximum temperature was non-linear (Table 3, max summer temp²), and there was an interaction with humidity (max summer temperature x summer vapour pressure). The association between mean maximum summer temperature and humidity indicated a switch towards larger bill size at higher humidity in hotter environments (Fig. S3c, d).

There was also a significant interaction between days $\geq 35^{\circ}\text{C}$ and summer rainfall (summer rainfall x days $\geq 35^{\circ}\text{C}$ interaction, Table 3, Fig. 5e, f). Bill size increased with increasing exposure to days $\geq 35^{\circ}\text{C}$ in climates when average summer rainfall is less than 100mm (Fig. 3e, f).

Tropical zone: We did not consider cold extremes (i.e. days $<5^{\circ}\text{C}$ and days $<0^{\circ}\text{C}$) in the tropical zone analysis, as there were very few populations that have experienced these conditions (Fig. S2). The best model of tropical analysis contained only wing length, sex and year of capture and none of the climate variables were present. However, the second-best model was almost equally favoured ($\Delta\text{AICc} = 1.18$), and indicated that wet season vapour pressure is associated with bill size variation and this relationship is mediated by mean

maximum summer temperature (Fig. S3e, f; Table 3). As humidity increases, there was a switch towards larger bills at higher mean maximum summer temperatures, a pattern that was also observed across temperate populations with mean maximum summer temperature (Fig. S3e, f).

Evolutionary history, climate extremes and bill size variation

There was a strong effect of phylogeny (λ of 0.895, 95% credible interval = 0.853 - 0.935) on bill size, independent of body size, across species of Meliphagides (Fig. S4). Thus, more closely related species have similar relative bill sizes, apparent in the phylogenetic tree in Fig. S4.

A substantial improvement in AICc was noted after inclusion of a random slope for the non-phylogenetic species term (m5), in addition to a random intercept (Δ AICc of model without the species term arid zone = 140.18; temperate zone: 255.74; Table S6), indicating that the associations we observed between bill size and climate, likely differ among species. However, when comparing responses among species (Fig. 4), there were similarities in bill size patterns across species for those experiencing similar conditions. In the arid zone, the association between bill size and the frequency of daily minima below 5°C is relatively similar between species, for individuals experiencing high rainfall (Fig. 4a). Likewise in the temperate zone, the association between bill size and the frequency of daily maxima above 35°C is similar in low rainfall environments, whereby the majority of species showed an increase in bill size with increasing exposure to hot extremes (Fig. 4b). The bill size pattern with humidity was relatively similar at both exposures i.e. 10 and 40 days with temperatures $\geq 35^\circ\text{C}$ (Fig. 4c). There was no obvious reduction in AICc with addition of random slopes to the phylogenetic species term to m5 for both arid and temperate models (m6; Table S6), indicating that phylogeny has no effect on species responses to climate extremes in these analyses.

Discussion

We examined the relationship between bill size and climate extremes to explore the adaptive significance of bill size in relation to its role in thermoregulation in a large and diverse radiation of Australian passerines, Meliphagides. Overall, across the continent, bill size variation was associated with both climate extremes and climate averages. Bill size was most strongly associated with average minimum winter temperature with smaller bills in environments with colder winters. However, the nature of the associations with temperature extremes varied among climate zones, were moderated by rainfall and humidity and in some cases were non-linear. There was a strong effect of phylogeny on bill size across Meliphagides species but, there was no phylogenetic signal for associations between bill size and climate.

Patterns of bill size are consistent with Allen's Rule

Our study, based on 9847 individuals, provides strong evidence that bird bills conform to Allen's rule at a continental scale in Southern Hemisphere passerines. In particular, Meliphagides inhabiting northerly latitudes, closer to the equator, displayed larger bills (relative to body size) than those in more southerly latitudes. We also detected a non-linear relationship between bill size and latitude, with a reduction in the rate of change evident at

higher latitudes. Such inconsistency implies that local climate underlies the bill size association with latitude. Elevation can confound bill size patterns across latitude, as it creates a vertical climate gradient (Laiolo and Rolando 2001). Here, we report a negative relationship between bill size and elevation in line with previous studies, confirming that Allen's rule applies to both latitudinal and elevational gradients (Symonds and Tattersall, 2010). In addition to latitude and elevation, we noted a significant, negative (although smaller) association between bill size and direct distance to the coastline, as observed elsewhere (Onley et al., 2020).

The strong associations between bill size and climate across space suggests that the latitude effect characteristic of Allen's rule is a proxy for climate. Winter conditions, including both minimum winter temperature and exposure to winter extremes (days $<5^{\circ}\text{C}$) best explained bill size variation across the continent. Of the climatic predictors, the association with mean minimum winter temperature was strong with the largest effect size and shows that smaller bills are associated with lower winter minimum temperatures. Our results concur with the continental-wide analysis of bill size in Australian Meliphagides by Friedman et al. (2017) who found that bill size variation was strongly associated with minimum winter temperature. However, our more comprehensive analyses, sampling multiple populations from across the entirety of each species' range, suggest that continental-wide analyses obscure the significant role of local climatic regimes in driving bill size variation.

Bill size and cold extremes (prediction 1)

Our study indicated a significant *positive* association between bill size and increasing frequency of days $<5^{\circ}\text{C}$ in the continental analysis. Note though that this pattern occurs after already controlling for minimum winter temperature. Overall, bill size is smaller than average in environments with increasing frequency of extreme cold days $<5^{\circ}\text{C}$, but not as small as expected given average coldness of the local climate. Consequently, upon controlling for average minimum temperature, relative bill size is negatively associated with more cold extreme days, consistent with prediction 1. There are many potential explanations for this result. For example, it may point to a complex non-linear effect of temperature or a correlation between days $<5^{\circ}\text{C}$ and an unmeasured variable. These could include a constraint on smallness after a size threshold is surpassed, a trade-off between optimal bill sizes in different seasons, or a functional constraint related to food processing in cold climates.

In the climate zone analyses, the frequency of exposure to cold extremes was associated with bill size variation only in the arid zone. Here, bill size reduction was associated with increasing exposure to days $<5^{\circ}\text{C}$ only in environments with high winter rainfall (see below for discussion). There was no effect of cold extremes in the temperate zone, despite our expectations. Although both arid and temperate zone populations experienced similarly severe cold winters, a greater proportion of populations in the arid zone were subject to such conditions compared with the temperate zone, at least in our sample (see Fig. S2). Perhaps this reflects the large latitudinal range of the temperate zone classification we used, obscuring any effect of cold extremes in our temperate analysis. Alternatively, this result might reflect a trade-off between optimal bill sizes in different seasons, with stronger selection for larger bills in summer.

Bill size and hot extremes (prediction 2)

In our continent-wide analysis, we found that bill size decreased with increasing maximum summer temperature, contrary to prediction, and there was no association with hot extremes

(days >35 or days >40°C). However, Gardner et al. (2016) found that the effect of maximum summer temperature on bill size appears to be dependent on its interaction with rainfall or humidity. Therefore, the broad spatial scale of our continental analysis may have obscured the significance of local climatic regimes in driving bill size variation.

In climate zone analyses we found no evidence for a positive association between bill size and high temperature *per se*. Rather, hot extremes (days >35°C) in the temperate zone were associated with bill size variation in interaction with other climate variables, humidity and rainfall (see next section). In these cases, the interactive effect of extreme temperature was non-linear, with reversal in the response of bill size, in line with prediction 2. Thus, relationships between bill size and hot extremes are complex but consistent with thermal physiology.

We did not observe a strong association between bill size and hot extremes in the arid zone where such extremes are common. This was unexpected, given growing evidence for the importance of bills in heat dissipation in hot conditions (Tattersall et al. 2009; van de Ven et al. 2016; Pavlovic et al. 2019). This result might represent a trade-off between optimal bill sizes in different seasons, given the arid zone is characterized by climatic extremes in both winter and summer, and we found strong selection for smaller bills in winter in the arid zone. Large bills might compromise winter survival, so birds may need to rely on other methods to dissipate heat in summer when ambient temperatures are high. Heat loss may also be achieved through non-evaporative heat dissipation via the legs, and Allen's Rule predicts increases in leg size in relation to temperature (Greenberg et al. 2012). Our results highlight the need to consider interactions among multiple traits when interpreting patterns of trait size variation and their role in thermal performance.

Temperature extremes interact with other climate variables (prediction 3).

Effects of winter extremes are mediated by rainfall in arid zone birds (prediction 3a)

In the arid zone, the strongest predictor of bill size was exposure to days <5°C and, consistent with our prediction (3a) this association was mediated by winter rainfall. In particular, bill size decreased with increasing exposure to days <5°C but only in environments with relatively high winter rainfall. Despite lower energy intake in winter due to reduced food availability, birds need to increase energy expenditure to maintain optimal body temperatures (Williams et al. 2015). Energy requirements for thermoregulation are greater in cold, wet environments where plumage insulation is compromised (Lustick and Adams 1977; Webb and King 1984), and this is likely to have consequences for fitness. Indeed, Gardner et al. (2017) found that white-browed scrubwrens (*Sericornis frontalis*) that were exposed to higher frequencies of cold wet days <5°C in winter were less likely to survive. Mechanisms that aid heat conservation, like smaller bills, may therefore be crucial in such conditions in line with our findings.

Effects of summer extremes are mediated by humidity and rainfall in temperate zone birds (prediction 3b)

We found strong support for prediction 3b, that hot extremes interact with other climate variables to influence bill size patterns. In particular, we found a positive association between bill size and increasing frequency of days >35°C only in dry environments where summer rainfall was <100 mm. Our result supports the idea that larger bills may be adaptive in hot,

arid environments where water availability is limited in summer due to improvement in water conservation (Greenberg et al. 2012).

Similarly, we found a positive association between relative bill size and humidity in summer in the temperate zone (when average days $\geq 35^{\circ}\text{C}$ set to mean) with larger bills in more humid environments. Latent heat loss via evaporation becomes less effective as humidity increases, potentially increasing the importance of heat dissipation via radiative structures such as the bill (Cooper and Withers 2008; Gerson et al 2014). The effect of humidity on bill size was non-linear and mediated by increasing exposure to hot extremes with a switch toward smaller bills in hotter, humid conditions. Interestingly, the switch towards smaller bills occurred earlier across the humidity gradient in locations with hot summers characterized by many extreme days (approximately 22hPa at 40 days exposure to days $\geq 35^{\circ}\text{C}$ in our sample) and later in locations with relatively cooler summers with fewer extreme days (approximately 27hPa at 10 days exposure to days $\geq 35^{\circ}\text{C}$), consistent with prediction 2. The value of larger bills that compensate for reduced efficiency of evaporative cooling declines with increasing exposure to hot extremes, because bills become a heat sink when air temperature exceeds body temperature. This may underlie the switch from large to small bills at different frequencies of hot extremes along the humidity gradient. Our findings are consistent with Gardner et al. (2016) who found that humidity had a much stronger association with bill size than did temperature per se, but temperature mediated the association between humidity and bill size.

No effect on bill size of hot extremes associated with humidity in tropics

The best model for tropical zone Meliphagides that included climate variables showed a significant association between bill size and humidity, similar to the temperate zone. Unlike temperate birds, however, there was no switch towards smaller bills with exposure to hot extremes. Perhaps individuals in our sample did not experience the critical temperature threshold necessary for such a switch, even though they were frequently exposed to temperatures $>35^{\circ}\text{C}$. Indeed, there were few days in our tropical sample with maxima $>40^{\circ}\text{C}$, when strong effects might be observed. Moreover, tropical birds in our sample were smaller, on average, than temperate individuals (Table S7) and therefore likely to be more efficient at dissipating body heat via convection (Scholander 1955). The advantage of smaller size, together with less exposure to maxima $>40^{\circ}\text{C}$ might make them less vulnerable to temperature extremes than the temperate individuals (James 1970). The observed interaction between maximum summer temperature and summer humidity (larger bills in hot environments coinciding with high humidity but no reversal in the bill size response), is consistent with this suggestion.

Overall, our results suggest that bills have an important role in balancing heat budgets, specifically in hot dry, hot humid and cold wet environments. This suggests that shifts between reliance on convective, evaporative or radiative cooling are associated with different climatic regimes, consistent with predictions from thermal physiology.

Adaptation of bill size to climate: evolutionary vs. plastic effects

We found a strong phylogenetic signal for bill size, independent of body size, across Meliphagides species, with more closely related species showing greater similarities in bill size. Such patterns have been interpreted in relation to diet and feeding ecology, although a

recent macro-evolutionary study found diet contributed very little (~12%) to variation in bill morphology across multiple lineages (Navalón et al. 2019).

In contrast to the effect of phylogeny on bill size *per se*, associations between relative bill size and climate extremes showed no phylogenetic signal among closely related species. This suggests that observed climate-related, bill size patterns occurred independently within species, in response to the local conditions experienced.

These findings are significant in relation to the question of whether bill size responses to climate are driven by plasticity or microevolution. The size and shape of bills has been shown to be highly heritable (Boag and Grant 1978), although there is some evidence for developmental plasticity (James 1991). We cannot rule out plasticity for patterns we observed. However, the broad ecological, geographic and phylogenetic scale of our study does suggest an adaptive evolutionary response to climate driven by strong selection for the role of bill size in thermal physiology.

Conclusion

Our study found bill size patterns across Meliphagides conform to Allen's rule across broad geographic space, some 33 degrees of latitude (or ca. 4000km). However, we clearly demonstrate that some of the fine scale variation in bill size is overlooked in the broader continental level analysis, illustrating the importance of considering different climate regimes at sub-continental geographic scales. The associations between bill size and climate observed at the level of climate zones are different from continent-wide associations, yet consistent with studies relating to physiology and a thermoregulatory role for avian bills. Our results suggest that radiative heat loss via the bill may be particularly useful for birds living in dry climates (rainfall <100mm) in the temperate zone where use of evaporative cooling is constrained due to limited water availability and also for birds living in humid environments with fewer days of hot extremes exceeding body temperature. Further, heat loss via bills is a greater concern for birds experiencing cold winters, particularly within the arid zone. We demonstrate the importance of including extremes of climate in analyses, in addition to climate means, and accounting for possible interactions and non-linearity to better understand fine scale variation in trait size variation across space. Our study is the first to provide strong evidence that climate extremes may have contributed to the evolution of bill morphology in relation to its role in thermoregulation. The increase in the frequency and intensity of climate extremes, a signature of rapid contemporary climate change, may lead to changes in bill size, but this proposition is yet to be tested.

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FIGURES AND TABLES

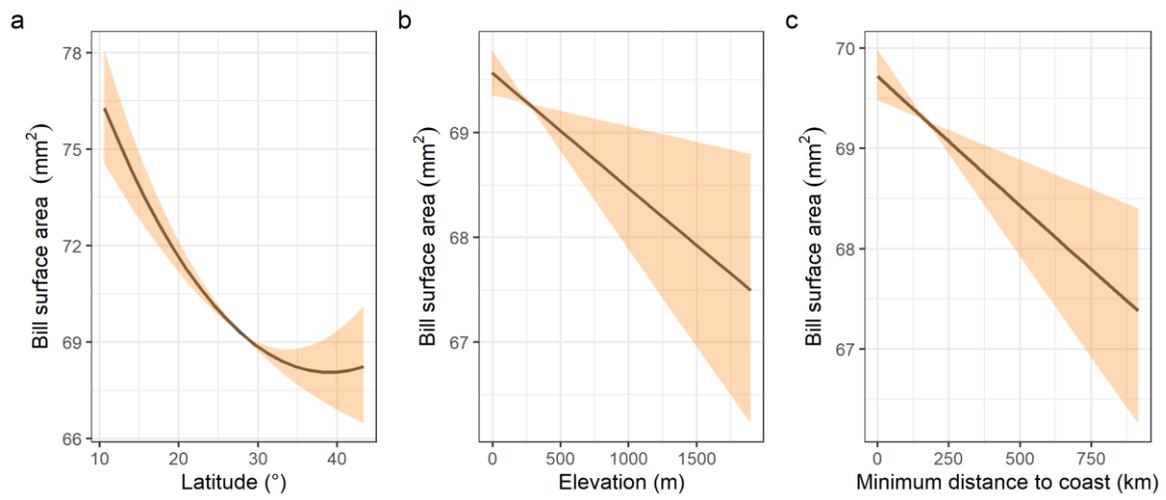


Figure 1. Relationships between relative bill size and a) latitude, b) elevation, c) minimum distance to coast. Shaded area shows 95% credible intervals around fitted values, when all other predictors (including their parameter estimates) are held constant.

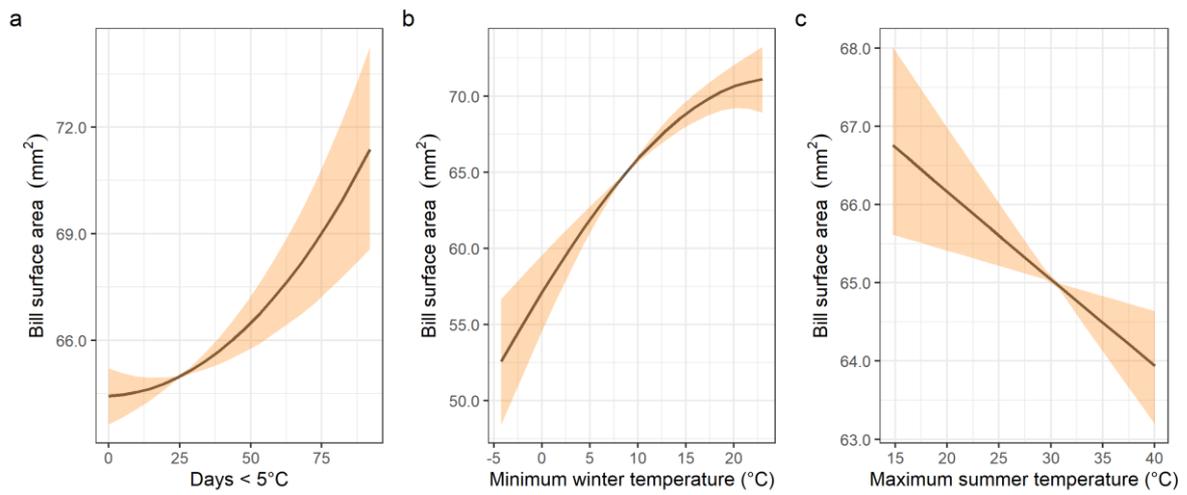


Figure 2. Relationships between relative bill size, after controlling for other variables in models, and a) days $<5^{\circ}\text{C}$, b) mean minimum winter temperature, c) mean maximum summer temperature across the continent. Shaded area shows 95% credible interval when posterior mean of non-focal parameters used for predictions. Note that the polynomial terms for days $<5^{\circ}\text{C}$ and mean minimum winter temperature in the best model of the continent-wide analysis caused the non-linear relationships in (a) and (b).

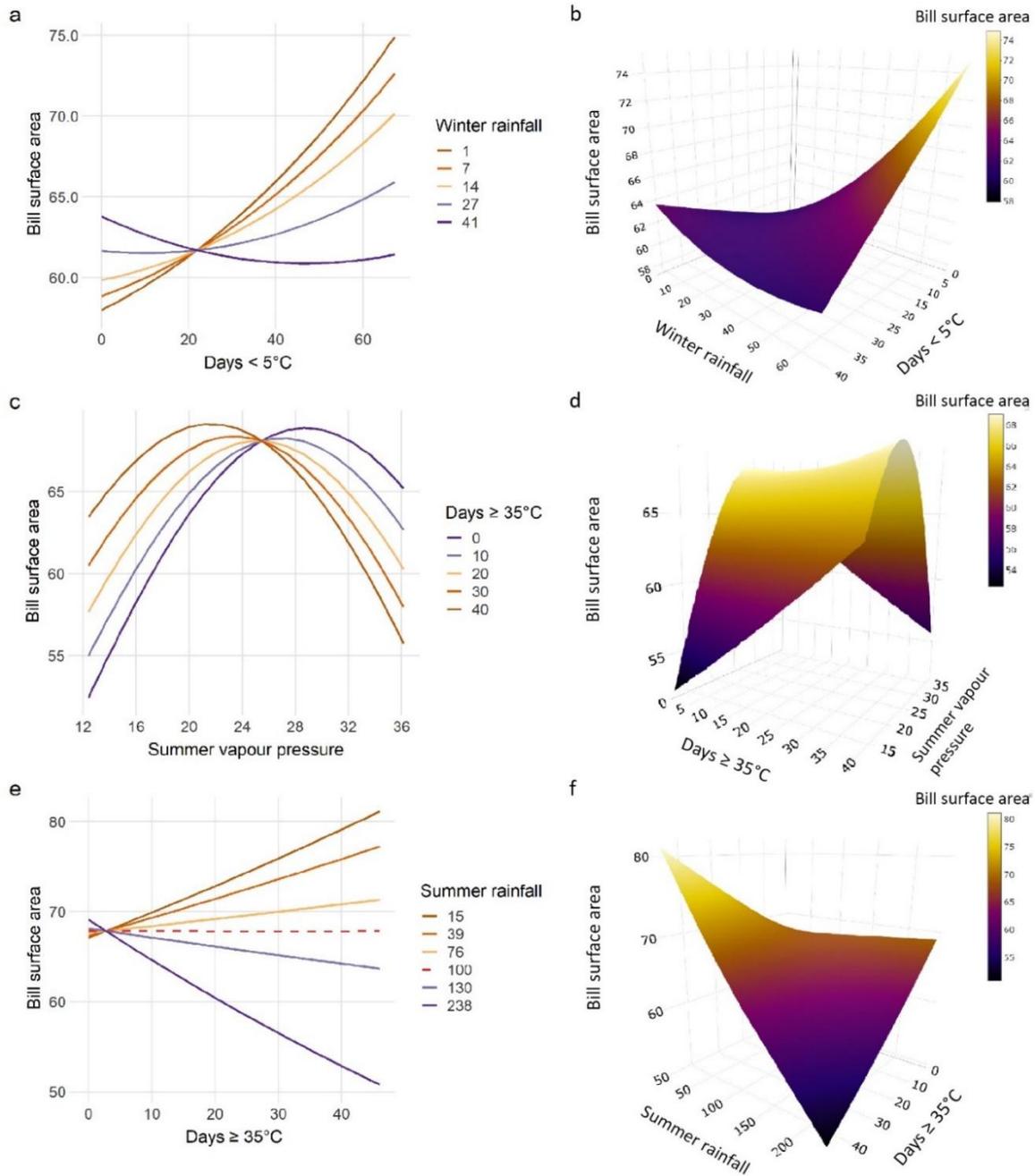


Figure 3. Associations between relative bill size and frequency of extreme temperatures within climate zones. Shown are relationships between bill size and (a) days < 5°C in interaction with winter rainfall (mm) at five quantiles, 5th, 25th, 50th, 75th, and 95th across 50 species within the arid zone and corresponding 3D representation in (b); (c) frequency of days ≥ 35°C in interaction with mean summer vapour pressure (hPa) at five quantiles i.e. 5th, 25th, 50th, 75th, and 95th across 57 species within the temperate zone and corresponding 3D representation in (d); (e) frequency of days ≥ 35°C in interaction with summer rainfall (mm) at five quantiles, 5th, 25th, 50th, 75th, and 95th across 57 species within the temperate zone and corresponding 3D representation in (f). Red-dash line in (e) shows the amount of rainfall above which bill size shows an increase with increasing hot extremes.

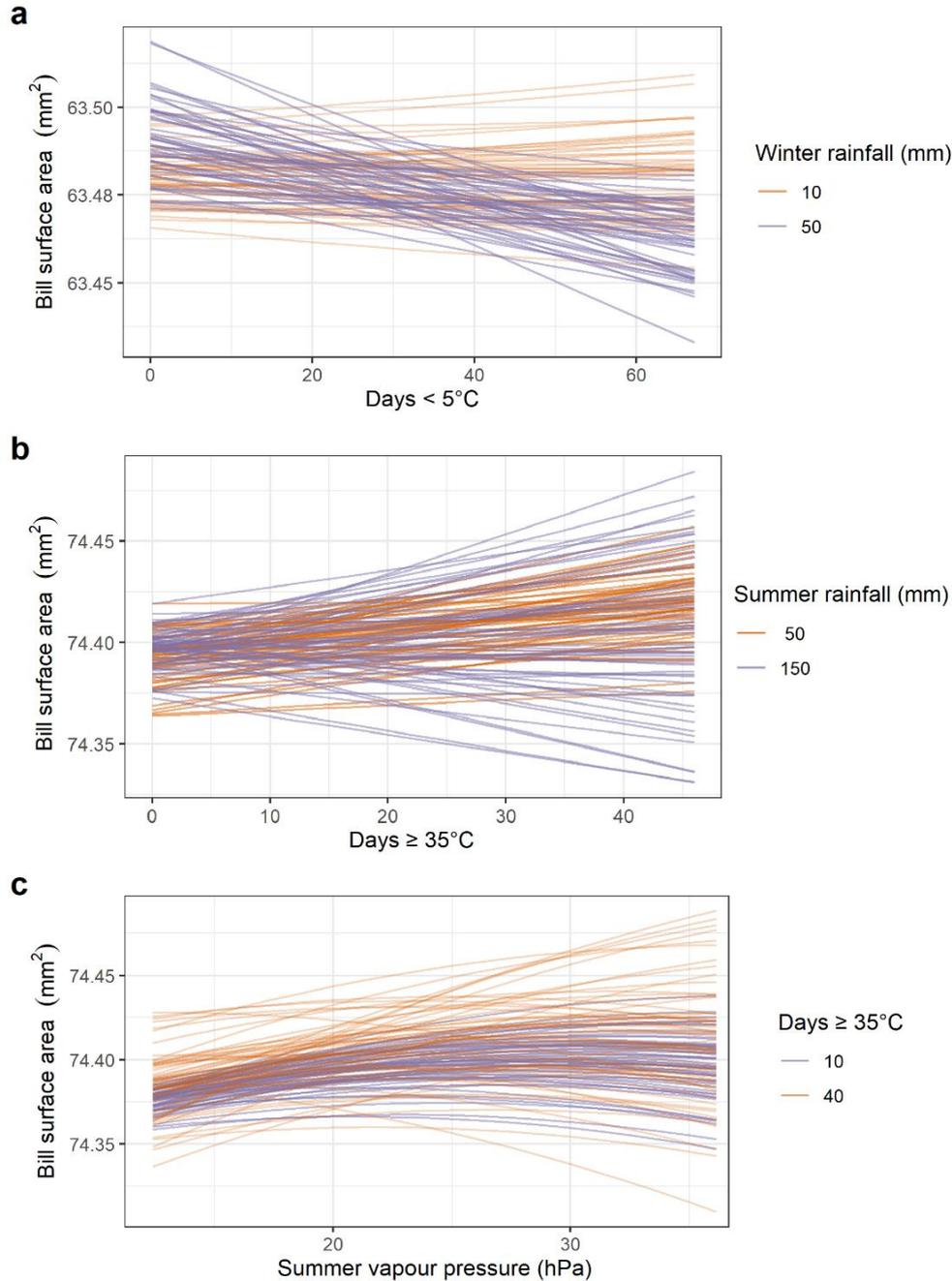


Figure 4. Species variation in the bill size response to extreme temperatures. Shown are bill size associations with (a) frequency of exposure to daily minima $<5^\circ\text{C}$ in arid zone birds at 10 mm (orange) and 50 mm (blue lines) of winter rainfall, (b) frequency of exposure to daily maxima $\geq 35^\circ\text{C}$ in temperate zone birds at 50 mm (orange lines) and 100 mm (blue lines) of summer rainfall and (c) summer vapour pressure in temperate zone birds when exposure to daily maxima $\geq 35^\circ\text{C}$ is 10 (blue lines) or 40 days (orange lines) in summer. Each line (orange or blue) presents the model predicted mean bill size of individual species after controlling for body size, sex, year of capture and IBRA region.

Table 1. The output of models m1 and m2, demonstrating associations between relative bill size and geographic variables across species of Meliphagides. All continuous variables except year of capture were standardized. The posterior mean estimates of predictors and associated 95% credible intervals are shown. The estimates where the 95% credibility intervals do not contain zero are highlighted in bold.

Parameter	m1: AIC= -9727.019			m2: AIC= -9730.772		
	estimate	l-95% CI	u-95% CI	estimate	l-95% CI	u-95% CI
Intercept	-0.280	-1.835	1.514	-0.286	-1.903	1.423
Latitude	-0.047	-0.056	-0.037	-0.042	-0.051	-0.031
Latitude^2				0.013	0.006	0.021
Elevation	-0.007	-0.011	-0.002	-0.006	-0.010	-0.001
Longitude	0.002	-0.005	0.010	0.000	-0.008	0.007
Distance to coast	-0.016	-0.022	-0.010	-0.011	-0.018	-0.005
Guild						
nectarivore	0.433	-0.243	1.315	0.435	-0.271	1.197
Guild:latitude	0.008	-0.002	0.017	0.008	-0.002	0.017
Year of capture	0.000	-0.001	0.000	0.000	-0.001	0.000
Sex						
male	0.050	0.043	0.057	0.050	0.043	0.058
Season						
spring	0.008	-0.001	0.016	0.008	-0.001	0.017
summer	0.021	0.010	0.032	0.021	0.010	0.033
winter	-0.018	-0.027	-0.010	-0.018	-0.026	-0.009
Wing length	0.449	0.425	0.476	0.448	0.424	0.470

Table 2. Parameter estimates for the best model for analysis of relative bill size in the continent-wide analysis and associated credibility intervals. The estimates for climate variables, where 95% credibility intervals do not contain zero are highlighted in bold. All continuous variables except year of capture are standardized.

	Parameter	estimate	95% CI
Continent	Intercept	-0.169	-1.788; 1.447
	Days <5°C	0.023	0.009; 0.040
	Days <5°C ^2	0.010	-0.004; 0.015
	Min. winter temperature	0.085	0.063; 0.106
	Min. winter temperature ^2	-0.013	-0.022; -0.004
	Max. summer temperature	-0.012	-0.020; -0.004
	Year of capture	-0.0003	-0.0007; 0.0004
	Sex		
	male	0.051	0.045; 0.059
	Season		
	spring	0.009	0.001; 0.017
	summer	-0.021	0.011; 0.033
	winter	-0.017	-0.026; -0.009
	Wing length	0.440	0.414; 0.465

Table 3. Parameter estimates for the top model for arid and temperate zones, and the second best model (the only model with climate variables among all models with $\Delta AICc \leq 2$) for the tropical analysis, and associated credibility intervals. The estimates for climate variables, where 95% credibility intervals do not contain zero are highlighted in bold. All continuous variables except year of capture are standardized.

	Parameter	estimate	95% CI
Arid zone	Intercept	-0.079	-2.092; 1.787
	Days <5°C	0.042	0.008; 0.070
	Days <5°C ^2	0.010	-0.001; 0.019
	Min. winter temperature	0.084	0.034; 0.130
	Min. winter temperature ^2	-0.024	-0.041; -0.007
	Mean summer vapour pressure	0.012	-0.002; 0.025
	Winter rainfall	-0.001	-0.015; 0.011
	Year of capture	-0.001	-0.001; 0.000
	Sex		
	male	0.052	0.039; 0.062
	Season		
	spring	0.017	0.004; 0.031
	summer	0.034	0.009; 0.053
	winter	-0.028	-0.041; -0.012
	Wing length	0.395	0.355; 0.435
Days <5°C: Winter rainfall	-0.038	-0.056; -0.021	
Min. winter temperature: Winter rainfall	-0.060	-0.088; -0.037	
Temperate zone	Intercept	-0.171	-1.673; 1.367
	Days ≥35°C	0.002	-0.018; 0.023
	Summer rainfall	-0.007	-0.021; 0.008
	Summer vapour pressure	0.044	0.021; 0.068
	Summer vapour pressure ^2	-0.030	-0.058; 0.002
	Max. summer temperature	-0.044	-0.069; -0.017
	Max. summer temperature^2	-0.051	-0.082; -0.018
	Year of capture	0.000	0; 0.001
	Sex		
	male	0.054	0.044; 0.065
	Season		
	spring	0.001	-0.013; 0.013
	summer	0.009	-0.006; 0.023
	winter	-0.020	-0.034; -0.007
	Wing length	0.467	0.430; 0.505
Days ≥35°C: Summer vapour pressure	-0.013	-0.023; -0.006	
Days ≥35°C: Summer rainfall	-0.031	-0.046; -0.015	
Summer rainfall: Max. summer temperature	0.005	-0.007; 0.016	
Summer vapour pressure: Max. summer temperature	0.075	0.015; 0.138	
Tropical zone	Intercept	-0.288	-1.795; 1.301
	Max. summer temperature	-0.008	-0.034; 0.016
	Wet season vapour pressure	0.004	-0.018; 0.027
	Wet season vapour pressure ^2	-0.043	-0.069; -0.016
	Year of capture	-0.001	-0.002; -0.001
	Sex		
	male	0.029	0.01; 0.048
	Wing length	0.589	0.517; 0.666
Max. summer temperature: Wet season vapour pressure	0.042	0.014; 0.066	

References

- Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Review*, 1, 108-140.
- Bartoń, K. 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bears, H., Drever, M. C., & Martin, K. (2008). Comparative morphology of Dark-Eyed Juncos *Junco hyemalis* breeding at two elevations: A Common Aviary Experiment. *Journal of Avian Biology*, 39(2), 152-162. <https://doi.org/10.1111/j.2008.0908-8857.04191>.
- Benkman, C. (1993). Adaptation to single resources and the evolution of Crossbill (*Loxia*) Diversity. *Ecological Monographs*, 63, 305-325. <https://doi.org/10.2307/2937103>.
- Boag, P. T., & Grant, P. R. (1978). Heritability of external morphology in Darwin's finches. *Nature*, 274(5673), 793-794. <https://doi.org/10.1038/274793a0>.
- Cardilini, A. P. A., Buchanan, K. L., Sherman, C. D. H., Cassey, P., & Symonds, M. R. E. (2016). Tests of ecogeographical relationships in a non-native species: what rules avian morphology? *Oecologia*, 181(3), 783-793. <https://doi.org/10.1007/s00442-016-3590-9>.
- Campbell-Tennant, D. J. E., Gardner, J. L., Kearney, M. R., & Symonds, M. R. E. (2015). Climate-related spatial and temporal variation in bill morphology over the past century in Australian parrots. *Journal of Biogeography*, 42(6), 1163-1175. <https://doi.org/10.1111/jbi.12499>.
- Cooper, C., & Withers, P. (2008). Allometry of evaporative water loss in marsupials: implications of the effect of ambient relative humidity on the physiology of brushtail possums (*Trichosurus vulpecula*). *Journal of Experimental Biology*, 211(17), 2759-2766. <https://doi.org/10.1242/jeb.019463>.
- Cunningham, S. J., Gardner, J. L., & Martin, R. O. (2021). Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, 19(5), 300-307. <https://doi.org/10.1002/fee.2324>.
- Danner, R. M., & Greenberg, R. (2015). A critical season approach to Allen's rule: bill size declines with winter temperature in a cold temperate environment. *Journal of Biogeography*, 42(1), 114-120. <https://doi.org/10.1111/jbi.12389>.
- Dawson, W. R. (1982). Evaporative losses of water by birds. *Comparative Biochemistry and Physiology. A, Comparative Physiology*, 71(4), 495-509. [https://doi.org/10.1016/0300-9629\(82\)90198-0](https://doi.org/10.1016/0300-9629(82)90198-0).
- de Villemereuil, P., Morrissey, M. B., Nakagawa, S., & Schielzeth, H. (2018). Fixed-effect variance and the estimation of repeatabilities and heritabilities: issues and solutions. *Journal of Evolutionary Biology*, 31(4), 621-632. <https://doi.org/10.1111/jeb.13232>.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013).

Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36: 27-46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

Fan, L., Cai, T., Xiong, Y., Song, G., & Lei, F. (2019). Bergmann's rule and Allen's rule in two passerine birds in China. *Avian Research*, 10(1), 34. <https://doi.org/10.1186/s40657-019-0172-7>.

Friedman, N. R., Harmáčková, L., Economo, E. P., & Remeš, V. (2017). Smaller beaks for colder winters: Thermoregulation drives beak size evolution in Australasian songbirds. *Evolution*, 71(8), 2120-2129. <https://doi.org/10.1111/evo.13274>.

Gardner, J. L., Amano, T., Peters, A., Sutherland, W. J., Mackey, B., Joseph, L., Stein, J., Ikin, K., Little, R., Smith, J., & Symonds, M. R. E. (2019). Australian songbird body size tracks climate variation: 82 species over 50 years. *Proceedings of the Royal Society B: Biological Sciences*, 286(1916), 20192258. <https://doi.org/10.1098/rspb.2019.2258>.

Gardner JL, Clayton M, Allen R, Stein J, Bonnet T. (2022). The effects of temperature extremes on survival in two semi-arid Australian bird communities over three decades, with projections to 2104. *Global Ecology & Biogeography*, <https://doi.org/10.1111/geb.13591>.

Gardner, J. L., Rowley, E., de Rebeira, P., de Rebeira, A., & Brouwer, L. (2017). Effects of extreme weather on two sympatric Australian passerine bird species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723), 20160148. <https://doi.org/10.1098/rstb.2016.0148>.

Gardner, J. L., Symonds, M. R. E., Joseph, L., Ikin, K., Stein, J., & Kruuk, L. E. B. (2016). Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. *Climate Change Responses*, 3(1), 11. <https://doi.org/10.1186/s40665-016-0026-z>.

Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology*, 87(6), 782-795. <https://doi.org/10.1086/678956>.

Gómez-Blanco, D., Santoro, S., Borrás, A., Cabrera, J., Senar, J. C., & Edelaar, P. (2019). Beak morphology predicts apparent survival of crossbills: due to selective survival or selective dispersal? *Journal of Avian Biology*, 50 <https://doi.org/10.1111/jav.02107>.

Gosler, A. G. (1987). Pattern and process in the bill morphology of the Great Tit *Parus major*. *Ibis*, 129(s2), 451-476. <https://doi.org/10.1111/j.1474-919X.1987.tb08234.x>.

Graham, M.H. (2003), Confronting multicollinearity in ecological multiple regression. *Ecology*, 84: 2809-2815. <https://doi.org/10.1890/02-3114>.

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's Finches. *Science*, 313(5784), 224-226. <https://doi.org/10.1126/science.1128374>.

Greenberg, R., & Danner, R. M. (2012). The influence of the California marine layer on bill size in a generalist songbird. *Evolution*, 66 3825-3835. <https://doi.org/10.1111/j.1558-5646.2012.01726.x>.

Greenberg, R., Cadena, V., Danner, R. M., & Tattersall, G. J. (2012). Heat loss may explain bill size differences between birds occupying different habitats. *PLoS ONE*, 7, e40933. <https://doi.org/10.1371/journal.pone.0040933>.

Greenberg, R., M. Etterson, and R. M. Danner. 2013. Seasonal dimorphism in the horny bills of sparrows. *Ecology and Evolution*. 3:389-98.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Chojnowski, J. L., Cox, W. A., Han, K. L., Harshman, J., Huddleston, C., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C., & Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768. <https://doi.org/10.1126/science.1157704>.

Hadfield, J. D. (2019). MCMC Generalised Linear Mixed Models. R package version 2.27. <https://cran.r-project.org/web/packages/MCMCglmm/index.html>.

Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23(3), 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>.

Hagan, A. A., & Heath, J. E. (1980). Regulation of heat loss in the duck by vasomotion in the bill. *Journal of Thermal Biology*, 5(2), 95-101. [https://doi.org/10.1016/0306-4565\(80\)90006-6](https://doi.org/10.1016/0306-4565(80)90006-6).

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965-1978. <https://doi.org/10.1002/joc.1276>.

Housworth, Elizabeth A., Martins, Emília P., & Lynch, M. (2004). The phylogenetic mixed model. *The American Naturalist*, 163(1), 84-96. <https://doi.org/10.1086/380570>.

James FC. (1970). Geographic size variation in birds and its relationship to climate. *Ecology*, 51365–390. (doi:10.2307/1935374).

James, F. C. (1991). Complementary descriptive and experimental studies of clinal variation in birds. *American Zoologist*, 3. <https://doi.org/10.1093/icb/31.4.694>.

Janse van Vuuren, A. K., Kemp, L. V., & McKechnie, A. E. (2020). The beak and unfeathered skin as heat radiators in the southern ground-hornbill. *Journal of Avian Biology*, 51(6). <https://doi.org/10.1111/jav.02457>.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448. <https://doi.org/10.1038/nature11631>.

Köppen, W. (1936). Das geographische System der Klimate. In *Handbuch der Klimatologie*, edited by Köppen, W. and Geiger, R., (Germany:Borntraeger), Vol 1 Part C, 1-44.

Kriticos, D. J., Webber, B. L., Leriche, A., Ota, N., Macadam, I., Bathols, J., & Scott, J. K. (2012). CliMond: global high-resolution historical and future scenario climate surfaces for

bioclimatic modelling. *Methods in Ecology and Evolution*, 3(1), 53-64.
<https://doi.org/10.1111/j.2041-210X.2011.00134.x>.

Laiolo, P., & Rolando, A. (2001). Ecogeographic correlates of morphometric variation in the Red-billed Chough *Pyrrhocorax pyrrhocorax* and the Alpine Chough *Pyrrhocorax graculus*. *Ibis*, 143(3), 602-616. <https://doi.org/10.1111/j.1474-919X.2001.tb04888.x>.

Lustick, S., & Adams, J. (1977). Seasonal variation in the effects of wetting on the energetics and survival of starlings (*Sturnus vulgaris*). *Comparative Biochemistry and Physiology Part A: Physiology*, 56(2), 173-177. [https://doi.org/10.1016/0300-9629\(77\)90181-5](https://doi.org/10.1016/0300-9629(77)90181-5).

Marki, P. Z., Jønsson, K. A., Irestedt, M., Nguyen, J. M. T., Rahbek, C., & Fjeldså, J. (2017). Supermatrix phylogeny and biogeography of the Australasian Meliphagides radiation (Aves: Passeriformes). *Molecular Phylogenetics and Evolution*, 107, 516-529. <https://doi.org/10.1016/j.ympev.2016.12.021>.

Matthysen, E. (1989). Season variation in bill morphology of nuthatches *Sitta europaea*: dietary adaptations or consequences? *Ardea*, 77, 117-125.

McNab, B. K. (2001). Energetics of toucans, a barbet, and a hornbill: implications for avian frugivory. *The Auk*, 118(4), 916-933, 918. <https://doi.org/10.1093/auk/118.4.916>.

McKechnie, A. E., Gerson, A. R., McWhorter, T. J., Smith, E. K., Talbot, W. A., & Wolf, B. O. (2017). Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation in heat tolerance. *Journal of Experimental Biology*, 220(13), 2436-2444. <https://doi.org/10.1242/jeb.155507>.

Morrissey, M., & Ruxton, G. (2018). Multiple Regression Is Not Multiple Regressions: The meaning of multiple regression and the non-problem of collinearity. *Philosophy, Theory and Practice in Biology*, 10(3). <https://doi.org/10.3998/ptpbio.16039257.0010.003>.

Navalón, G., Bright, J. A., Marugán-Lobón, J., & Rayfield, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution*, 73(3), 422-435. <https://doi.org/10.1111/evo.13655>.

Onley, I. R., Gardner, J. L., & Symonds, M. R. E. (2020). Spatial and temporal variation in morphology in Australian whistlers and shrike-thrushes: is climate change causing larger appendages? *Biological Journal of the Linnean Society*, 130(1), 101-113. <https://doi.org/10.1093/biolinnean/blaa028>.

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526-528. <https://doi.org/10.1093/bioinformatics/bty633>.

Pavlovic, G., Weston, M. A., & Symonds, M. R. E. (2019). Morphology and geography predict the use of heat conservation behaviours across birds. *Functional Ecology*, 33(2), 286-296. <https://doi.org/10.1111/1365-2435.13233>.

Ryding, S., Klaassen, M., Tattersall, G.J., Gardner, J.L., & Symonds, M.R.E. (2021) Shape-shifting: changing animal morphologies as a response to climatic warming. *Trends in Ecology and Evolution*, 36(11), 1036-1048. <https://doi.org/10.1016/j.tree.2021.07.006>

Scholander PF, Hock R, Walters V, Johnson F, Irving L. (1950). Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin* 99, 237–258. (doi:10.2307/1538741)

SEWPaC (2012) Interim biogeographic regionalisation for Australia (IBRA), Version 7. Australian Government Department of Sustainability Environment Water Population and Communities, <https://www.environment.gov.au/land/nrs/science/ibra#ibra>.

Subasinghe, K., Symonds, M. R. E., Vidal-García, M., Bonnet, T., Prober, S. M., Williams, K. J., & Gardner, J. L. (2021). Repeatability and validity of phenotypic trait measurements in birds. *Evolutionary Biology*, 48(1), 100-114. <https://doi.org/10.1007/s11692-020-09527-5>.

Symonds, M. R. E., & Tattersall, G. J. (2010). Geographical variation in bill size across bird species provides evidence for Allen's rule. *The American Naturalist*, 176. <https://doi.org/10.1086/653666>.

Tattersall, G. J., Andrade, D. V., & Abe, A. S. (2009). Heat exchange from the Toucan bill reveals a controllable vascular thermal radiator. *Science*, 325(5939), 468-470. <https://doi.org/10.1126/science.1175553>.

Tattersall, G.J., Arnaout, B. and Symonds, M.R.E. (2017), The evolution of the avian bill as a thermoregulatory organ. *Biological Reviews*, 92, 1630-1656. <https://doi.org/10.1111/brv.12299>.

Tattersall, G. J., Chaves, J. A., & Danner, R. M. (2018). Thermoregulatory windows in Darwin's finches. *Functional Ecology*, 32(2), 358-368. <https://doi.org/10.1111/1365-2435.12990>.

Thackway, R. & Cresswell, I. D. (1995). An interim biogeographic regionalisation for Australia: a framework for setting priorities in the national reserves system cooperative program, version 4.0. Australian Nature Conservation Agency, Canberra.

van de Ven, T. M. F. N., Martin, R. O., Vink, T. J. F., McKechnie, A. E., & Cunningham, S. J. (2016). Regulation of heat exchange across the Hornbill beak: Functional similarities with Toucans? *PLoS One*, 11(5), e0154768. <https://doi.org/10.1371/journal.pone.0154768>.

Wathen, P., Mitchell, J. W. and Porter, W. P. (1971). Theoretical and experimental studies of energy exchange from Jackrabbit ears and cylindrically shaped appendages. *Biophysical Journal*, 11(12), 1030-1047. [https://doi.org/10.1016/S0006-3495\(71\)86276-8](https://doi.org/10.1016/S0006-3495(71)86276-8).

Webb, D. R., & King, J. R. (1984). Effects of wetting of insulation of bird and mammal coats. *Journal of Thermal Biology*, 9(3), 189-191. [https://doi.org/10.1016/0306-4565\(84\)90020-2](https://doi.org/10.1016/0306-4565(84)90020-2).

Whittow G.C. (1986) Regulation of body temperature. In: Sturkie P.D. (eds) *Avian Physiology*. Springer, New York, NY. https://doi.org/10.1007/978-1-4612-4862-0_9.

Williams C.M., Henry H.A.L., Sinclair B.J. (2015) Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biol. Rev.* 90, 214–235. (doi:10.1111/brv.12105).

Spatial variation in avian bill size is associated with temperature extremes in a major radiation of Australian passerines

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SUPPLEMENTAL MATERIAL

METHODS

Study System

Meliphagides consists of a diverse range of about 276 species (of which 145 are Australian) from five families; fairy-wrens and grasswrens, honeyeaters, thornbills, gerygones and allies, pardalotes and bristlebirds, with diverse morphologies and life histories (Marki et al. 2017). The group is widely distributed across the Australian continent, spanning a broad range of habitats in tropical, arid and temperate climate zones. Some species are confined to a specific climate zone, for example the grey-headed honeyeater *Ptilotula keartlandi* is only found in the arid zone, whereas others show wider distributions over multiple climate zones.

Bird Data

Specimens are housed in major museum collections in Australia: Australian Museum, Sydney; Queensland Museum, Brisbane; Australian National Wildlife Collection, Canberra; Museum Victoria, Melbourne; South Australian Museum, Adelaide; Western Australian Museum, Perth.

Statistics

Bill size patterns across geographic space

$Bill_{latitude} + longitude + elevation + minimumdistance_{coast} + body_{guild} + sex + season + year + 1 \vee species + 1 \vee IBRA + 1 \vee year + res_i$

[m1]

$Bill_{latitude} + latitude^2 + longitude + elevation + minimumdistance_{coast} + body_{guild} + sex + season + year + 1|species + 1|IBRA + 1 \vee year + res_i$

[m2]

Testing associations with climate

$$\begin{aligned}
& \text{BillDays35C} + \text{Days35C}^2 + \text{Days40C} + \text{Days40C}^2 + \sum .\text{vapour} + \sum . \\
& < +\text{Days.35C:} \sum .\text{vapour} + \text{Days40C:} \sum .\text{vapour} + \text{Days35C:} \sum . \\
& < +\text{Days40C:} \sum . \\
& < + \sum .\text{temp} + \sum .\text{temp}^2 + \sum .\text{temp:} \sum .\text{vapour} + \sum .\text{temp:} \sum . \\
& < +\text{Days5C} + \text{Days5C}^2 + \text{Days0C} + \text{Days0C}^2 + \text{Win.} < +\text{Days5C:Win.} \\
& < +\text{Days0C:Win.} < +\text{Win.temp} + \text{Win.temp}^2 + \text{Win.temp:Win.} \\
& < +\text{controlvariables} + \text{res}_i
\end{aligned}$$

[m3]

Testing the effect of phylogeny and species variation in bill size response

We estimated the phylogenetic signal (λ) using Eq 2. We included the variance of fixed effects in the denominator of Eq 2 when quantifying the phylogenetic signal to avoid underestimation of total phenotypic variance, as proposed in de Villemereuil et al. (2018).

$$\frac{\text{var. species.phylo}}{\text{var. effects} + \text{var. species.phylo} + \text{var. species.non - phylo} + \text{var. randomeffects} + \text{residuals}} \quad [\text{Eq2}]$$

We also tested if there were differences among species in how they responded to climate extremes within each climate zone, by comparing the AICc values of the best model from the climate zone analysis (*general structure indicated in m4*) with a separate model [m5], adding interaction terms between species *non-phylo* and all climate variables that were present in the best model from climate zone analysis in addition to all fixed (both climate and control fixed effects) and random terms that were present in the best model (*See Table 3 for climate variables in best models from climate zone analysis and for detailed random effect structure of m5, Table 4*).

To determine if evolutionary history plays a role in species responses, we included an interaction term between *species.phylo* and climate variables in the subsequent model [m6], and reported if this inclusion caused a substantial decrease in AICc values compared to AICc values of m5 as described in Gardner et al. 2016 (*See Table 4 for detailed random effect structure*). All models ran for 1001000 iterations using weakly informative priors, with a thinning interval of 1000 and burn-in phase of 1000.

$$\text{Billeffects} + 1|\text{species.non.phylo} + 1 \vee \text{species.phylo} + 1|\text{IBRA} + 1 \vee \text{year}$$

[m4]

$$\text{Billeffects} + 1|\text{Climate: species.non.phylo} + 1 \vee \text{species.phylo} + 1|\text{IBRA} + 1 \vee \text{year}[\text{m5}]$$

*Billeffects + 1|Climate: species.non.phylo + 1 v Climate: species.phylo + 1|IBRA + 1 v
year[m6]*

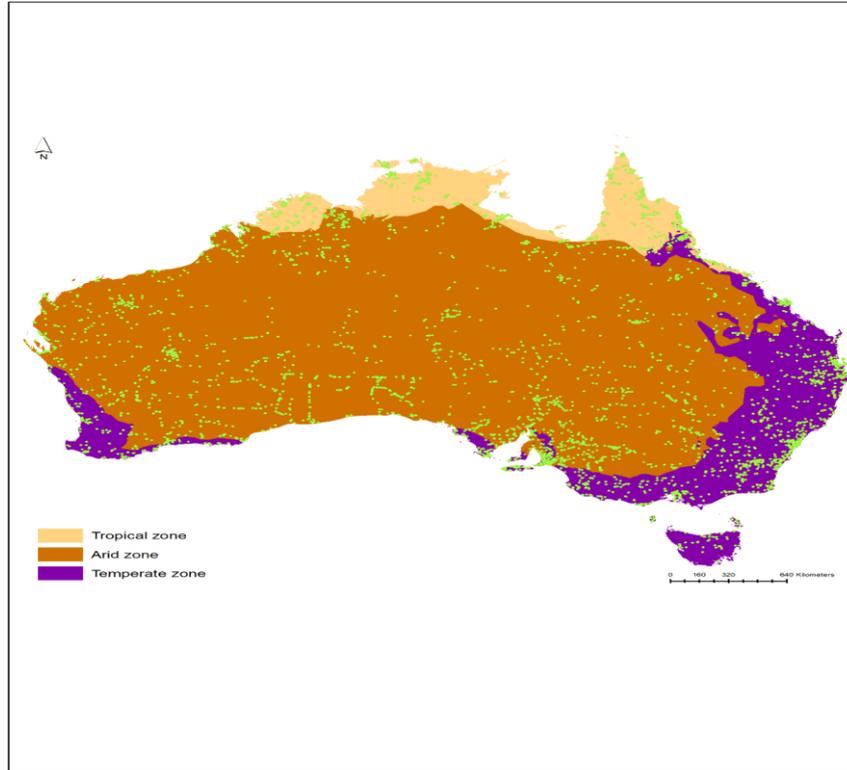


Figure S1. A map showing climate zones following the Köppen-Geiger climate classification (Köppen 1936) and the locations of measured individual *Meliphagides* in green dots.

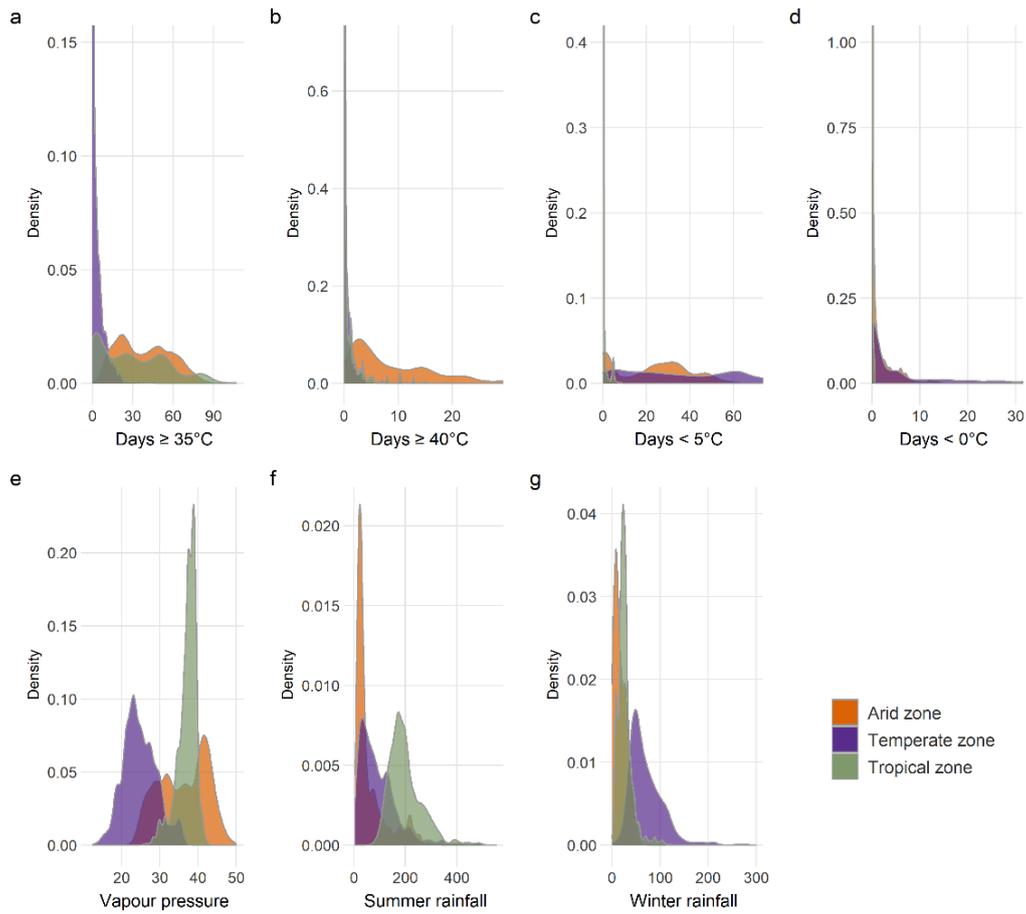


Figure S2. Density distributions showing the proportion of individuals that experienced particular climatic conditions in three climate zones: arid ($n = 4382$), temperate ($n = 4120$), tropics ($n = 1195$). Fig. shows the distribution of: a) average number of days $\geq 35^{\circ}\text{C}$ and b) $\geq 40^{\circ}\text{C}$ in the warm season, c) average number of days $< 5^{\circ}\text{C}$ and d) $< 0^{\circ}\text{C}$ in the cold season, e) mean vapour pressure in the warm season, f) rainfall in warm and g) cold seasons experienced by populations in arid, temperate and tropical climate zones.

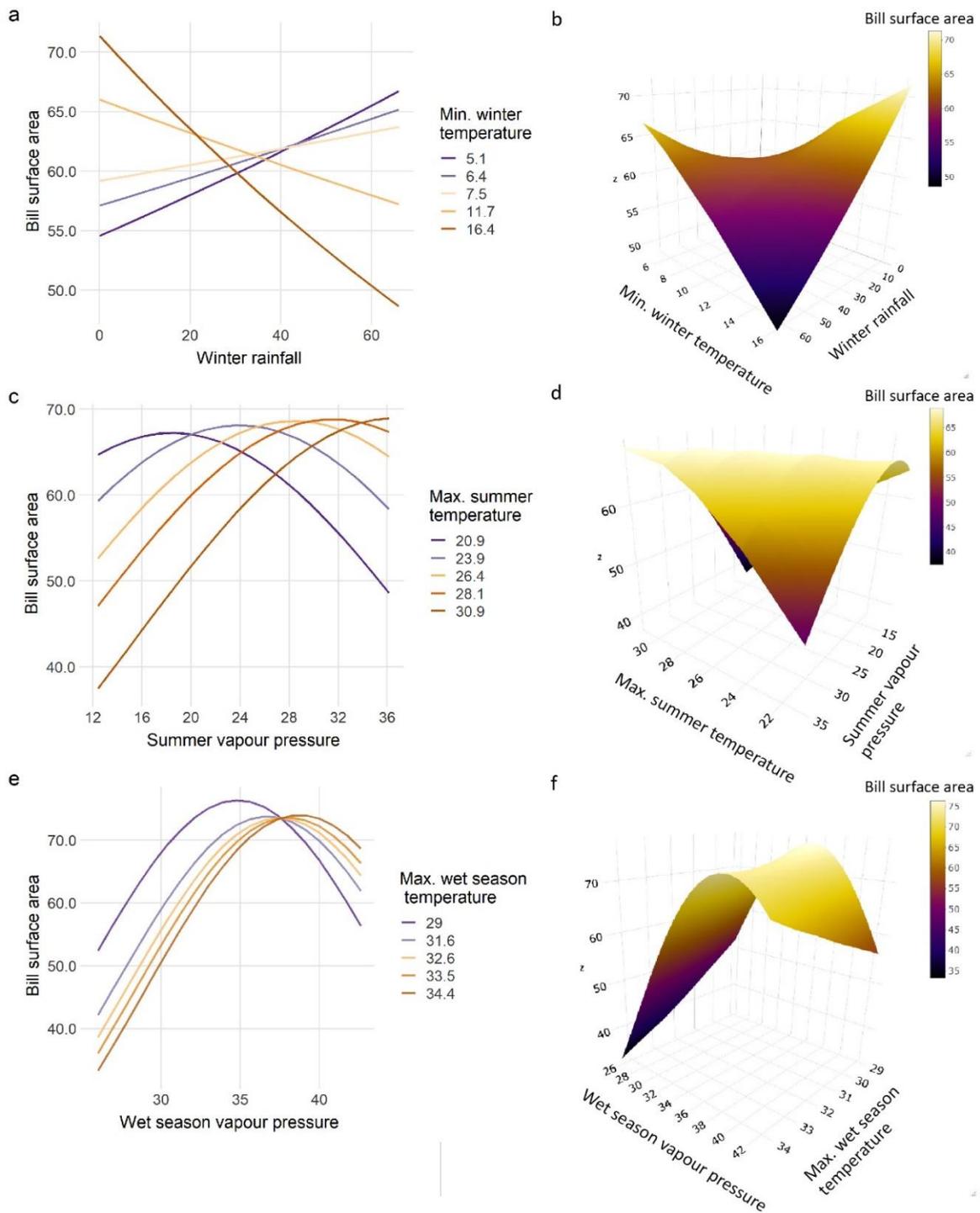


Figure S3. Associations between relative bill size in Meliphagides and seasonal mean temperature: (a) shows the relationship between bill size and mean minimum winter temperature in interaction with mean winter rainfall across 50 species in the arid zone; (c) mean maximum summer temperature in interaction with mean summer vapor pressure across 57 species within the temperate zone; (e) mean maximum wet season temperature in interaction with mean wet season vapor pressure across 27 species within the tropical zone. The 3D representation of (a), (c) and (e) are given in (b), (d) and (f), respectively.

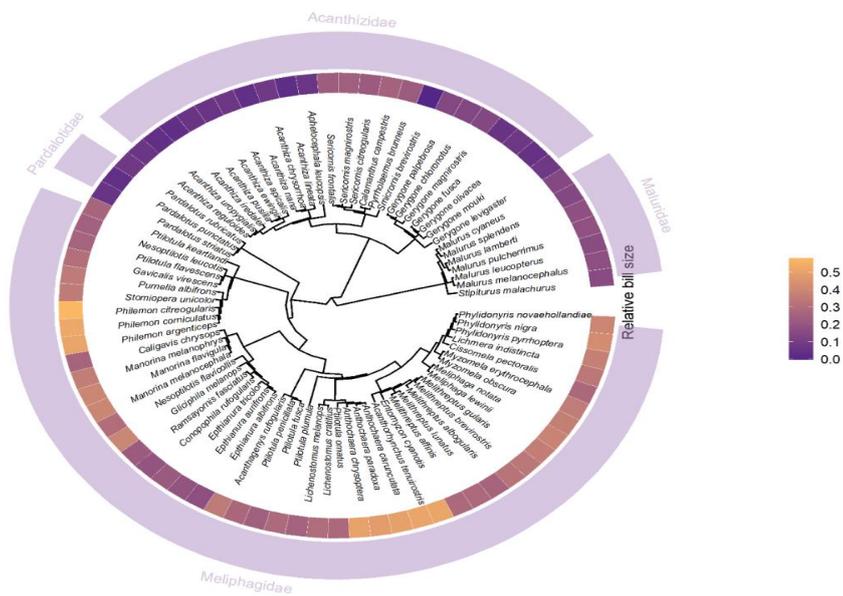


Figure S4. Phylogenetic distribution of relative bill size across study species. The colour gradient, from purple to yellow, indicates increasing relative bill size. Clustering of colours across the phylogeny indicates that closely related species have similar relative bill sizes. Relative bill sizes included here are the best linear unbiased prediction (BLUP) of bill surface area of species after accounting for variation in body size, sex, season, IBRA region, year of capture and sample size.

Table S1. Mean wing length (mm) and sample sizes of all species included in the study.

Species	Common name	Family	Mean wing length (mm)	Number of individuals
<i>Acanthagenys rufogularis</i>	Spiny-cheeked Honeyeater	Meliphagidae	110.5	151
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	Meliphagidae	64.6	243
<i>Anthochaera carunculata</i>	Red Wattlebird	Meliphagidae	152.1	153
<i>Anthochaera chrysoptera</i>	Little Wattlebird	Meliphagidae	126.7	88
<i>Anthochaera paradoxa</i>	Yellow Wattlebird	Meliphagidae	174.3	25
<i>Caligavis chrysops</i>	Yellow-faced Honeyeater	Meliphagidae	78.9	162
<i>Cissomela pectoralis</i>	Banded Honeyeater	Meliphagidae	65.5	46
<i>Conopophila rufogularis</i>	Rufous-throated Honeyeater	Meliphagidae	70.7	84
<i>Entomyzon cyanotis</i>	Blue-faced Honeyeater	Meliphagidae	146.4	133
<i>Epthianura albifrons</i>	White-fronted Chat	Meliphagidae	69.0	54
<i>Epthianura aurifrons</i>	Orange Chat	Meliphagidae	63.1	63
<i>Epthianura tricolor</i>	Crimson Chat	Meliphagidae	67.1	85
<i>Gavicalis virescens</i>	Singing Honeyeater	Meliphagidae	89.2	167
<i>Gliciphila melanops</i>	Tawny-crowned Honeyeater	Meliphagidae	78.4	43
<i>Lichenostomus cratitius</i>	Purple-gaped Honeyeater	Meliphagidae	81.7	43
<i>Lichenostomus melanops</i>	Yellow-tufted Honeyeater	Meliphagidae	85.0	122
<i>Lichmera indistincta</i>	Brown Honeyeater	Meliphagidae	65.9	209
<i>Manorina flavigula</i>	Yellow-throated Miner	Meliphagidae	126.1	270
<i>Manorina melanocephala</i>	Noisy Miner	Meliphagidae	135.8	165
<i>Manorina melanophrys</i>	Bell Miner	Meliphagidae	94.2	52
<i>Meliphaga lewinii</i>	Lewin's Honeyeater	Meliphagidae	97.6	148
<i>Meliphaga notata</i>	Yellow-spotted Honeyeater	Meliphagidae	83.1	49
<i>Melithreptus affinis</i>	Black-headed Honeyeater	Meliphagidae	76.8	31
<i>Melithreptus albogularis</i>	White-throated Honeyeater	Meliphagidae	71.2	145
<i>Melithreptus brevirostris</i>	Brown-headed Honeyeater	Meliphagidae	69.3	166
<i>Melithreptus gularis</i>	Black-chinned Honeyeater	Meliphagidae	84.0	69
<i>Melithreptus lunatus</i>	White-naped Honeyeater	Meliphagidae	75.3	84

<i>Myzomela erythrocephala</i>	Red-headed Honeyeater	Meliphagidae	57.6	65
<i>Myzomela obscura</i>	Dusky Honeyeater	Meliphagidae	66.8	78
<i>Nesoptilotis flavicollis</i>	Yellow-throated Honeyeater	Meliphagidae	100.4	36
<i>Nesoptilotis leucotis</i>	White-eared Honeyeater	Meliphagidae	90.1	160
<i>Philemon argenticeps</i>	Silver-crowned Friarbird	Meliphagidae	135.7	88
<i>Philemon citreogularis</i>	Little Friarbird	Meliphagidae	129.6	175
<i>Philemon corniculatus</i>	Noisy Friarbird	Meliphagidae	150.8	67
<i>Phylidonyris nigra</i>	White-cheeked Honeyeater	Meliphagidae	74.6	52
<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	Meliphagidae	76.7	153
<i>Phylidonyris pyrrhoptera</i>	Crescent Honeyeater	Meliphagidae	72.0	104
<i>Ptilotula flavescens</i>	Yellow-tinted Honeyeater	Meliphagidae	72.5	145
<i>Ptilotula fusca</i>	Fuscous Honeyeater	Meliphagidae	80.2	101
<i>Ptilotula keartlandi</i>	Grey-headed Honeyeater	Meliphagidae	76.6	70
<i>Ptilotula ornatus</i>	Yellow-plumed Honeyeater	Meliphagidae	82.4	108
<i>Ptilotula penicillata</i>	White-plumed Honeyeater	Meliphagidae	80.1	246
<i>Ptilotula plumula</i>	Grey-fronted Honeyeater	Meliphagidae	76.4	162
<i>Purnella albifrons</i>	White-fronted Honeyeater	Meliphagidae	79.1	79
<i>Ramsayornis fasciatus</i>	Bar-breasted Honeyeater	Meliphagidae	70.0	40
<i>Stomiopera unicolor</i>	White-gaped Honeyeater	Meliphagidae	95.5	84
<i>Malurus cyaneus</i>	Superb Fairy-wren	Maluridae	50.5	161
<i>Malurus lamberti</i>	Variegated Fairy-wren	Maluridae	47.9	423
<i>Malurus leucopterus</i>	White-winged Fairy-wren	Maluridae	46.6	128
<i>Malurus melanocephalus</i>	Red-backed Fairy-wren	Maluridae	42.6	137
<i>Malurus pulcherrimus</i>	Blue-breasted Fairy-wren	Maluridae	50.3	69
<i>Malurus splendens</i>	Splendid Fairy-wren	Maluridae	51.2	163
<i>Stipiturus malachurus</i>	Southern Emu-wren	Maluridae	42.9	52
<i>Acanthiza apicalis</i>	Inland Thornbill	Acanthizidae	52.1	212
<i>Acanthiza chrysorrhoa</i>	Yellow-rumped Thornbill	Acanthizidae	58.1	125
<i>Acanthiza ewingii</i>	Tasmanian Thornbill	Acanthizidae	53.0	41
<i>Acanthiza iredalei</i>	Slender-billed Thornbill	Acanthizidae	49.5	46

<i>Acanthiza lineata</i>	Striated Thornbill	Acanthizidae	52.0	182
<i>Acanthiza nana</i>	Yellow Thornbill	Acanthizidae	49.5	101
<i>Acanthiza pusilla</i>	Brown Thornbill	Acanthizidae	50.9	153
<i>Acanthiza reguloides</i>	Buff-rumped Thornbill	Acanthizidae	52.7	99
<i>Acanthiza uropygialis</i>	Chestnut-rumped Thornbill	Acanthizidae	50.8	159
<i>Aphelocephala leucopsis</i>	Southern Whiteface	Acanthizidae	58.2	282
<i>Calamanthus campestris</i>	Rufous Fieldwren	Acanthizidae	53.5	81
<i>Gerygone chloronotus</i>	Green-backed Gerygone	Acanthizidae	51.5	58
<i>Gerygone fusca</i>	Western Gerygone	Acanthizidae	55.6	179
<i>Gerygone levigaster</i>	Mangrove Gerygone	Acanthizidae	53.7	63
<i>Gerygone magnirostris</i>	Large-billed Gerygone	Acanthizidae	55.1	55
<i>Gerygone mouki</i>	Brown Gerygone	Acanthizidae	50.1	64
<i>Gerygone olivacea</i>	White-throated Gerygone	Acanthizidae	56.1	94
<i>Gerygone palpebrosa</i>	Fairy Gerygone	Acanthizidae	53.7	64
<i>Pyrrholaemus brunneus</i>	Redthroat	Acanthizidae	56.9	73
<i>Sericornis citreogularis</i>	Yellow-throated Scrubwren	Acanthizidae	67.3	70
<i>Sericornis frontalis</i>	White-browed Scrubwren	Acanthizidae	55.7	140
<i>Sericornis magnirostris</i>	Large-billed Scrubwren	Acanthizidae	56.3	133
<i>Smicrornis brevirostris</i>	Weebill	Acanthizidae	49.9	196
<i>Pardalotus punctatus</i>	Spotted Pardalote	Pardalotidae	58.0	331
<i>Pardalotus rubricatus</i>	Red-browed Pardalote	Pardalotidae	63.5	77
<i>Pardalotus striatus</i>	Striated Pardalote	Pardalotidae	63.4	573

Table S2. Parameter estimates for all models with $\Delta AICc \leq 2$ in continent wide analysis. All continuous variables except year of capture are standardized.

(Intercept)	Days $\geq 35^{\circ}C$	Days $\geq 35^{\circ}C^{\wedge}2$	Days $\geq 40^{\circ}C$	Days $\geq 40^{\circ}C^{\wedge}2$	Days $< 0^{\circ}C$	Days $< 0^{\circ}C^{\wedge}2$	Days $< 5^{\circ}C$	Days $< 5^{\circ}C^{\wedge}2$	Summer rainfall	Tmax	Tmax $^{\wedge}2$	Summer humidity	Summer humidity $^{\wedge}2$	Winter rainfall	Tmin	Tmin $^{\wedge}2$
-0.156	NA	NA	NA	NA	NA	NA	0.024	0.009	NA	-0.010	NA	NA	NA	NA	0.085	-0.013
-0.156	NA	NA	NA	NA	NA	NA	0.022	0.010	NA	NA	NA	-0.011	NA	NA	0.086	-0.013
-0.144	NA	NA	NA	NA	NA	NA	0.017	0.009	NA	NA	NA	NA	NA	NA	0.073	-0.010
-0.214	0.004	NA	NA	NA	NA	NA	0.024	0.009	NA	-0.014	NA	NA	NA	NA	0.086	-0.013
-0.147	0.020	NA	NA	NA	NA	NA	0.024	0.010	NA	-0.031	-0.008	NA	NA	NA	0.089	-0.013

Days $\geq 35^{\circ}C$: Summer rainfall	Days $\geq 35^{\circ}C$: Summer humidity	Days $\geq 40^{\circ}C$: Summer rainfall	Days $\geq 40^{\circ}C$: Summer humidity	Days $< 0^{\circ}C$: Winter rainfall	Days $< 5^{\circ}C$: Winter rainfall	Summer rainfall:Tmax	Tmax:Summer humidity	Winter rainfall:Tmin	Guild	Season	Sex	Wing length	Year of capture	df	logLik	AICc	delta
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.445	-0.0003	16	4898.776	-9765.496	0.000
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.446	-0.0003	16	4898.511	-9764.967	0.529
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.447	-0.0003	15	4897.394	-9764.740	0.756

NA	+	+	0.446	-	17	4899.34	-	0.87									
													0.0003		1	9764.619	7
NA	+	+	0.445	-	18	4900.08	-	1.38									
													0.0003		9	9764.109	7

Table S3. Parameter estimates for all models with $\Delta AICc \leq 2$ in arid zone analysis. All continuous variables except year of capture are standardized.

Intercept	Days $\geq 35^{\circ}\text{C}$	Days $\geq 35^{\circ}\text{C}^2$	Days $\geq 40^{\circ}\text{C}$	Days $\geq 40^{\circ}\text{C}^2$	Days $< 0^{\circ}\text{C}$	Days $< 0^{\circ}\text{C}^2$	Days $< 5^{\circ}\text{C}$	Days $< 5^{\circ}\text{C}^2$	Summer rainfall	Tmax	Tmax 2	Summer humidity	Summer humidity 2	Winter rainfall	Tmin	Tmin 2
-0.143	NA	NA	NA	NA	NA	NA	0.042	0.010	NA	NA	NA	0.012	NA	-0.001	0.085	-0.024
-0.039	NA	NA	NA	NA	NA	NA	0.043	0.009	NA	0.009	NA	NA	NA	-0.001	0.089	-0.024
-0.093	NA	NA	NA	NA	0.008	NA	NA	NA	NA	NA	NA	0.009	NA	0.011	0.054	NA
-0.082	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.048	NA
-0.144	NA	NA	NA	NA	NA	NA	0.014	NA	NA	NA	NA	0.018	NA	0.002	0.040	NA
-0.065	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.010	NA	0.011	0.048	NA
-0.130	NA	NA	NA	NA	0.007	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.053	NA
-0.151	NA	NA	NA	NA	NA	NA	0.017	NA	NA	NA	NA	NA	NA	NA	0.064	NA
-0.122	NA	NA	NA	NA	NA	NA	0.047	0.011	NA	NA	NA	NA	NA	-0.004	0.100	-0.028
-0.089	NA	NA	NA	NA	NA	NA	0.051	NA	NA	NA	NA	NA	NA	-0.001	0.104	-0.023
-0.087	NA	NA	NA	NA	NA	NA	0.011	NA	NA	NA	NA	0.017	-0.006	0.003	0.038	NA

Days \geq 35°C:Summer rainfall	Days \geq 35°C:Summer humidity	Days \geq 40°C:Summer rainfall	Days \geq 40°C:Summer humidity	Days<0°C:Winter rainfall	Days<5°C:Winter rainfall	Summer rainfall:Tmax	Tmax:Summer humidity	Winter rainfall:Tmin	Guild	Season	Sex	Wing length	Year of capture	df	AICc	delta
NA	NA	NA	NA	NA	-0.037	NA	NA	-0.058	NA	+	+	0.394	-0.001	19	-3824.545	0.000
NA	NA	NA	NA	NA	-0.037	NA	NA	-0.059	NA	+	+	0.396	-0.001	19	-3824.012	0.534
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.398	0.000	15	-3823.987	0.558
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.402	0.000	12	-3823.926	0.620
NA	NA	NA	NA	NA	-0.023	NA	NA	-0.039	NA	+	+	0.397	-0.001	17	-3823.742	0.804
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.400	0.000	14	-3823.325	1.220
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.400	0.000	13	-3823.231	1.315
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	+	+	0.402	0.000	13	-3822.949	1.597
NA	NA	NA	NA	NA	-0.036	NA	NA	-0.057	NA	+	+	0.398	-0.001	18	-3822.827	1.718
NA	NA	NA	NA	NA	-0.027	NA	NA	-0.047	NA	+	+	0.397	-0.001	17	-3822.706	1.840
NA	NA	NA	NA	NA	-0.023	NA	NA	-0.043	NA	+	+	0.397	-0.001	18	-3822.628	1.917

Table S3. continued

Table S4. Parameter estimates for all models with $\Delta AICc \leq 2$ in temperate zone analysis. All continuous variables except year of capture are standardized.

Intercept	Days $\geq 35^{\circ}C$	Days $\geq 35^{\circ}C^2$	Days $\geq 40^{\circ}C$	Days $\geq 40^{\circ}C^2$	Days $< 0^{\circ}C$	Days $< 0^{\circ}C^2$	Days $< 5^{\circ}C$	Days $< 5^{\circ}C^2$	Summer rainfall	Tmax	Tmax 2	Summer humidity	Summer humidity 2	Winter rainfall	Tmin	Tmin 2
-0.246	0.002	NA	NA	NA	NA	NA	NA	NA	-0.007	-0.044	-0.051	0.044	-0.030	NA	NA	NA
-0.217	0.003	NA	NA	NA	NA	NA	NA	NA	-0.006	-0.045	-0.024	0.042	NA	NA	NA	NA
-0.148	0.002	NA	NA	NA	NA	NA	NA	NA	-0.007	-0.041	-0.053	0.045	-0.031	0.007	NA	NA
-0.181	0.005	NA	NA	NA	NA	NA	0.027	NA	-0.011	-0.055	-0.057	0.054	-0.044	NA	0.026	NA
-0.214	0.000	NA	NA	NA	-0.028	NA	NA	NA	-0.006	-0.047	-0.071	0.062	-0.064	0.011	-0.030	0.020
-0.178	0.003	NA	NA	NA	NA	NA	NA	NA	-0.006	-0.042	-0.025	0.043	NA	0.006	NA	NA
-0.547	0.002	NA	NA	NA	NA	NA	NA	NA	-0.007	-0.044	-0.049	0.044	-0.028	NA	NA	NA
-0.193	0.002	NA	NA	NA	NA	NA	NA	NA	-0.008	-0.046	-0.051	0.047	-0.029	NA	-0.001	NA
-0.533	0.002	NA	NA	NA	NA	NA	NA	NA	-0.007	-0.040	-0.054	0.044	-0.032	0.006	NA	NA
-0.212	0.001	NA	NA	NA	-0.027	NA	NA	NA	-0.009	-0.050	-0.062	0.056	-0.055	NA	-0.026	0.016
-0.540	0.002	NA	NA	NA	NA	NA	NA	NA	-0.007	-0.044	-0.023	0.041	NA	NA	NA	NA

Table S4. continued

Days \geq 35°C:Summer rainfall	Days \geq 35°C:Summer humidity	Days \geq 40°C:Summer rainfall	Days \geq 40°C:Summer humidity	Days $<$ 0°C:Winter rainfall	Days $<$ 5°C:Winter rainfall	Summer rainfall:Tmax	Tmax:Summer humidity	Winter rainfall:Tmin	Guild	Season	Sex	Wing length	Year of capture	df	AICc	delta
-0.031	-0.014	NA	NA	NA	NA	0.006	0.076	NA	NA	+	+	0.465	0.000	21	-4233.683	0.000
-0.029	-0.012	NA	NA	NA	NA	0.006	0.018	NA	NA	+	+	0.464	0.000	20	-4233.526	0.157
-0.030	-0.013	NA	NA	NA	NA	0.007	0.077	NA	NA	+	+	0.464	0.000	22	-4233.227	0.456
-0.032	-0.014	NA	NA	NA	NA	0.007	0.093	NA	NA	+	+	0.464	0.000	23	-4233.019	0.665
-0.031	-0.014	NA	NA	NA	NA	0.007	0.128	0.011	NA	+	+	0.465	0.000	26	-4232.887	0.796
-0.029	-0.011	NA	NA	NA	NA	0.007	0.017	NA	NA	+	+	0.465	0.000	21	-4232.855	0.828
-0.031	-0.014	NA	NA	NA	NA	0.006	0.072	NA	+	+	+	0.465	0.000	22	-4232.689	0.995
-0.032	-0.014	NA	NA	NA	NA	0.006	0.075	NA	NA	+	+	0.465	0.000	22	-4231.842	1.842
-0.031	-0.013	NA	NA	NA	NA	0.007	0.079	NA	+	+	+	0.463	0.000	23	-4231.750	1.933
-0.031	-0.012	NA	NA	NA	NA	0.007	0.106	NA	NA	+	+	0.465	0.000	24	-4231.745	1.938
-0.030	-0.012	NA	NA	NA	NA	0.006	0.017	NA	+	+	+	0.463	0.000	21	-4231.696	1.987

Table S5. Parameter estimates for all models with $\Delta AICc \leq 2$ in tropical zone analysis. All continuous variables except year of capture are standardized.

Intercept	Days $\geq 35^{\circ}\text{C}$	Days $\geq 35^{\circ}\text{C}^2$	Days $\geq 40^{\circ}\text{C}$	Days $\geq 40^{\circ}\text{C}^2$	Days $< 0^{\circ}\text{C}$	Days $< 0^{\circ}\text{C}^2$	Days $< 5^{\circ}\text{C}$	Days $< 5^{\circ}\text{C}^2$	Wet season rainfall	Tmax	Tmax 2	Wet season humidity	Wet season humidity 2	Dry season rainfall	Tmin	Tmin 2
-0.212	NA	NA	NA	NA					NA	NA	NA	NA	NA	NA	NA	NA
-0.191	NA	NA	NA	NA					NA	-0.009	NA	0.004	-0.044	NA	NA	NA
-0.445	NA	NA	NA	NA					NA	NA	NA	NA	NA	NA	NA	NA

Days $\geq 35^{\circ}\text{C}$: Wet season rainfall	Days $\geq 35^{\circ}\text{C}$: Wet season humidity	Days $\geq 40^{\circ}\text{C}$: Wet season rainfall	Days $\geq 40^{\circ}\text{C}$: Wet season humidity	Days $< 0^{\circ}\text{C}$: Dry season rainfall	Days $< 5^{\circ}\text{C}$: Dry season rainfall	Wet season rainfall:Tmax	Tmax: Wet season humidity	Dry season rainfall:Tmin	Guild	Season	Sex	Wing length	Year of capture	df	logLik	AICc	delta
NA	NA	NA	NA			NA	NA	NA	NA	NA	+	0.583	-0.0014	8	755.746	-1495.370	0.000
NA	NA	NA	NA			NA	0.043	NA	NA	NA	+	0.586	-0.0015	12	759.231	-1494.199	1.171
NA	NA	NA	NA			NA	NA	NA	+	NA	+	0.579	-0.0014	9	755.923	-1493.693	1.677

Table S6. Comparison of models (m5, m6, m7) of bill size with increasing complexity of random effects structure, to test if bill size association with extremes vary among species and if there is a phylogenetic effect. Fixed effects are the variables appeared on top model in climate zone analysis (*see parameters in Table 3*); random effects include IBRA region, year of capture, *species-non.phylo* and *species-phylo* (species effect associated with phylogeny). Variation in associations between species was included by adding extremes as an interaction term to *species-non.phylo* and *species-phylo* as shown in the table. Comparisons were carried out only on populations across temperate and arid zones, but not on tropical populations as their bill sizes were not affected by frequency of exposure to extremes.

	Model	AIC
Arid zone	m4 random= \sim <i>species.non.phylo</i> + <i>species.phylo</i> + IBRA + year + res	-3821.855
	m5 random= \sim us(1+Days <5°C + Min. winter temperature + Winter rainfall + Days <5°C:Winter rainfall + Min.winter temperature:Winter rainfall): <i>species.non.phylo</i> + <i>species.phylo</i> + IBRA + year + res	-3961.181
	m6 random= \sim us(1+Days <5°C+ Min. winter temperature + Winter rainfall + Days < 5°C:Winter rainfall + Min.winter temperature:Winter rainfall): <i>species.non.phylo</i> + us(1+Days < 5°C+ Min. winter temperature+ Winter rainfall + Days <5°C:Winter rainfall + Min.winter temperature:Winter rainfall): <i>species.phylo</i> + IBRA + year + res	-3960.453
Temperate zone	m4 random= \sim <i>species.non.phylo</i> + <i>species.phylo</i> + IBRA + year + res	-4232.182
	m5 random= \sim us(1+Days \geq 35°C + Max. summer temperature + Summer humidity + Summer rainfall + Days \geq 35°C: Summer humidity + Max. summer temperature : Summer humidity+ Days \geq 35°C: Summer rainfall + Max. summer temperature: Summer rainfall): <i>species.non.phylo</i> + <i>species.phylo</i> + IBRA + year + res	-4487.924
	m6 random= \sim us(1+Days \geq 35°C + Max. summer temperature + Summer humidity + Summer rainfall + Days \geq 35°C: Summer humidity + Max. summer temperature : Summer humidity + Days \geq 35°C: Summer rainfall + Max. summer temperature: Summer rainfall): <i>species.non.phylo</i> + us(1+Days \geq 35°C + Max. summer temperature + Summer humidity + Summer rainfall + Days \geq 35°C: Summer humidity + Max. summer temperature : Summer humidity + Days \geq 35°C: Summer rainfall + Max. summer temperature: Summer rainfall): <i>species.phylo</i> + IBRA + year + res	-4485.425

Table S7. Results of MCMCglmm comparing average body sizes of Meliphagides in three climate zones i.e. arid, temperate and tropical. The intercept represents the expected average body size of Meliphagides in the arid zone after controlling for effects due to differences in the number sampled from each species, the capture year and the IBRA regions between the sampled individuals. The estimates for the temperate zone and tropical zone represent the difference in body size relative to the expected body size of Meliphagides in the arid zone. The estimates for climate zone, where 95% credibility intervals do not contain zero, are highlighted in bold.

Parameter	estimate	l-95% CI	u-95% CI
Intercept	75.067	69.107	81.153
Temperate zone	0.785	0.4459	1.1227
Tropical zone	-1.203	-1.675	-0.801