

# THE INFLUENCE OF THE CALIFORNIA MARINE LAYER ON BILL SIZE IN A GENERALIST SONGBIRD

Russell Greenberg<sup>1,2</sup> and Raymond M. Danner<sup>3,4</sup>

<sup>1</sup>*Smithsonian Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20008*

<sup>2</sup>*E-mail: greenbergr@si.edu*

<sup>3</sup>*Smithsonian Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20008*

<sup>4</sup>*Virginia Tech, Blacksburg, Virginia 24061*

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The hypothesis is tested that birds in hotter and drier environments may have larger bills to increase the surface area for heat dissipation. California provides a climatic gradient to test the influence of climate on bill size. Much of California experiences dry warm/hot summers and coastal areas experience cooler summers than interior localities. Based on measurements from 1488 museum skins, song sparrows showed increasing body-size-corrected bill surface area from the coast to the interior and declining in the far eastern desert. As predicted by Newton's convective heat transfer equation, relative bill size increased monotonically with temperature, and then decreased where average high temperatures exceed body temperature. Of the variables considered, distance from coast, average high summer temperature, and potential evapotranspiration showed a strong quadratic association with bill size and rainfall had a weaker negative relationship. Song sparrows on larger, warmer islands also had larger bills. A subsample of radiographed specimens showed that skeletal bill size is also correlated with temperature, demonstrating that bill size differences are not a result of variation in growth and wear of keratin. Combined with recent thermographic studies of heat loss in song sparrow bills, these results support the hypothesis that bill size in California song sparrows is selected for heat dissipation.

**KEY WORDS:** Allen's Rule, geographic variation, heat dissipation, mediterranean climate, thermography.

The avian bill is primarily adapted for obtaining and processing food. Thus, it is not surprising that differences in the size and shape of bills between closely related taxa have been shown to relate to forage and dietary differences (Grant 1986; Smith 1990; Remsen 1991; Benkman 1993; Giuliano et al. 2002). In addition to its feeding function, the avian bill is an uninsulated extremity. Poorly insulated extremities may be a source of intense heat loss and thus a reduction in their size will conserve and an increase will dissipate a disproportionate amount of heat (Bartholomew and Wilke 1956; Baudinette et al. 1976; Hill et al. 1980; Buchholz 1996; Nudds and

Oswald 2007). The tissue within the ramphotheca is vascularized (Lucas and Stettenheim 1972) and thermographic studies have determined that heat loss from blood flow within the bill can be substantial (Hagan and Heath 1980; Scott et al. 2008; Tattersall et al. 2009).

Few studies, however, have examined how bill size might vary with geographic patterns in ambient temperature. Snow (1954) demonstrated that European tits have larger bills in warmer climates. Over a half century later, Symonds and Tattersall (2010) found that bill size decreases with low minimum temperature

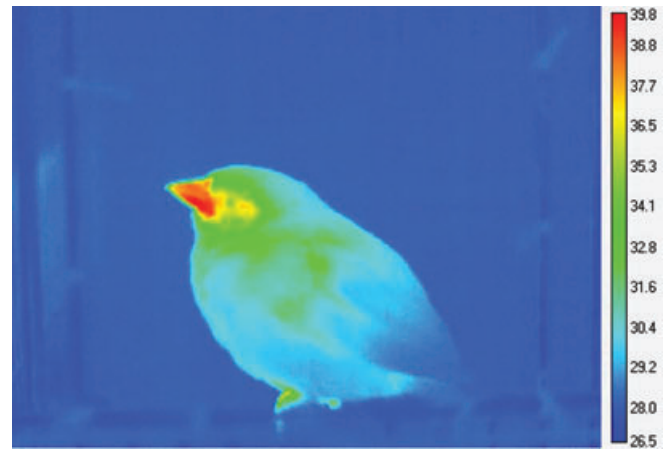


among species within several orders of birds. VanderWerf (2012) further documented a relationship between bill size and temperature in Elepaio (*Chasiempis* spp.) along elevational gradients in Hawaii.

The few previous studies have tended to focus on heat conservation (Snow 1954; Symonds and Tattersall 2010); smaller bills lose less heat. However, greater attention to issues of hyperthermia and heat dissipation (Speakman and Król 2010) should lead to the examination of the hypothesis that increased bill size facilitates metabolic heat loss under hot conditions. Greenberg et al. (2012) presented a striking correlation between high summer temperature and bill size among and within species of salt marsh dwelling sparrows (Emberizinae). Heat loss per se may not be as much of an issue in smaller endotherms (Speakman and Król 2010), but water loss due to evaporation from the skin and respiratory tract can be very high in small endotherms, such as passerines (Bartholomew and Cade 1963; Dawson 1982; Williams and Tieleman 2005). A 20 g passerine loses approximately 20% of its body weight daily due to evaporative water loss and species found in arid and salt marsh environments, where fresh water is limiting, consume between 50% and 100% of their weight in water when it is presented ad libitum, which is substantially more than similar birds in other environments (Bartholomew and Cade 1963). Given that the bill releases “dry” heat without evaporative water loss, heat loss from the bill may be an important alternative mechanism for heat dissipation when and where fresh water is limiting. Newton’s convective heat transfer equation states that the rate of heat loss over time is proportional to the difference in temperature between two substances, such as a bill and surrounding air. When air temperature is cooler than bill, heat is dissipated, but when air is warmer than the bill, heat will be absorbed. Based on this, we predicted that where the bill is hotter than air and there is potential for heat stress, a larger bill will be advantageous for heat dissipation. But where temperatures commonly exceed sparrow body temperatures (40–42°C), then smaller bills will absorb less heat.

Intraspecific comparisons make the strongest test for the effects of climate on body size and shape (Rensch 1938; Mayr 1956). The song sparrow (*Melospiza melodia*), a widespread and abundant North American songbird well known for its high degree of geographic variation (Miller 1956; Aldrich 1984; Smith 1998) is an ideal candidate species for an analysis of the effect of climate on bill size in birds. A song sparrow’s bill can be up to 10°C over ambient temperature (Fig. 1) and account for up to 9% of the total heat loss. Furthermore, two subspecies were compared (*M. m. atlantica* and *M. m. melodia*) and the former subspecies, which breeds in xeric coastal dune and salt marsh edge environments, had a 16.7% larger bill that released over 32% more heat from its bill than the latter (Greenberg et al. in press).

California has the ideal climate to test the joint effect of heat and water stress on bill size. For much of California, precipitation



**Figure 1.** Image of an Eastern song sparrow (*Melospiza melodia melodia*) taken with a FLIR T-300 demonstrates that the bill is vasodilated and is 10°C above ambient. Image was taken in study described in Greenberg et al. (in press).

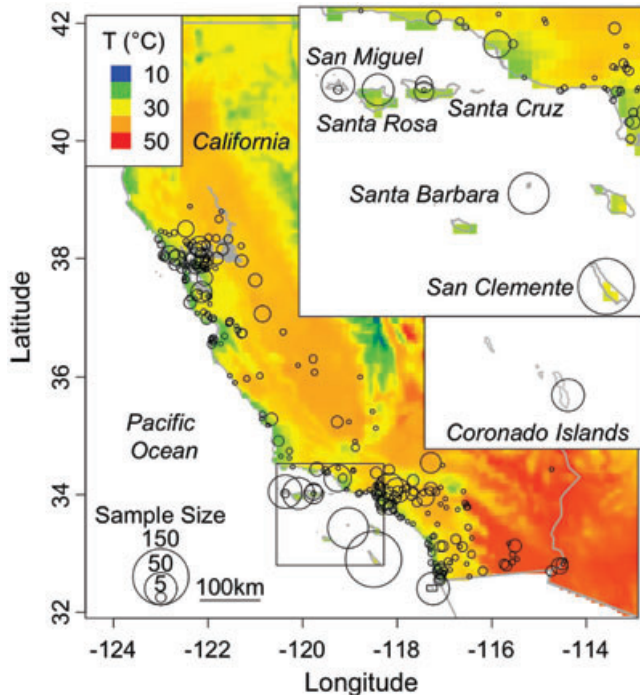
falls during the winter; summers are dry and ranging from warm along the coast to hot in the interior. Importantly, the warmest temperatures occur during periods of environmental moisture deficits (evapotranspiration > precipitation). The California Current and cold-water upwelling create cool coastal air, often augmented by cloudy conditions, and this marine layer reduces summer temperatures in areas closer to the coast. The distance of interior intrusion of the marine layer varies with the topography of the Coast Ranges, but the Central Valley and southern deserts are unaffected by coastal air masses and experience hot summers (Fig. 2). A large amount of variation in summer heat and winter precipitation allows the examination of the climatic correlates of morphological variation.

In this study, we asked the following questions: (1) Is the spatial pattern of bill size variation explained better by climatic than geographic variables? (2) Is maximum temperature an important predictor of bill size variation compared to other climatic variables? (3) Does bill size variation conform to the pattern predicted from the conductive heat loss equation (increasing until temperatures commonly exceed body temperature)? and (5) Do populations on islands show discrete variation consistent with the mainland trends?

## Methods

### STUDY AREA

Song sparrow specimens represented 250 localities from the Mexican border to Sonoma County along the coast (including the Channel Islands and Coronado Islands) and the Mohave and Sonoran Deserts to Yolo and Sacramento Counties in the interior. The area is approximately 875 km (6.8° latitude) from North to South and up to 220 km from the coast to the most interior



**Figure 2.** Map of sample sizes and localities for specimens used in measurements and average monthly high temperature (1981–2010) for the hottest month of the year at 4 km resolution (Prism Climate Group 2011).

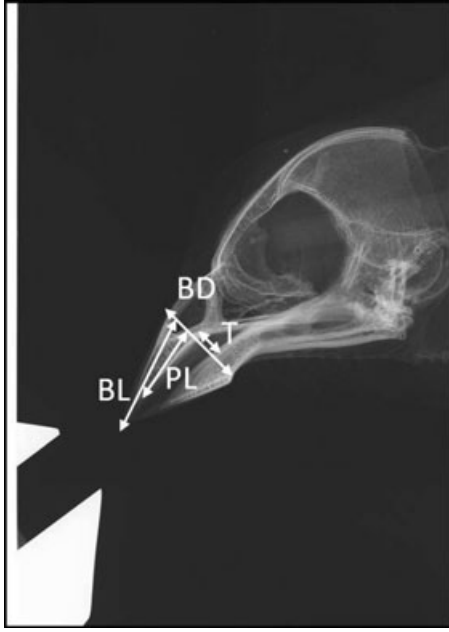
sites. The region of California covered by this study incorporates warm and hot dry summer subtropical climates to semiarid to arid conditions in the Central Valley and southeastern desert regions (modified Köpplen system, Kesseli 1942). The primary analysis was focused on the subspecies *M. m. heermanni* and *M. m. gouldii* on the California mainland. We also included data on *M. m. fallax*, a more distantly related subspecies found in riparian habitat in the Sonoran desert region (Patten and Pruett 2009). We focused some analysis on the island populations (*M. m. graminea*) because the islands have differentiated environments, populations have a distinct complement of mtDNA haplotypes from mainland birds (Fry and Zink 1998; Wilson 2008), and gene flow among sparrows on the different islands is extremely restricted (Wilson 2008; Wilson et al. 2009). We analyzed material from six islands, including three island populations where song sparrows are now extinct.

#### DATA

Bill measurements were taken from 1488 museum study skins by the lead author (data archived at <http://nationalzoo.si.edu/scbi/migratorybirds/research/data/>). Bill length (BL), bill depth (BD), and bill width (BW) were measured at the anterior edge of the nares with digital dial calipers (0.01 mm precision). Wing chord and tarsometatarsus length (joint of tibiotarsus and tarsometatarsus to the last complete scute before the articulation

of the halux) were also measured and collecting locality and date, sex, weight, and age were recorded from the specimen tag. Bill measurements were converted to an estimate of surface area of the distal portion of the bill using the following approximate formula for the lateral surface area of a nearly circular elliptical cone  $((BW + BD)/4) \times BL \times \pi$ . Specimens were selected to obtain adequate representation from the California islands (Channel and Coronado Islands,  $n = 462$ ), the coast to the outer and inner Coast Ranges and the Central Valley of Northern California ( $35.1\text{--}38.8^\circ\text{N}$ ,  $n = 481$ ), Coast, Coast Range, interior valleys and deserts of Southern California ( $32\text{--}35^\circ\text{N}$ ,  $n = 480$ ), and the Colorado River/Salton Sea region of California and Arizona ( $n = 65$ ) (Fig. 2 for geographic distribution). Collection date was first assigned a number between 1 and 365 with the year beginning on August 16, the approximate end of the breeding season. Date was then twice transformed. First, we created the variable  $dt$  in radians using the formula:  $dt = 2\pi \frac{\text{date}}{365}$  then  $dt$  was transformed to COSDT and SINDT, respectively, as  $\cos(dt)$  and  $\sin(dt)$ . The two terms COSDT and SINDT together comprise a single effect that we refer to below as date. The term date (a combination of  $cdt$  and  $sdt$ ) creates an oscillating response that forces the predicted value for bill size to be equivalent at  $\text{date} = 0$  and  $\text{date} = 365$  (Zar 1999).

Bill size can vary due to stable differences in skeletal structure or more seasonally variable differences in the growth and wear of the keratin sheath (ramphotheca) (Matthysen 1989). In addition to the standard bill measurements, we took digital radiographs of the head of a subsample of 161 sparrow specimen using a Kevex Microfocus x-ray source (PXS10–16W) with a 6 micron focal spot along with a Varian System Flat Panel Amorphous Silicon Digital X-Ray Detector (PaxScan 4030R) with a  $28.2 \times 40.6$  cm pixel area. This produced a 7.1 MB 8 bit TIFF file which was captured by Viva k.03 software. The image was transferred to ImageJ (Rasband 2011) where we measured both the bony (pre- and inferior maxillary bones) and ramphothecal (keratin) elements of the bill to determine which tissue type contributed to any differences in bill size between the subspecies. In these images, skeletal elements are visible within the outline of the ramphotheca. The measurements used in this article are BD at the anterior edge of the nasal cavity, tomium depth ( $T$ , distance between premaxillary and inferior maxillary bones at the same location as the BD measurement), and premaxillary (PL) and rhinothecal (BL) lengths from the anterior edge of the nasal cavity. A sample skull showing four sample measurements is depicted in Figure 3. An estimate of surface area of the cone of the skeletal bill was obtained as follows:  $(BD - T)/2 \times PL \times \pi$ , substituting  $BD/2$  for radius because only a lateral image was taken. This results in a slight underestimation as BW is slightly less than BD, but is unlikely to have biased the results. Total bill surface area was the same except we substituted BL for PL and BD for  $BD - T$ .



**Figure 3.** Radiograph of a sparrow showing the measurements taken for calculations of skeletal bill size. BL, bill length; PL, premaxillary length; BD, bill depth; T = tomium.

Temperature and rainfall data for the specimen data locations were 30 years averages estimated at a resolution of 4 km (1981–2011, Prism Climate Group 2011). All collecting localities were covered by the Prism dataset except the Coronado Islands. Climate data for the Coronado Islands were obtained from the Secretaria de Marina (SEMAR) of the Mexican government (<http://meteorologia.semar.gob.mx/meteorologia/coronado.htm>) and the Scripps Institution of Oceanography (<http://www.cordc.ucsd.edu/projects/sboo/coronadoislands/metstation.php>), which collectively ran weather stations from 2001 to 2011. Climatic variables included mean high temperature for the hottest month of the year (MAXTEMP), mean low temperature for the coldest month of the year (MINTEMP), and annual precipitation (PRECIP).

Evapotranspiration potential (ETo) data were downloaded from the California Irrigation Management Information System ([www.cimis.water.ca.gov](http://www.cimis.water.ca.gov)). Data were in the form of 2 km resolution maps, which were constructed following the Penman–Monteith ETo equation using maximum and minimum temperatures, altitude, wind speed, humidity data (to calculate vapor pressure deficits), and net radiation (Hart et al. 2009). We calculated the mean ETo value from 2003 to 2011 for each month and extracted the point estimate for each measurement locality for the month with the maximum value (this was always July).

Geographic variables for specimen locations included: Latitude (LAT), distance from coast (DIST), specimen origin from island or mainland (ISLAND), island size (ISIZE), and maximum island elevation (IELEV). DIST was measured on images in

Google Earth ([www.google.com/earth](http://www.google.com/earth)) and was used instead of longitude because the California coast from the Mexican border to Sonoma County is oriented at an approximately 45° angle from North. DIST was set to 0 for island populations.

### STATISTICAL ANALYSIS

All analyses were performed with Statistica version 10 (Statsoft, Inc. 2011). Bill size was standardized by two other features that are known to correlate with overall body size (wing chord and tarsus length). A principle component analysis (PCA) was conducted on these two variables and the first axis was used as an indicator of body size (variable weight was 0.78 for both variables; the first factor explained 63.5% of the total variance). We used the standardized residuals of the least-squared regression between PCA factor scores and bill surface area. The use of residuals can lead to a biased estimate of regression parameters when the variables are correlated (Freckleton 2002). However, with an  $r^2$  of 0.04 between PCA and bill size, this bias is negligible. The residuals were inspected and found to be normally distributed and homoscedastic. The relationship between PCA and bill surface area showed no signs of being curvilinear. Bill surface area was then used as the dependent variable in linear models with both combinations of both categorical data (SEX, ISLAND) and continuous variables (DATE, MAXTEMP, MINTEMP, PRECIP, LAT, DIST, ISIZE, IELEV). Models did not include interaction terms. Diagnostics based on residual plots were conducted on the top models to insure that they conformed to the assumptions of normally distributed errors, linearity, and homoscedasticity. We used an information theoretical approach (Akaike Information Criteria (corrected) [AICc], Burnham and Anderson 2002) to compare models that incorporated subsets of the possible explanatory variables for size-corrected bill surface area. Relative model probabilities were estimated using the evidence ratio (ratio of model weights). Inspection of scatter plots suggested that the dependent variables have curvilinear relationships with both MAXTEMP and DIST, so we included quadratic terms ( $x + x^2$ ) for those variables in candidate models, but transformed this expression by subtracting the mean of  $x$  from the  $x$  term. This reduced the collinearity between  $x$  and  $x^2$  (variance inflation factor went from 25 to 1.4) without changing the performance of the overall model. Some other potential covariates were highly intercorrelated (Tables S1, S2 present correlation tables). Where variance inflation factors were greater than 4, we either transformed the variables to reduce collinearity or selected one variable to include in the candidate models.

For the analysis of the whole dataset, we used the following strategy for the analyses: (1) we developed and selected the best models using only climatic or geographic variables based on AIC weights; (2) we examined the evidence ratio of AIC for the best climate versus the best geographic model to test the hypothesis

that the climate model explained more of the variation in bill size than the geographic model; (3) we compared standardized regression coefficients for the parameters in the global models for climate and geography to estimate the relative importance of individual variables; (4) and we added climatic variables to the top-ranked geographic model and used evidence ratios to determine which climate variable results in the greatest improvement in model fit.

We took a different approach for model selection for bill size variation across the California islands, using only one set of models. Because of collinearity, two potential variables were not included (IELEV and MINTEMP). With a reduced number of variables, we determined that only one (LAT) was locational (ISIZE is an environmental and not a locational variable). Thus, separate model selection for geographic and climatic variables was unwarranted. The variables in the single model set included MAXTEMP, ISIZE, LAT, and PRECIP

Because both SEX (Arcese et al. 2002) and DATE (Matthysen 1989) are known to influence bill size, we included these variables in all models. With the provision that certain parameters were paired (such as the  $x$  and  $x^2$  terms for DIST and MAXTEMP and the sine and cosine terms for DATE), all possible models were included for model selection. Model weights for the top and null (SEX and DATE) models and their evidence ratios are presented in the text, along with adjusted  $R^2$  values and standardized regression coefficients ( $\beta$ ) for the top model. Log-likelihood, AICc,  $\Delta$ AICc, and model weight ( $w$ ) are presented for all models (Tables S3–S7), along with the  $\beta$ s for the parameters of interest. Betas were derived by model averaging when the complete model held less than 95% of the total model weight (Tables S7–S8).

## Results

### GEOGRAPHICAL PATTERNS OF BILL SIZE VARIATION

The full geographic model had almost all of the model weight ( $w = 1.0$ ,  $R^2_{\text{adj}} = 0.27$ ,  $df = 7$ , 1480) and this model had  $3.74 \times 10^{95}$  greater probability than the null model (SEX and DATE alone). Standardized  $\beta$ s for individual variables indicate that DIST ( $0.71 \pm 0.04$ ) and DIST<sup>2</sup> ( $-0.55 \pm 0.04$ ) had much more effect on the full model regression equation than presence on island ( $-0.13 \pm 0.02$ ) and latitude ( $-0.08 \pm 0.02$ ). Figure 4A shows the quadratic relationship between bill size and distance from the coast.

### CLIMATE CORRELATES OF BILL SIZE VARIATION

The full climate model, which included a quadratic term MAXTEMP, MINTEMP, and PRECIP, was the best model ( $w = 0.995$ , adjusted  $R^2 = 0.39$ ,  $df = 7$ , 1480). Based on the evidence ratio, the top model was approximately  $3.0 \times 10^{162}$  times more likely than the null model including only sex and date. The best cli-

matic model had essentially all of the model weight (1.00) when compared to the best geographic model ( $\Delta$ AIC = 337.3, evidence ratio  $1.71 \times 10^{169}$ ). Based on standardized  $\beta$  in the full model, MAXTEMP was the most important variable ( $0.614 \pm 0.03$ ) followed by the MAXTEMP<sup>2</sup> ( $-0.382 \pm 0.03$ ), with MINTEMP ( $0.024 \pm 0.02$ ) and PRECIP ( $0.117 \pm 0.02$ ) contributing little to the model. Figure 4B shows the quadratic relationship between bill size and MAXTEMP.

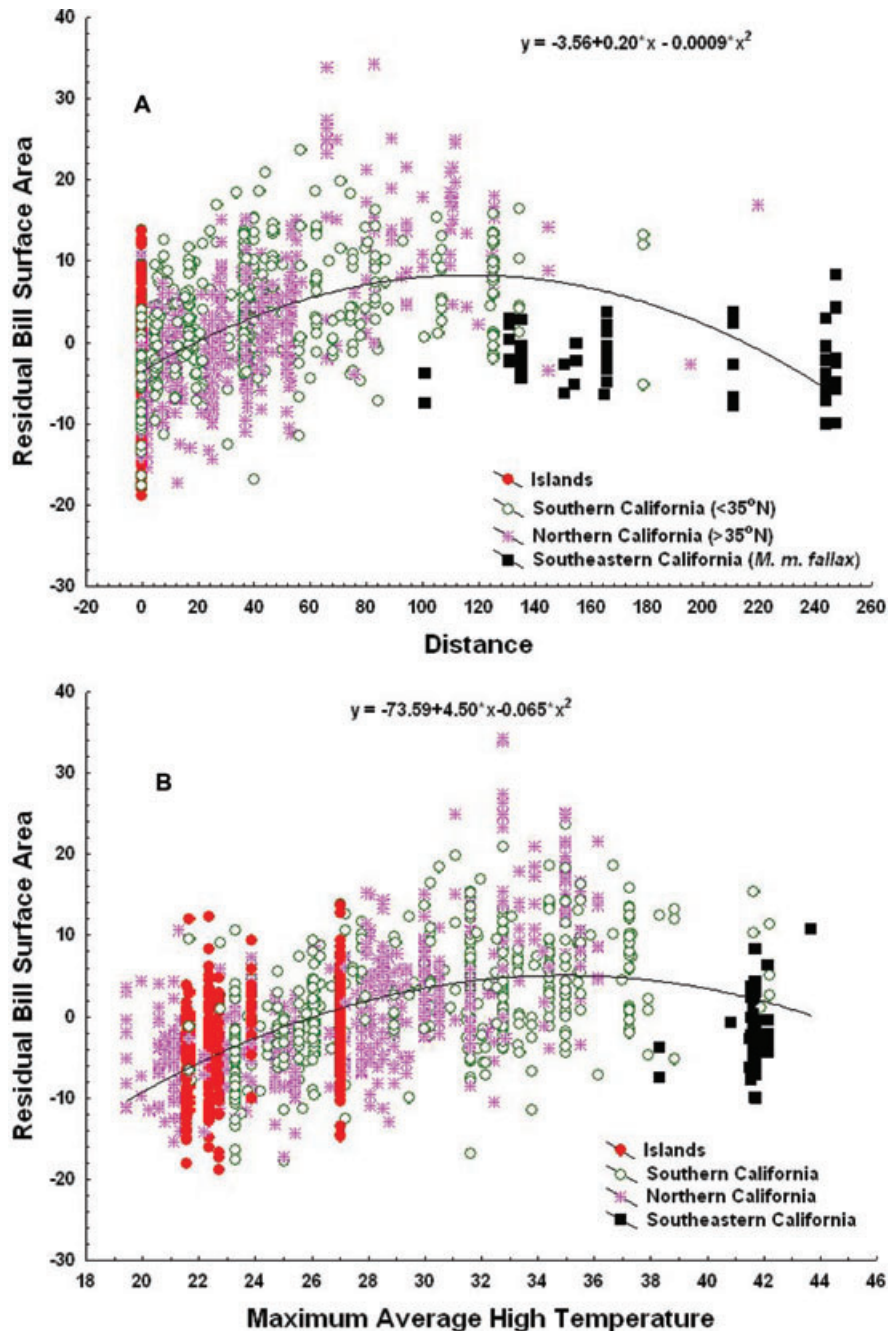
Another way to look at the importance of particular climatic variables is to examine how much variation in bill size is explained beyond variables indicating specimen collection location. This is a conservative approach, as some of the variation explained by the geographic model may be the result of correlated variation in climate. We compared models for size-corrected bill areas using best geographic model (see above) as a base model and individually added climatic variables to see which climatic variable provides the greatest improvement of the overall fit. The model with MAXTEMP<sup>2</sup> was  $1.82 \times 10^{67}$  more likely than the geographic model alone, and  $6.75 \times 10^{50}$  and  $1.28 \times 10^{58}$  times more likely than the models with PRECIP and MINTEMP added, respectively. Importantly, the model with MAXTEMP<sup>2</sup> was  $9.06 \times 10^{25}$  more likely than the model with MAXTEMP, providing additional support that the quadratic relationship between bill size and high temperatures (see Table S9).

### VARIATION AMONG ISLAND POPULATIONS

For variation in body-size-corrected bill surface areas for island populations, the best model combined MAXTEMP and ISIZE garnering 65% of the model weight ( $W = 0.646$ ,  $R^2_{\text{adj}} = 0.33$ ,  $df = 5$ , 455, Fig. 5) followed by MAXTEMP + ISIZE + LAT ( $W = 0.251$ ,  $R^2_{\text{adj}} = 0.33$ ,  $df = 6$ , 454). The evidence ratio between these two models is only 2.56, but the top model has only two variables and thus is more parsimonious. The top model was  $1.44 \times 10^{95}$  times more likely than the null model. This model with both ISIZE and MAXTEMP was  $1.22 \times 10^{32}$  and  $6.73 \times 10^{34}$  times more likely than the model with only ISIZE or MAXTEMP, respectively. The model-averaged  $\beta$  and unconditional standard errors for MAXTEMP and ISIZE were 0.351 (0.06) and 0.342 (0.06), respectively, compared to 0.02 (0.04) and 0.01 (0.03) for LAT and PREC. Further evidence that MAXTEMP and ISIZE were the variables of paramount importance is that they appear in the top four models. In contrast, all models with PRE and LAT without MAXTEMP and ISIZE were ranked lower than the null model (SEX + DATE only).

### COMPARISON OF SKELETAL VERSUS TOTAL BILL SIZE

A comparison of skeletal and total bill surface areas to average maximum high temperature (Fig. 6) shows that both increased significantly with temperature ( $r = 0.72$  and  $0.67$ , respectively,  $t = 13.1$ ,  $11.4$ ;  $P < 0.001$  for both). Skeletal bill surface area



**Figure 4.** (A) Distance from coast versus bill surface area and (B) average high temperature for the hottest month versus bill surface area in song sparrows. Second-degree polynomial regression lines are presented.

increased with a shallower slope than total bill surface area (0.88 vs. 1.41; ANCOVA for interaction between measurement type (skeletal or total) and temperature:  $F_{1,321} = 13.48$ ,  $P = 0.0028$ ).

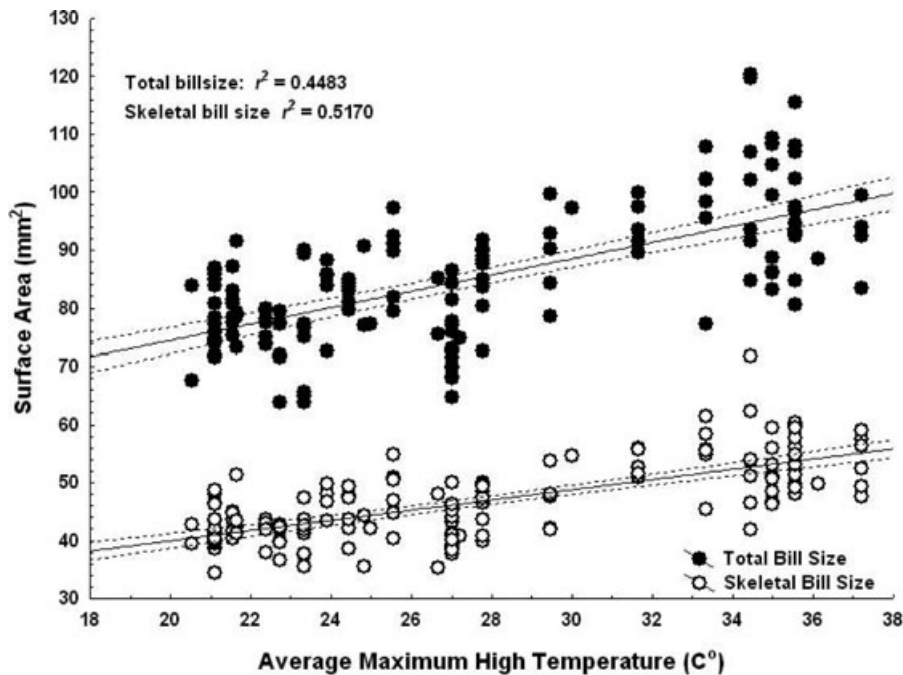
## Discussion

### PATTERN IN RELATIVE BILL SIZE

The climatic model for bill size variation received far greater support than the geographic model. Among the climatic variables,

the MAXTEMP<sup>2</sup> was the most important based on a comparison of  $\beta$ s. Competing models with climate variables added individually to the full geographic model provided strong support for the overriding importance of MAXTEMP<sup>2</sup> in explaining bill size variation.

Size-corrected bill surface area increased with distance from coast with the greatest increase occurring within the first 80–100 km. Bill size on the islands was similar to that found along the coast of the mainland. Between 20°C and 35°C for MAXTEMP, uncorrected bill surface area increased at a rate of approximately



**Figure 5.** Average high temperature for the hottest month versus skeletal and total size (anterior to the nasal cavity). Regression line and 95% confidence interval are presented.

0.64 mm<sup>2</sup> for every degree Celsius, resulting in bills that averaging 23.5% higher in surface area in the warmest versus the coolest sites in this range.

Including the *M. m. fallax* specimens from the far eastern deserts, we found a decline from the linear increase predicted from other populations and the entire bill size–temperature gradient formed a curve that could be modeled with a quadratic term (MAXTEMP<sup>2</sup>). This decline at the highest temperatures is to be expected if conductive heat transfer during the hottest conditions is important for selecting bill size. As maximum bill temperature exceeds ambient temperature for a significant amount of time, the differential between the two will reverse and heat transfer will proceed from the environment to the bill.

The pattern of interisland variation further supports the hypothesis about the effect of temperature on the evolution of song sparrow bill size in two ways: (1) bill size generally increased with average island maximum high temperatures; and (2) bill size is notably larger on large islands. A model that combines these two variables is strongly supported in the AICc analysis. As Fischer et al. (2009) demonstrated, the marine layer has very heterogeneous impact on different parts of Santa Cruz Island (one of the large islands) depending on topography, slope aspect, and distance from the island edge). It is reasonable to assume that the effect of the marine layer will be more homogeneous on the small islands with less topographic relief. With regards to the influence of phylogeny and relatedness of island populations on the pattern, although a phylogeny of the island sparrows has not been com-

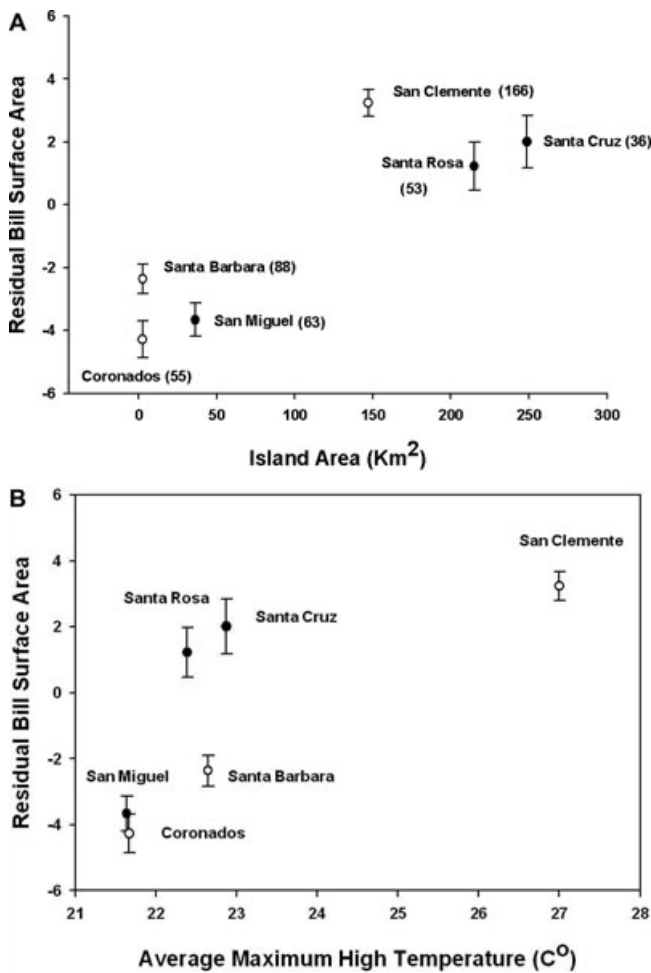
pleted, mtDNA haplotypes are unshared between the southern and northern island groups (Wilson 2008), yet bill size is unrelated to a latitudinal gradient among the islands.

The geographic and climatic patterns of bill size variation is based on body-size-corrected values and therefore are not a consequence of a positive allometric relationship driven by a shift in overall body size, as has been found for other shape variables in song sparrows (Smith 1998).

Total bill size and the size of the skeletal bill elements showed a similar pattern of increase with higher maximum temperatures. The similarity in pattern argues against the hypothesis that the variation in bill size along the temperature gradient results from differential wear or growth of the horny cover of the bill. It is interesting to note that the relationship between total BL and temperature has both a steeper slope than that of the skeletal elements, suggesting that plasticity in the keratin covering may play a role in the observed patterns.

#### SONG SPARROW BILLS AS A HEAT RADIATOR

The predicted strong correlation between bill size and high summer temperatures found across California song sparrows supports the heat dissipation hypothesis for bill size variation. Part of the hypothesis is that heat dissipation from the bill minimizes evaporative water loss. ETo, a more direct indicator of evaporative water loss, also varies across the coast to interior gradient. ETo values, which are based on temperature and relative humidity, air pressure, solar radiation, and wind, are an appropriate indicator



**Figure 6.** Surface area of song sparrow bills as a function of (A) island size and (B) maximum mean high summer temperatures.

of the potential cost of evaporative water loss. In this case,  $E_{\text{To}}$  showed the same relationship to bill size as high temperature, but the two variables were so highly correlated that it is impossible to partition the effects of the two variables (due to their collinearity). Rainfall had a much smaller effect on bill size ( $\beta = -0.117$ ) than high temperature, but it was in the direction of bill size increasing with increased aridity.

The correlation between bill size and temperature is a necessary but not sufficient finding for the hypothesis. There is increasing support, however, for the importance of bird bills, including those of the song sparrow, in heat dissipation. Thermographic studies have demonstrated that because of vasodilation of the blood vessels underlying the ramphotheca, bird bills can be substantially hotter than the insulated body surfaces and the ambient air temperature (Hagan and Heath 1980; Scott et al. 2008; Tattersall et al. 2009). Song sparrows from the eastern United States have been shown to have bills  $5^{\circ}\text{C}$ – $10^{\circ}\text{C}$  higher than ambient (Greenberg et al. in press). In a comparison of two subspecies of song sparrow, Greenberg et al. (in press) demonstrated

32% greater heat loss in the subspecies with a 13.5% larger bill (measured at the nares, thus comparable to this study). The bill size difference at the extremes of the gradient in California is 23.5% which is much greater than the difference between the two eastern subspecies even though average body size is similar (approximately 19.5 g for both California mainland, eastern and Atlantic).

Although a complete water budget has not been developed, Greenberg et al. (in press) provided a rough estimate of a 7.7% increase in water conserved over the eastern song sparrow by the Atlantic song sparrow due to the greater amount of heat lost from its bill. Once again, given the greater differential in bill size, the savings in water could be substantially greater in the interior song sparrows of California.

The data from song sparrows also provide insight into the question: which season is of paramount importance in selecting for bill size. Some studies have argued that bill size decreases with cold winter temperatures to reduce heat loss (Snow 1954; Symonds and Tattersall 2010). A similar case has been made for tarsus size in seabirds (Nudds and Oswald 2007). In the case of the song sparrows, high summer temperature is the important explanatory variable, and models with minimum winter temperature are generally not well supported. Because in the gradient studied, the two variables are negatively correlated ( $-0.26$ ), the relationship between song sparrow bill size and winter temperature is negative, the opposite of what would be predicted from a heat conservation hypothesis.

#### ECOLOGICAL ATTRIBUTES THAT CONTRIBUTE TO BILL SIZE VARIATION DUE TO HEAT DISSIPATION

Although the thermal issues we discuss could affect the bill of any bird species, certain ecological attributes may lead to the expression of thermal properties as a clear temperature-based gradient in bill size. The song sparrow is a dietary generalist that tends to occupy communities with low avian species diversity. Less precise matching of bill size to a particular resource might allow thermal properties to play a larger role in determining optimal bill size. This is a similar argument to one proposed by Schluter and Smith (1986) when they suggested that selection on BD and BW, associated with foraging on seeds of different strength, was found to be weak in song sparrows compared to similar measures in Galapagos Finches.

#### POSSIBLE INDIRECT EFFECTS OF CLIMATE

The strength of the correlation between bill size and temperature, independent of latitude and the mainland and found in isolated island populations, is most parsimoniously explained by the direct physiological effect of climate. However, an indirect effect of climate could at least help explain the gradient bill size variation, if a key food resource also varies with high temperatures in a way



that would influence bill function. However, no data currently exists that suggest that either the spectrum of seeds available or the actual seeds consumed by song sparrows covary with high summer temperatures in the region we studied.

### PLASTICITY VERSUS ADAPTATION

One additional alternative, suggested by Allen (1877) himself, is that large bills are a direct result of plasticity rather than adaptation to a hotter climate. Reciprocal transplantation of nestlings (James 1983) and rearing under different climate conditions in the laboratory (James 1991) has shown that in addition to a genetic component, there is an environmental component to bill growth in the Red-winged Blackbird (*Agelaius phoeniceus*). Recent common garden experiments with two subspecies of the swamp sparrow (*Melospiza georgiana*), a congener of the song sparrow, however, demonstrated that bill size differences comparable to what we report were stable under the laboratory rearing conditions (Ballentine and Greenberg 2010).

### PREDICTIONS FOR THE HEAT DISSIPATION HYPOTHESIS

The next step in investigating the heat dissipation/water conservation hypothesis for California song sparrows is to examine the thermal properties of bills and impact heat loss might have on the heat and water budgets of sparrows from different populations along the temperature gradient. If the physiological mechanism is further supported, then field tests of the fitness consequences is needed to establish the importance of heat dissipation in the selection for bill size. Even if these values of increased heat loss and water savings are not enough to effect survival, it is likely that they will allow the performance of fitness-related activities during high temperature periods, such as provisioning of young, and the patrolling of territories by males (for a similar argument, see Darnell and Munguia 2011). Singing is particularly expensive for respiratory water loss and thus may be most impacted by marginal increases in water conservation. A demographic prediction is that birds with bigger bills (controlled for body-size variation) will have greater reproductive output than birds with smaller bills in hotter, drier areas, whereas a trophic-based hypothesis might predict that over-winter survival will be the more important correlate of selection on bill size.

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## Supporting Information

The following supporting information is available for this article:

**Figure S1.** Comparison of residual bill surface area plotted against maximum monthly average potential evapotranspiration (2003–2011, [www.cimis.water.ca.gov](http://www.cimis.water.ca.gov)) and maximum monthly average high temperature (1981–2011) (Prism Climate Group 2011).

**Table S1.** Correlation matrix for covariates used in overall linear models ( $N = 1488$ ).

**Table S2.** Correlation matrix for nonforced covariates used in island-restricted linear models ( $N = 461$ ).

**Table S3.** Linear models describing bill surface area of California song sparrows as a function of geographic variables (SEX and DATE in all models), with log-likelihood, number of parameters ( $k$ ), AICc values, and model weights.

**Table S4.** Linear models describing bill surface area of California song sparrows as a function of climatic variables (SEX and DATE in all models), with log-likelihood, number of parameters ( $k$ ), AICc values, and model weights ( $w$ ).

**Table S5.** Models describing size-corrected bill surface area of California song sparrows as a function of all geographic variables, SEX and DATE with climate variables added: log-likelihood, number of parameters ( $k$ ), AICc values, and model weights ( $w$ ) ( $N = 1488$ ).

**Table S6.** Models describing bill surface area of California islands song sparrows as a function of climatic and geographic variables (controlled for sex and date effects), with log-likelihood, number of parameters ( $k$ ), AICc values, and model weights ( $w$ ).

**Table S7.** Betas of covariates used in complete geographic linear models ( $N = 1488$ ).

**Table S8.** Model-averaged betas of covariates used in complete island linear models ( $N = 461$ ).

**Table S9.** Betas of covariates used in complete climatic linear models ( $N = 1488$ ).

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

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