



High summer temperature explains bill size variation in salt marsh sparrows

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Physiological factors are rarely proposed to account for variation in the morphology of feeding structures. Recently, bird bills have been demonstrated to be important convective and radiant heat sinks. Larger bills have greater surface area than smaller bills and could serve as more effective thermoregulatory organs under hot conditions. The heat radiating function of bills should be more important in open habitats with little shade and stronger convective winds. Furthermore, as a means of dumping heat without increasing water loss through evaporation, bills might play a particularly important thermoregulatory role in heat loss in windy habitat where fresh water is limited. North American salt marshes provide a latitudinal gradient of relatively homogeneous habitat that is windy, open, and fresh-water limited. To examine the potential role of thermoregulation in determining bill size variation among ten species or subspecies of tidal marsh sparrows, we plotted bill size against maximum summer and minimum winter temperatures. Bill surface areas increases with summer temperature, which explained 82–89% of the variance (depending upon sex) when we controlled for genus membership. Latitude alone predicted bill surface area much more poorly than summer temperature, and winter temperatures explained < 10% of the variance in winter bill size. Tidal marsh sparrow bill morphology may, to a large degree, reflect the role of the bill in expelling excess body heat in these unbuffered, fresh-water-limited environments. This new example of Allen's rule reaffirms the importance of physiological constraints on the evolution of vertebrate morphologies, even in bird bills, which have conventionally been considered as products of adaptation to foraging niche.

Size variation among bird species' bills is often related to differences in foraging behavior and diet, and studies of the avian bill provide some of the strongest evidence of the effects of food supply and resource competition on a morphological feature. Short-term changes in average bill size within species have been associated with changes in resource availability (Boag and Grant 1981), the addition and subtraction of potentially competitive species (Grant and Grant 2006), and changes in social competition (Clegg and Owens 2002). Indeed the diversity of bill morphology among closely related birds has become a textbook example of adaptation to a diversity of ecological niches (Freed et al. 1987).

The avian bill may also play a role in body-temperature regulation, by acting as a radiator for excess heat (Hagan and Heath 1980, Scott et al. 2008, Tattersall et al. 2009) in a manner similar to other poorly insulated extremities in animals, including the flippers of seals and sea lions (Whittow et al. 1972), the ear pinnae of hares (Hill et al. 1980), the head wattles of chickens and turkeys (Buckholz 1996), and the legs and feet of birds (Baudinette et al. 1976). The avian bill is covered in a cornified layer that is underlaid by heavily vascularized tissue (Lucas and Stettenheim 1972). In what is probably an extreme case of the thermal capabilities of bird

bills, Tattersall et al. (2009) demonstrated that adult toucans *Ramphastos toco* vasodilated the tissue underlying the ramphotheca during high temperatures and reduced flow in the face of cold temperatures. Up to 60% of excess body heat was dissipated at high temperature through the bill. The possible role that heat loss has in shaping bill morphology was documented by Symonds and Tattersall (2010) who showed a relationship between bill size and latitude, altitude, and temperature among all but one of the seven taxonomic groups of birds they examined. In this case, the authors emphasized that to reduce heat loss bill size is smaller in colder climates. The relationship between bill shape and size and temperature and humidity has also been established for red-winged blackbirds *Agelaius phoeniceus* by James (1991).

If the avian bill can be used as a radiator to expel excess heat under thermally stressful conditions, this function should be particularly important in birds that occupy climatically poorly-buffered habitats where opportunities to escape direct insolation are reduced. Further, thermal stress is closely related to water loss, as evaporative cooling is one of the most important physiological responses to high temperatures (Bartholomew and Cade 1963). Heat loss via the bill and other extremities may reduce evaporative water

loss and be advantageous as an alternative mechanism of thermoregulation in water-limited environments. In one of the classic examples of Allen's rule, North American jackrabbits (*Lepus* spp.) live in xeric environments and have a relatively small amount of water available for evaporative cooling (Schmidt-Nielson et al. 1965). Limits on evaporative cooling appear to be compensated by the release of heat from their large ears (Hill et al. 1980), which thereby avoids reliance on increased evaporation through nasal or oral sinuses. Among jackrabbits, ear size is larger in taxa that live in warmer environments (Stevenson 1986), but the equal importance of xeric environments in explaining this and other examples of Allen's rule has been largely overlooked.

The Emberizid sparrows of North American salt marshes provide an excellent comparative system to study the possible role of climatic factors in bill-size evolution. Salt marshes offer a thermal gradient of structurally similar habitat along a latitudinally broad range of the three North American coastlines (Fig. 1). Close examination of these taxa has led to the description of at least 10 different subspecies or subspecies groups (from three genera), which reflect at least seven different tidal-marsh invasions. Tidal marsh sparrows show consistently larger bills and greater bill size dimorphism than both their closest relatives and emberizids

in general (Grenier and Greenberg 2005, Greenberg and Olsen 2010). In addition, salt marsh sparrows display striking variation in their relative bill size in an ecosystem that does not appear to reflect the same level of variation in food resources. We explore this variation to examine whether bill size variation is related to high summer temperature, low winter temperature, or latitude as a test of the importance of thermoregulation and osmoregulation on the evolution of avian morphology

Methods

Morphological measurements

Measurements were taken from 1380 specimens (see Supplementary material Appendix 1 for mean, SD, and sample size). Breeding season measurements are from specimens collected April–July and are, for the most part, the same measurements used in Greenberg and Olsen (2010). In some cases, subsequent work has allowed us to augment the sample size with data from additional specimens. Measurements for wintering birds were obtained from museum skins collected between late November and early March. Separate means for measurements from winter

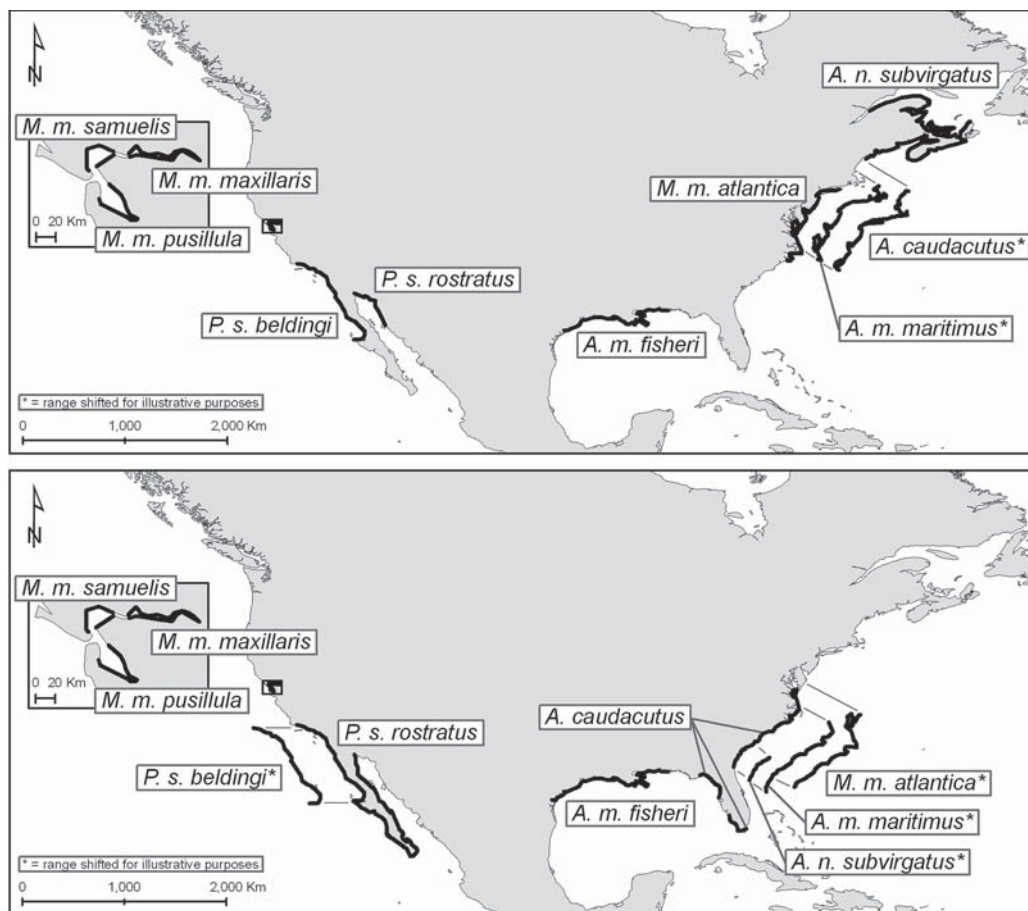


Figure 1. Maps of the summer (top) and winter (bottom) ranges of ten salt marsh sparrow taxa used in this study. * denotes that range was shifted for illustrative purposes. Ranges are based on American Ornithologists Union (1957) and Greenlaw and Woolfenden (2007). Not all salt marsh taxa are depicted, hence the gaps in the distribution of *Ammodramus maritimus* and *Passerculus sandwichensis*.

specimens were used because bill size often varies seasonally in sparrows in general (Davis 1954, Morton and Morton 1987) and salt marsh sparrows in particular (Greenberg unpubl.). The taxa used in the analysis include four subspecies of song sparrow (Atlantic song sparrow *Melospiza melodia atlantica*, Alameda song sparrow *M. m. pusillula*, San Pablo song sparrow *M. m. samuelis*, and Susuin song sparrow *M. m. maxillaris*); two subspecies of savannah sparrow (large-billed savannah sparrow *Passerculus sandwichensis rostratus*, and Belding's savannah sparrow *P. s. beldingi*) and four subspecies (in three separate species) of *Ammodramus* (Acadian Nelson's sparrow *A. nelson subvirgatus*, saltmarsh sparrow *A. caudacutus*, Atlantic seaside sparrow *A. maritimus maritimus*, and Gulf Coast seaside sparrow *A. m. fisheri*). Tidal marsh sparrows that do not breed in salt marshes (salinity > 10 ppt), such as the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*), were not included. Not all salt marsh subspecies were included. Subspecies that were not included were members of already represented subspecies groups where the climate was similar. For example only one of four Atlantic coast subspecies and one of five Gulf Coast subspecies of seaside sparrows were included. Similarly, only one of three subspecies of both Belding's and large-billed savannah sparrow were used. There is no reason to believe that inclusion of these subspecies would substantially change any of the results of these analyses.

Length, depth, and width of the bills were measured at the anterior edge of the nares using digital calipers (0.01 mm precision). Bill surface area was calculated by using the approximate formula for the lateral surface area of a (nearly circular) elliptical cone $((BD + BW)/4) \times BL$. Body mass data were taken from published and unpublished studies totaling 924 individuals (see Supplementary material Appendix 1 for mean surface area (mm³), SD, and sample size).

Temperature and latitude data

Recent thirty-year monthly average temperatures were obtained from several websites for weather stations close to the collecting sites of each specimen (www.climate.weatheroffice.gc.ca/climate_normals/index_e.html), www.weather.com and www.climateemp.info). For each collecting location, we calculated the mean maximum daily temperature for the month of July for breeding specimens and the mean, minimum daily January temperatures for nonbreeding specimens. We developed three descriptive statistics relating these climate data to each salt-marsh sparrow taxon: A) overall temperature averages across all specimens of each taxon, which therefore produced a temperature mean that is weighted by the portion of the range where the taxa was most frequently collected; B) the median of the maximum and minimum average high temperatures (or low temperatures in winter) from all of the collecting sites; and C) the maximum (breeding) or minimum (winter) average temperature encountered at any single collecting site. For the breeding season, all three measures are highly correlated (r for the average and median was 0.98 and for the average and maximum was 0.91). We present results based only on the weighted average in this paper,

since the bill sizes are likewise weighted by the collection locations. Mean maximum summer temperatures were only weakly correlated with mean breeding latitude ($r = 0.47$), and mean minimum winter temperatures showed only a moderate correlation with mean winter latitude ($r = 0.59$). We therefore used temperature and latitude separately as predictive variables for bill surface area. Average summer high and winter low temperatures are presented along with average latitude for each taxon in Supplementary material Appendix 2.

Statistical analysis

We used an information-theoretic approach to model selection within an ANOVA/ANCOVA design. Relative bill size was the dependent variable, mass, latitude and temperature were continuous predictors, and genus was a categorical predictor. Models tested include the intercept-only, individual variables and genus combined with either temperature or latitude. Model performance was assessed using the Akaike's information criterion (AIC) corrected for sample size (AIC_C; Anderson 2008). From this, the ΔAIC_C and model weights were calculated. For specific comparisons, we took the ratio of the model weights (evidence ratio). As a descriptive statistic of scatter in the linear relationship between variables, we present the r^2 for the models with the best support based on ΔAIC_C values.

As there is significant sexual dimorphism in bill size among the tidal marsh sparrow taxa (Greenberg and Olsen 2010) and seasonal variation in bill size (Greenberg unpubl.), we analyzed the sexes and seasons separately.

Results

The best model for relative bill size in male salt-marsh sparrow taxa during the breeding season included only mean maximum summer temperature (hereafter 'summer temperature') as the predictive variable (Table 1, Fig. 2). For males, the summer temperature model held 74.8% of the model weight followed by the temperature-genus model with 19.2% of the weight ($\Delta AIC_C = 2.71$). The evidence ratio of this model compared to the intercept-only model (no predictive variables) was 93.6 for temperature, 24.6 for summer temperature + genus, and only 4.8 for the temperature + mass. The corrected r^2 was 0.89 for the summer temperature-genus model and only 0.70 for the summer temperature-only model. For breeding females (Table 2,

Table 1. Statistics associated with the information-theoretic analysis of regression models for summer bill size in males of ten salt marsh sparrow taxa. Only the intercept model and models with ΔAIC_C less than the intercept model are presented in Tables (for all models see Supplementary material Appendix 3).

Model	logL	Parameters	AIC _C	ΔAIC_C	Model weight
temperature (temp)	-8.74	3	27.48	0	0.7439
temp + genus	-2.59	5	30.19	2.71	0.1917
temp + mass	-8.70	5	33.40	5.92	0.038
intercept	-15.42	2	36.56	9.08	0.0079

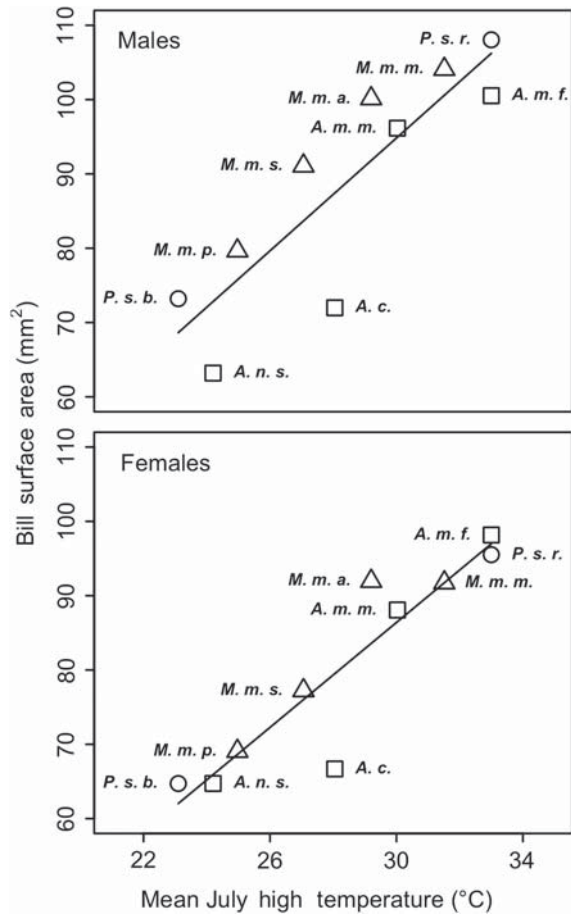


Figure 2. Mean average high July temperature versus mean breeding season bill surface area in males and females of salt marsh sparrow taxa (\square = *Ammodramus*, Δ = *Melospiza*, and \circ = *Passerculus*). The regression equations for males was $Y = -17.63 + 3.74X$ and for females $Y = -19.43 + 3.5X$.

Fig. 2), the summer temperature model held 67.0% of the model weight. Summer temperature + mass had a small ΔAIC_c (1.56), and thus this model performed almost as well as the summer temperature-only model. The evidence ratio supporting the summer temperature-only model over the intercept-only model was 1496.7, and the ratio for the summer temperature-mass model had an evidence ratio of 685.5 suggesting a high likelihood that summer temperature is an important variable. The evidence ratio of the temperature-genus model over the intercept-only model was 2.5, indicating a lower probability that genus is an important predictor of bill surface area. The r^2 was 0.82

Table 2. Statistics associated with the information theoretic analysis of regression models for summer bill surface area in females of ten salt marsh sparrow taxa.

Model	logL	Parameters	AIC_c	ΔAIC_c	Model weight
temp	-5.29	3	20.58	0	0.6785
temp + mass	-3.07	4	22.15	1.57	0.3102
lat + mass	-7.13	4	30.25	9.67	0.0054
mass	-10.39	3	30.77	10.19	0.0042
temp + genus	-4.27	5	33.55	12.97	0.0010
intercept	-14.75	2	35.21	14.624558	0.0004

for the summer temperature-only model and 0.85 for the summer temperature-mass model.

The winter analysis for both sexes (Table 3 and 4) indicated that the mass-only models had the highest weights (71.6% for males and 92.5% for females). The r^2 for mass were 0.45 and 0.65 and for temperature were 0.03 and 0.09 (male and female, respectively). The large scatter associated with the temperature/bill size relationship for winter specimens can be seen in Fig. 3. This evidence suggests that bill size may be related to mass but is unrelated to low winter temperature or latitude.

Discussion

Patterns of bill size variation

Among salt marsh sparrows, bill surface area is positively correlated with high summer temperatures. Furthermore, the relationship between bill surface area and temperature can be found within the three different genera of salt marsh sparrows. The close association between bill size and high temperatures supports the hypothesis that bills may have a thermoregulatory function. There was little support for either minimum winter temperatures or breeding or winter latitude as important correlates of bill size. An expected relationship between bill surface area and mass may have simply been overwhelmed by the strength of the temperature-bill size relationship during the breeding season, but mass appears as the only important explanatory variable for the winter analysis.

Along the east coast of North America, summer temperatures generally decrease with latitude. Temperatures, however, are decoupled from latitude along the Pacific Coast, which explains the poor correlation between temperature and latitude. The California Current brings relatively cold waters down the coast of California and northern Baja California. As a result, the shores of the San Francisco estuaries and the coastal marshes of southern Baja California have unexpectedly low summer temperatures. In the San Francisco Bay region, a sharp temperature gradient occurs between the areas adjacent to the San Francisco Bay and areas on the opposite side of the inner Coast Range. Areas interior to the Bay are not influenced by the marine layer and temperatures soar during the summer months. Such a distinct temperature divide can be found between the San Pablo and South San Francisco Bay estuaries and Suisun Bay, each of which possesses a unique endemic tidal-marsh sparrow. The thermoregulatory hypothesis predicts distinct differences in bill size across this region to match the dramatic shifts in temperature. The three distinct song sparrow subspecies of the San Francisco Bay region conform precisely to these predictions, with the large-billed Suisun song sparrow occupying

Table 3. Statistics associated with the information theoretical analysis of regression models for winter bill surface area in males of ten salt marsh sparrow taxa.

Model	logL	Parameters	AIC_c	ΔAIC_c	Model weight
mass	-11.50	3	33.00	0	0.7164
intercept	-15.11	2	35.93	2.93	0.1655

Table 4. Statistics associated with the information theoretical analysis of regression models for winter bill surface areas in females of ten salt marsh sparrow taxa.

Model	logL	Parameters	AIC _c	ΔAIC _c	Model weight
mass	-8.15	3	26.29	0	0.9245
mass + temp	-8.14	4	32.28	6.00	0.0461
intercept	-14.03	2	33.77	7.48	0.0220

the highest temperature regions and the two smaller-billed subspecies occupying the cooler regions. Likewise, summer temperatures along the southern California and northern Baja California coast, where Belding's savannah sparrows breed with their relatively small bill, are cool compared to the region immediately inland. With no cold, offshore current and associated marine layer, however, the coastal marshes along the Sea of Cortez, where the large-billed savannah sparrow breeds, are exceedingly hot.

Although Tattersall et al. (2009) emphasized the toucan's ability to radiate heat when temperatures are high, Symonds and Tattersall (2010) focused on the effect of low temperatures on bill size in their comparative cross-taxa study. In salt marsh sparrows, bill size is unrelated to minimum winter temperatures. The lack of morphological adaptation to winter conditions may be related in part to migratory behavior. The salt marsh sparrow taxa are resident

in regions with moderate winters (west coast) and migrate from regions of extreme cold (northeast coast) to areas with more moderate winters. Wintering in moderate climates may prevent strong selection from extremely cold temperatures. During the breeding season, however, the tidal-marsh taxa spread out along the coastlines to occupy all climatic conditions including areas with summer highs that regularly exceed the high end of the thermal neutral zone of most songbirds.

Alternative hypotheses for why high summer temperature correlates with bill size

The strength of the correlation between temperatures and bill size suggests that bill size is an adaptation to cope with hot climatic conditions. We have focused on direct heat transfer from the bill surface as the most likely mechanism underlying variation in bill surface area. Other thermoregulatory adaptations may affect bill morphology, but are largely uninvestigated. For example, respiratory turbinates (Geist 2000) housed partially in the nasal cavity appear to be important in heat and water flux in birds (Geist 2000) and mammals. It has been suggested that marine carnivores have high surface area of respiratory turbinates because they live in a salt water environment where water conservation is at a premium (Van Valkenburgh 2011). This hypothesis has obvious implications for saltmarsh sparrows; however, little is known about morphological variation in birds and how this might impact overall bill size.

In addition to physiological factors, temperature regime may influence prey size and provide an ecological basis for bill size variation. The strength of the relationship between temperature and bill size in tidal marsh sparrows during the breeding season probably renders a food-based hypothesis far less parsimonious than a direct physiological response to temperature.

Factors favoring a climatic influence on bill size

If temperature regulation plays a role in selecting for bill size in birds, it is likely to vary with the ecology of the species and the environmental characteristics of their habitat. It is not surprising that Allen's rule (extremities vary in size with temperature) has not been consistently supported (Stevenson 1986, Zink and Remsen 1986, Symonds and Tattersall 2010) as the natural history of the species studied probably influences the importance of climate versus other sources of selection (Stevenson et al. 1986). We suggest six factors of tidal-marsh sparrows that may favor high temperature as a driving force in bill morphology evolution.

Generalized diet and foraging ecology: selection for bill shapes that enable birds to handle particular dietary items or forage in specialized microhabitats might counter selection for an optimized thermoregulatory device. Emberizid sparrows, however, are generally quite generalized in their diet and feeding behavior. Diet data on tidal marsh sparrows indicates they feed on a wide variety of invertebrates, as well as seeds, and forage in tidal mud, detritus, and grass and shrub foliage (Grenier and Greenberg 2006). Salt marsh sparrows often live in environments with low species

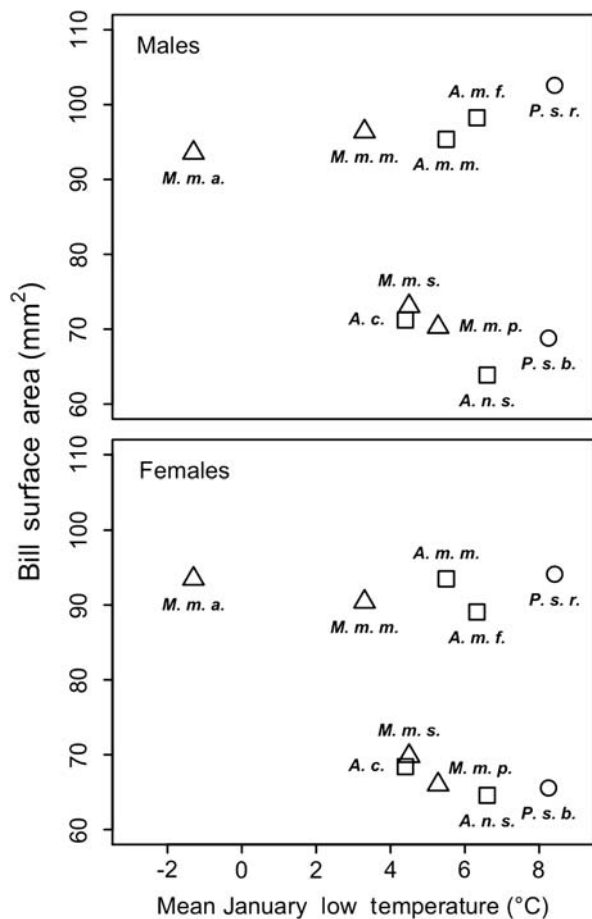


Figure 3. Mean average low January temperature versus mean winter bill surface area in males and females of salt marsh sparrow taxa (□ = *Ammodramus*, Δ = *Melospiza*, and ○ = *Passerculus*).

diversity and interspecific competition may play a relatively small role in restricting bill size (Greenberg and Olsen 2010).

Pronounced thermal gradient: tidal-marsh sparrows breed along the North American coastline from as far north as Nova Scotia and central California to as far south as the coast of the Gulf of Mexico and the Sea of Cortez. As a result, different populations of the same species and different species occupy environments with an impressive range in average daily high summer temperatures (from 21° to over 35°C), which allows for a wide diversity of the strength of selection for thermoregulatory adaptation.

Low thermal buffering: salt marshes are structurally very simple habitats offering little shade. Further, the ability to seek shade within this single, simple layer is hampered by the influx of high tides.

Small body size: because of their high surface area-to-volume ratio, small birds are less prone to thermal stress than larger birds. Small birds, however, process much more water on a weight-specific basis than do larger birds, and combined with their large relative surface area, this makes them particularly susceptible to the negative impacts of water loss (Williams and Tieleman 2005). Further, evaporative water loss does not completely eliminate excess metabolic heat when birds are above their thermal neutral zone (Bartholomew and Cade 1963), and therefore alternative ways to release heat that do not involve water loss should be advantageous.

Water limitation: salt marsh birds are surrounded by water, but its salinity may make it a limiting resource. Some species of salt marsh sparrow are capable of concentrating and voiding excess salt (Cade and Bartholomew 1959, Poulson 1969), however it is unclear how prevalent this is in the field (Goldstein 2006). Salt marsh sparrows generally have enlarged kidneys, particularly the medullary cortex, which processes large quantities of water, and their ad libitum water demands exceed, often greatly, those of similarly sized non-salt marsh passerines (Goldstein 2006). Thus, water conservation appears to be important for salt marsh sparrows, which would contribute to the advantage that convective and radiative heat loss from the bill would confer over increased evaporation.

Windy conditions: wind contributes greatly to evaporative water loss (Wolf and Walsburg 1996). Salt marshes are often windy compared to inland habitats, because the temperature differential between coastal waters and land help generate local convective winds. This would further increase the osmoregulatory advantage of a large bill as a primary thermoregulatory organ.

Possible selective advantage of bill-size variation

Sparrow bills are relatively much smaller than toucan bills and therefore the bill is likely to play a commensurately reduced role in heat loss. The surface area of a sparrow bill is approximately 1–2% of total surface area (Walsburg and King 1978). However, bills contribute significantly to the total unfeathered (poorly insulated) surface area – approximately 20–25% (unpubl.). Sparrow taxa that breed in areas with over 30°C average high summer temperatures

have bills that average 40% greater in surface area than taxa that breed in areas where high temperatures average <25°C. This increase in bill area could result in a relatively large increase in heat loss and contribute to a critical, albeit incremental, increase in ability to tolerate high temperatures. Although direct mortality for small birds during extreme heat events has been rarely documented (McKechnie and Wolf 2010), having a larger bill may confer important advantages even where the effects of heat are sublethal. For example, having a more effective way of releasing excess body heat should allow territorial males and provisioning pairs to remain active longer in the day and later in the breeding season. The sexual dimorphism of salt marsh sparrow bills (Greenberg and Olsen 2010) might result from the higher exposure of territorial males than females to direct insolation, as they remain active on song perches throughout the nesting cycle. This may be even more important in salt marshes than in other hot and dry environments, as birds in these habitats exhibit breeding seasons that are generally longer than those in nearby inland habitats due to high rates of nest loss from flooding and predation (Greenberg et al. 2006, Olsen et al. 2008).

Conclusions

Variation in salt marsh sparrow bill size is strongly related to variation in the mean, daily-high summer temperatures of their breeding habitats. This ecogeographic pattern may be explained by recent findings about the thermoregulatory role that bills can play. Birds are capable of vasodilating the vascularized tissue underlying the ramphothecus to increase convective and radiative heat loss under conditions of high ambient temperature. The absolute amount of heat loss due to an increase in bill surface area is likely to be small and the advantage manifested in an increase in activity during thermally stressful conditions. Further research needs to establish both the role of the bill in the thermal budget of individuals and the relationship between bill size and the activity patterns of birds in the field.

Such a thermoregulatory mechanism may be particularly important in birds that occupy open, thermally unbuffered environments that offer little refuge from direct insolation. As evaporative water loss cannot keep pace with heat generation at high temperatures, other contributing factors might include a small body size (high surface area to volume ratio), the lack of fresh water, and strong, consistent winds. For omnivorous, dietary-generalist species with few competitors, like these sparrows, selection may act to increase the surface area of the bill in the absence of strong counter-selection for a bill specialized for foraging. At this point, the thermoregulatory hypothesis for variation in bill size is supported by a strong correlation between bill surface area and high summer temperature. Further work is required to establish whether there is sufficient heat loss through the bill to influence fitness-related activities in salt marsh sparrows.

Although we have argued that specific conditions may underlie the striking relationship between bill size and high temperature in salt marsh sparrows, conditions probably exist in other systems that have similar environmental constraints. Further tests of the thermoregulatory hypothesis

of bill-size evolution and Allen's rule should consider specific environments and species groups that are more likely to conform to the above expectations and hence provide appropriate tests.

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Supplementary material (Appendix E7002 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.