



RESEARCH ARTICLE

Males with larger bills sing at higher rates in a hot and dry environment

David Luther * and Ray Danner

Biology Department, George Mason University, Fairfax, Virginia, USA

Both authors contributed equally to the paper.

* Corresponding author: dluther@gmu.edu

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ABSTRACT

Temperature and water availability affect the survival, reproductive success, and behavior of all animals; thus, traits that influence thermoregulation and water balance should be under strong selection. Avian bills can dissipate excess body heat through convection and radiation. We hypothesized that in hot, dry locations, bill size would be selected for its value in thermoregulation: males with larger bills would shed excess heat more efficiently, allowing greater activity levels during thermally challenging periods of the breeding season. We predicted that thermoregulatory challenges would require *Melospiza melodia atlantica*, which breeds in hot, dry sand dunes, to trade off between behaviors associated with breeding (song output) and behaviors related to thermoregulation, and that in the hot environment occupied by our study population, males with larger bills would sing at higher rates. We captured, measured, and marked individual birds and then observed singing behavior, microclimate, and microhabitat use to assess thermoregulatory challenges. Ambient weather indicated thermally challenging conditions, and birds displayed thermoregulatory behaviors, including reducing their song rates at higher temperatures. Birds with larger bills sang at higher rates than birds with smaller bills, and males with the largest bills in the population sang almost twice as many songs per minute than birds with the smallest bills. These results are consistent with the hypothesis that climate influences selection on the bill as a thermoregulatory organ.

Keywords: Allen's rule, bill morphology, sexual selection, thermoregulation, song output

Los machos con picos más largos cantan a tasas más altas en ambientes calurosos y secos

RESUMEN

La temperatura y la disponibilidad de agua afectan la supervivencia, el éxito reproductivo y el comportamiento de todos los animales, por lo que los rasgos que influyen la termorregulación y el balance hídrico deberían estar bajo fuerte selección. Los picos de las aves pueden disipar el exceso de calor corporal a través de convección y radiación. Nuestra hipótesis es que en lugares calurosos y secos, el tamaño del pico está seleccionado por su valor de termorregulación: los machos con picos grandes liberan el exceso de calor de manera más eficiente, permitiendo mayores niveles de actividad durante los períodos térmicamente desafiantes de la estación reproductiva. Predijimos que los desafíos de termorregulación requieren que *Melospiza melodia atlantica*, que se reproduce en dunas de arena calientes y secas, realice un balance entre comportamientos asociados con la reproducción (emisión del canto) y termorregulación, y en el ambiente caluroso ocupado por nuestra población de estudio, los machos con picos más largos cantaron a tasas más altas. Capturamos, medimos y marcamos aves individuales y luego observamos el comportamiento de canto, el microclima y el uso de microhábitats para evaluar los desafíos de termorregulación. El tiempo ambiental indicó condiciones térmicamente desafiantes, y las aves desplegaron comportamientos de termorregulación, incluyendo la reducción de las tasas de canto a mayores temperaturas. Las aves con picos más largos cantaron a tasas más altas que las aves con picos más pequeños, y los machos con los picos más largos en la población cantaron casi el doble de cantos por minuto que las aves con los picos más pequeños. Estos resultados son consistentes con la hipótesis de que el clima influencia la selección del pico como un órgano de termorregulación.

Palabras clave: emisión del canto, morfología del pico, Regla de Allen, selección sexual, termorregulación

INTRODUCTION

Temperature and water availability are fundamental abiotic factors that affect the survival, reproductive success, and behavior of animals (Grant 1982, Tingley et al. 2009, Pigot et al. 2010, Boucher-Lalonde et al. 2014). Traits that

influence thermoregulation and water balance are therefore expected to be under strong selection in many systems. Indeed, climatic selection of morphology is thought to underlie well-known global biogeographic patterns, including Allen's rule (Allen 1877) and Bergmann's rule (Bergmann 1847).

Allen's rule states that bodily proportions are selected to facilitate heat loss in hot environments or to retain heat in cold environments. Putative examples include biogeographic relationships between climate and the size of vascularized appendages that enhance thermoregulation. Despite a rich literature on such features (Steen and Steen 1965, Hill and Veghte 1976, Stitt 1976, Maloiy et al. 1982, Dawson et al. 2000, Tattersall et al. 2009, Weissenböck et al. 2010, Darnell and Munguia 2011), connections between thermoregulatory function and fitness are rarely demonstrated.

The avian bill, an iconic feature of ecology and evolution (Darwin 1859, Grant 1968), has recently been shown to play an important role in both thermoregulation and water balance. Birds can dissipate substantial amounts of excess heat through convection and radiation from the surface of the bill (Tattersall et al. 2009, Greenberg et al. 2012a). Heat loss from the surface of the bill does not carry water and is therefore hypothesized to conserve water, which is otherwise lost through a second major form of heat loss, respiration. Therefore, the function of the bill as a heat dissipater is expected to be especially advantageous for species that inhabit hot environments with limited fresh water. Studies have shown that bill size follows Allen's rule in some systems, where it is positively correlated with ambient temperatures across continental (Snow 1954, Symonds and Tattersall 2010, Greenberg et al. 2012b, Luther and Greenberg 2014) and regional spatial scales (Greenberg and Danner 2012, 2013, VanderWerf 2012), suggesting selection pressure on the bill for thermoregulation. To date, fitness effects of the bill as a thermoregulatory organ are unsubstantiated.

When animals cannot adequately dissipate excess body heat, they face tradeoffs between reproductive and thermoregulatory behaviors (Carrascal et al. 2001, Boyles et al. 2011, du Plessis et al. 2012). For some bird species, this tradeoff occurs during the breeding season, when temperatures become hot and activity levels are high. During the breeding season, males of many bird species in temperate latitudes spend substantial time singing from exposed perches and moving vigorously to defend territories in hot summer weather. Flight increases energy use (Berger and Hart 1974), as does singing (Oberweger and Goller 2001, Ward et al. 2003, Hasselquist and Bensch 2008), although it is debated whether the latter is substantial in all taxa (Ward et al. 2004). Increased energy use, along with increased insolation from exposed perches, is expected to increase body heat. Breeding activities therefore may require males to dissipate large amounts of excess heat in order to avoid hyperthermia. Further, hot weather hinders the loss of excess body heat through convection, because the heat gradient between animal and environment is reduced. Therefore, at high temperatures, birds increase the rate of heat loss through evaporative

cooling, such as panting and cutaneous water loss (Wolf and Walsberg 1996). In water-limited environments, individuals that rely primarily on evaporative heat loss would need to reduce activity levels or move to cooler microclimates in order to avoid dehydration. In contrast, individuals with larger heat-conducting body surfaces, which allow heat loss in the absence of water loss, should be better able to conserve water while shedding excess body heat and remaining active.

Given the thermoregulatory function of bird bills, we hypothesized that in hot environments, males with larger bills would be better able to remain active during the breeding season, and thus would experience greater reproductive success (Greenberg et al. 2012a, Greenberg and Danner 2012, 2013). We tested this hypothesis with the Song Sparrow (*Melospiza melodia*), which displays a high degree of morphological variation (Miller 1956), has larger bills in males than in females (Greenberg and Danner 2013, Danner and Greenberg 2015), and has been the focus of recent research into the evolution of bill morphology in response to climate (Greenberg and Danner 2012, Greenberg et al. 2012a, 2012b). Here, we focus on *M. m. atlantica*, a subspecies that is endemic to the mid-Atlantic Coast, where it inhabits back dunes and the back dune–salt marsh ecotone from Long Island, New York, to Beaufort, North Carolina, USA (Todd 1930). These habitats are thought to be physiologically stressful environments, subject to freshwater shortage, periods of intense heat, and little cover from insolation (McLachlan 1991). *M. m. atlantica* has a significantly larger bill than the closely related eastern subspecies (*M. m. melodia*; Greenberg et al. 2012a, Danner and Greenberg 2015), suggesting adaptation for thermoregulation and water conservation. Indeed, laboratory studies have revealed that the larger bill of the dune-endemic subspecies acts as a more effective thermoregulator in heat, releasing 32% more body heat than the bill of the smaller-billed eastern subspecies at 40°C (Greenberg et al. 2012a).

In this study, we first assessed the potential for *M. m. atlantica* to experience thermoregulatory challenges during the breeding season by describing the microclimates of breeding territories, microhabitat use, and thermoregulatory behaviors. We then tested whether males with larger bills sang more frequently, as higher song frequency could facilitate mate attraction and has the potential to increase reproductive success. Indeed, higher song rates elicit more interest from females in a closely related species (*Zonotrichia leucophrys*; Wasserman and Cigliano 1991) and, in other species, lead to earlier pair formation (*Sylvia atricapilla*; Hoi-Leitner et al. 1995; *Ficedula hypoleuca*; Alatalo et al. 1990), as well as a lower probability of lost paternity (*Hirundo rustica*; Møller et al. 1998) and greater partner reproductive investment (*Taeniopygia guttata*; Bolund et al. 2012). Male *M. m. atlantica* typically sing

from perches at the top of vegetation, where they are exposed to the sun. Perch locations are sometimes also exposed to wind, which could increase the rate of convective heat loss from body surfaces and facilitate cooling (Wolf and Walsberg 1996), so we also investigated whether wind influenced singing rate.

METHODS

Data Collection

We studied *M. m. atlantica* in the back dunes and back dune–salt marsh ecotones of Delaware Seashore State Park, Delaware, and Assateague National Seashore, Maryland, USA. Habitats consisted of open sand, American beachgrass (*Ammophila breviligulata*), northern bayberry (*Myrica pensylvanica*), wax myrtle (*Myrica cerifera*), Jesuit's bark (*Iva frutescens*), sawtooth blackberry (*Rubus argutus*), eastern poison ivy (*Toxicodendron radicans*), and occasional pines (*Pinus* spp.). We identified territorial male *M. m. atlantica* based on singing behavior, captured birds with mist nets, measured morphology (see below), applied unique colored leg bands for individual recognition, and then observed each individual twice daily during the breeding season from July 16 to August 2, 2012. Song Sparrow males were observed nesting and exhibiting mate attraction and territorial defense behaviors from April until mid-August. Song is expected to be important for mate selection early in the breeding season, when temperatures are milder. However, for species that have multiple broods and extrapair copulations, such as the Song Sparrow (Arcese et al. 2002), we would also expect singing behavior to be an important factor for reproductive success later in the breeding season, when temperatures and insolation are high. Because we were interested in thermoregulatory challenges in hot weather, we focused our research on the hottest portion of the breeding season.

We observed 21 male birds daily for 15 min in the morning, between 06:00 and 09:30, and 15 min in the afternoon, between 12:00 and 16:00. Individual Song Sparrows were observed within different time frames each day to minimize the possibility of routine bias among individuals. Each observation session was divided into 10 1.5-min intervals. Linear models revealed that no individual was observed at significantly cooler or hotter temperatures than any other ($F = 1.01$, $df = 21$ and 168 , $P = 0.45$; Tukey's post-hoc multiple comparisons: all $t < |2.76|$, all $P > 0.4$), and that observation sessions were not biased toward larger or smaller bills in relation to temperature, time of day, or date (all $F < |2.05|$, $df = 1$ and 188 , all $P > 0.15$).

We characterized the microclimates of territories at (1) typical singing locations, ~1.5 m above the ground on the periphery of bushes; (2) typical ground foraging locations, 5 cm above the sand; and (3) typical shaded perching

locations in a shrub. Our choice of typical locations was based on observations of multiple individuals prior to and during the study. Using a Kestrel 4000 portable weather monitoring system (Nielsen-Kellerman Kestrel Instruments, Boothwyn, Pennsylvania, USA), we measured ambient temperature (accuracy = 0.5°C , precision = 0.1°C) at all 3 locations, and wind (accuracy = 3.0%, precision = 0.1 km hr^{-1}) and relative humidity (accuracy = 3.0%, precision = 0.1%) at singing locations. We measured weather conditions every 1.5 min and averaged values for each 15-min observation period. To assess the potential for heat and water loss through evaporation, we calculated the vapor pressure deficit for singing locations following Allen et al. (2005; vapor pressure deficit = actual vapor pressure – saturation vapor pressure).

We recorded behavior and microhabitat use at the beginning of every 1.5-min interval. Behaviors analyzed in this study included foraging, singing, and perching. Microhabitat data collected included substrate (ground or structure, the latter of which was typically vegetation, but also included fences, signs, and a few other anthropogenic structures), height above the ground, and percent exposure. We waited at least 1 day after handling each bird before beginning behavioral observations. All data were recorded by hand in field notebooks.

We measured song rate by tallying the number of songs during the 1st, 9th, and 15th 1.5-min intervals of each 15-min observation session. Because our goal was to understand how birds perform maximally during putatively thermally challenging environmental conditions, and to account for short-term temporal variation in singing rate, we used the maximum singing rate during each observation period as our measure of song rate. Songs were counted if they started within each 1.5-min interval.

For each individual, we measured bill width, depth, and length from the anterior edge of the nares, and wing and tarsus lengths, using digital calipers (precision = 0.01 mm), and measured mass with a digital scale (precision = 0.1 g). We calculated bill surface area approximately as the surface area of a cone: length * pi * (width + depth) / 4. Relationships between bill surface area and body size measurements were weak and variable (mass: positive, $r^2 = 0.096$; wing length: negative, $r^2 = 0.078$; tarsus length: positive, $r^2 = 0.012$). Because larger animals produce more heat (Kleiber 1932), we scaled bill size relative to heat production by dividing bill surface area by expected daily energy consumption ($\text{mass}^{0.658}$; Speakman and Król 2010, Hudson et al. 2013). Other measures of bill size provided qualitatively similar results, including uncorrected bill size and the residuals of a regression between bill surface area and wing length.

We measured weather, microhabitat use, behavior, and song rates in the territories of 24 males during 515 15-min observation sessions across 17 days. Two males did not

sing at all during measurement intervals and were therefore excluded from all analyses that included song rate. We did not weigh 1 male, who was excluded from all analyses that included scaled bill size.

Data Analyses

For descriptions of weather, microhabitat use, and behavior, and to test hypotheses regarding song rate, we used an information-theoretic approach, including model selection and model averaging (Burnham and Anderson 2002). We performed all analyses with R (R Core Team 2015) and implemented the information-theoretic approach with package MuMIn (Bartoń 2014). For each description and test, we constructed a linear model that included all relevant predictor variables. We then fit all possible models that nested within the global model and ranked models based on how well they fit the data using Akaike's Information Criterion adjusted for small sample size (AIC_c ; Akaike 1973). We present effect sizes (B) or model-averaged effect sizes (β) and coefficients of determination for simple linear regressions (r^2) and multiple regressions (R^2) for top-ranking models. For models that included random effects, we calculated R^2 with function `r.squaredGLMM`, which follows the methods of Nakagawa and Schielzeth (2013). We report measures of support for models in 2 ways: (1) the weight of the model of interest (w_i), or the summed weights of models containing the variable of interest (the "importance value"); and (2) the evidence ratio (ER), which is a comparison of the weights of 2 models of interest and is interpreted as the number of times that 1 model in a set is more parsimonious than another. We calculated the evidence ratio as the weight of the model containing the variable of interest divided by the weight of an appropriate null model that did not contain that variable.

We described weather with summarized values and patterns throughout the day by averaging weather data within observation sessions and including date as an additive effect in linear models (function `lm` in R). We also described weather variation within the 15-min observation sessions. Ambient temperature was correlated with time of day ($R^2 = 0.75$; linear model including an additive effect of date), preventing us from definitively isolating the effects of these variables on behavior.

We described microhabitat use and behavior with a series of generalized linear mixed models (function `glmer`; Bates et al. 2015). These models included binary response variables (including 2 microhabitats or 2 behaviors) and we therefore used binomial error distributions (Zuur et al. 2009). To account for repeated sampling of the same individuals and repeated sampling within sessions, we included bird number and session number as random effects. Effect sizes from binomial models are presented as odds ratios, which are interpreted as the multiplicative

effect on the odds of the animal using the second listed microhabitat or behavior in relation to the first.

To test whether singing rate varied with respect to bill size, ambient temperature, and wind, we constructed a generalized linear model that included additive effects of these predictor variables. All models included a random effect of individual to account for repeated measurements of individuals. Because the number of songs is a count variable, we fit all models using a Poisson error distribution (Zuur et al. 2009). To evaluate whether the data were overdispersed with respect to our global model, we calculated the sum of squared Pearson residuals / residual degrees of freedom (>1 indicates overdispersion; glmm.wikidot.com).

RESULTS

The weather during our trials indicated a range of mild to thermally challenging conditions: minimum daily trial temperatures (mean = 23.6°C) were near the lower critical limit of *M. melodia*'s thermoneutral zone (24.1°C , measured in winter; Yarbrough 1971), increased throughout the day ($B = 1.1^\circ\text{C hr}^{-1}$, $w_i = 0.999$, $R^2 = 0.71$), and were near *M. m. atlantica*'s active body temperature ($42.5 \pm 0.9^\circ\text{C}$ SD; V. Cadena personal communication) on multiple days; temperatures fell during some trials in the late afternoon. Insolation was high during many trials (though unmeasured) and the sand became very hot, leading to maximum temperatures near the ground on a given day to be an average of 5°C higher than at 1.5 m above the ground. Further, as ambient temperature increased, typical perch locations in the shade became relatively cool ($B = -0.04^\circ\text{C per } 1^\circ\text{C rise in ambient temperature}$, $\text{ER} = 14$, $r^2 = 0.015$) compared with exposed perch locations. Relative humidity ranged from 23% to 100%, declined throughout the day ($B = -3.22\% \text{ hr}^{-1}$, $w_i = 0.999$, $R^2 = 0.50$), and was negatively related to temperature ($r^2 = 0.70$). Vapor pressure deficits at perch locations were low in the morning when temperatures were cooler, and ranged widely in the afternoon, though generally rose ($B = 0.25 \text{ kPa hr}^{-1}$, $w_i = 0.999$, $R^2 = 0.51$), with high deficit values of $\sim 6.67 \text{ kPa}$, indicating a broad range of potential for evaporation. Weather was highly uniform within 15-min sessions (mean session range \pm SD: ambient temperature = $0.07 \pm 0.33^\circ\text{C}$; relative humidity = $0.34 \pm 1.52\%$).

At higher temperatures, birds shifted from mating and feeding behaviors to those that facilitated thermoregulation: they moved off the ground to perch on structures ($B = 0.05 \pm 0.02 \text{ SE}$, odds ratio = $1.05^\circ\text{C}:1.00^\circ\text{C}$, $\text{ER} = 3.7$, $R^2 = 0.53$) that were elevated (mainly vegetation; $B = 0.03 \text{ m} \pm 0.01 \text{ SE per } 1^\circ\text{C}$, $w_i = 0.999$, $R^2 = 0.47$), and shifted from singing to quietly perching ($B = 0.04 \pm 0.01 \text{ SE}$, odds ratio = $1.04^\circ\text{C}:1.00^\circ\text{C}$, $\text{ER} = 19.0$, $R^2 = 0.38$) under greater cover ($B = -0.5\% \pm 0.1\% \text{ exposure per } 1^\circ\text{C}$, $w_i = 0.999$, $R^2 =$

0.14). There was also a trend for birds to shift from foraging to perching as temperatures increased, but the effect was small and not statistically supported ($B = 0.005 \pm 0.023$, odds ratio = $1.01^{\circ}\text{C}:1.00^{\circ}\text{C}$, $\text{ER} < 1.0$, $R^2 = 0.57$). Bill size did not influence the likelihood of transitions from foraging or singing to perching, or to moving among microhabitats (all $\text{ERs} < 1.0$).

We recorded the song rates and morphology of 21 individuals during 182 of the 515 15-min observation sessions. For each bird, we recorded an average of 12.0 ± 1.1 SE sessions (range: 1–20). The average of the maximum number of songs per 1.5-min interval was 3 (range: 1–8). The data were not overdispersed with respect to the global model (sum of squared Pearson residuals / residual degrees of freedom = 0.8, $P = 0.99$).

Singing rate was positively correlated with bill surface area ($\beta = 0.003 \pm 0.004$ unconditional SE; 1.014 songs per 1 unit of scaled bill size; Figure 1A) and tended to be negatively correlated with ambient temperature ($\beta = -0.034 \pm 0.063$ unconditional SE; 0.985 songs per 1°C ; Figure 1B). The top model for singing rate included bill size and temperature, was ranked ~ 3.4 AIC_c units higher than the top model without bill size (the temperature only model; Table 1), and had an R^2 of 0.07. It also had an ER of 5.2, and bill size had an importance value of 0.88, all of which support the hypothesis that singing rate was correlated with bill surface area. The top model with temperature was ~ 1.0 AIC_c unit higher than the top model without temperature (the bill size only model) and had an ER of 1.6, and temperature had an importance value of 0.71, which provides evidence that temperature also influenced song rate. Neither the interaction between bill size and temperature nor wind were supported as important predictors of song rate (both $\text{ERs} < 1.0$). The top model ranked only slightly higher than a model with time of day rather than temperature ($\Delta\text{AIC}_c = 0.4$), indicating that time of day was nearly equivalent at predicting song rate as temperature, but there was little variation in temperature across days, thus preventing us from definitively isolating the effects of temperature and time of day on behavior.

DISCUSSION

Our results provide novel support for a connection between climate, animal behavior, and morphology. We found that singing activity (an important aspect of breeding biology) in a hot, dry environment was related to bill size, and that the males with the largest bills in our sample sang almost twice as many songs per minute than the birds with the smallest bills. These findings are consistent with the hypothesis that climate exerts selection pressure on bill morphology for thermoregulatory benefits. These results present an original contribution to a rich

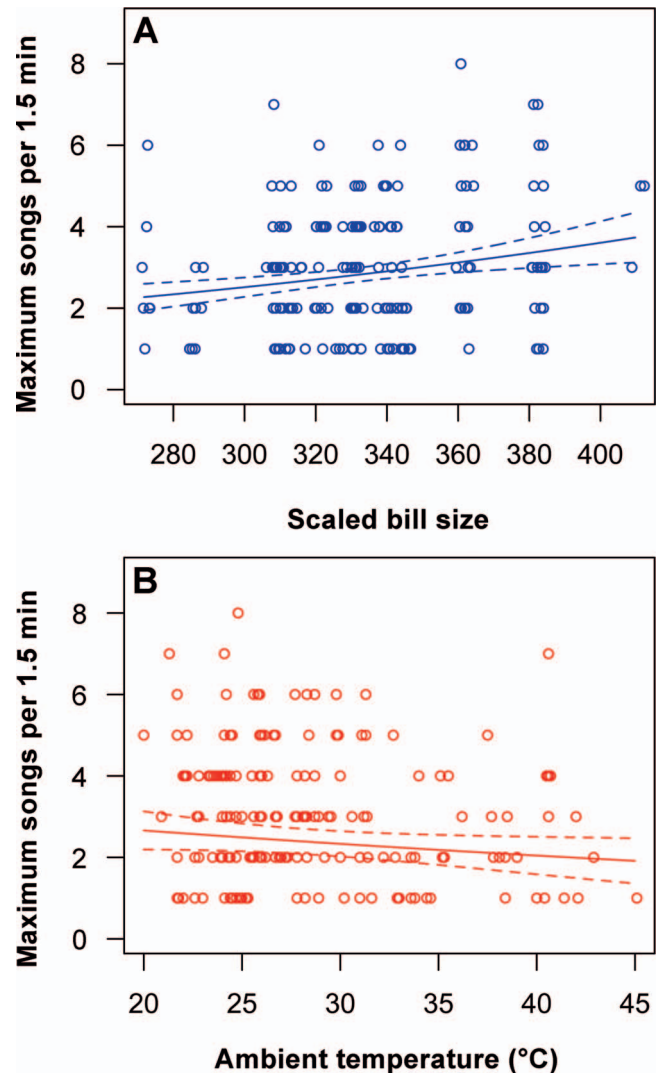


FIGURE 1. Singing rate of Atlantic Song Sparrows in Delaware and Maryland, USA, (A) increased with bill size and (B) decreased with ambient temperature. Singing rate is the maximum number of songs per 1.5-min interval during 15-min observation periods conducted in July–August, 2012. Scaled bill size is in units of mm^2 per kJ of energy use per day. Lines are model average predictions \pm unconditional SE, and circles are raw data for all individuals combined ($n = 21$).

literature on avian bill morphology (Darwin 1859, Grant 1968) and appendages that enhance thermoregulation in many species of birds, mammals, and invertebrates (Steen and Steen 1965, Hill and Veghte 1976, Stitt 1976, Maloiy et al. 1982, Dawson et al. 2000, Tattersall et al. 2009, Weissenböck et al. 2010, Darnell and Munguia 2011), but for which connections between thermoregulatory function and behaviors associated with mate attraction and fitness are rarely demonstrated.

Our results are consistent with the hypothesis that singing from exposed perches poses a thermoregulatory

TABLE 1. Ranking of models used to describe the singing rate of Atlantic Song Sparrows in Delaware and Maryland, USA, 2012. All models include a random effect of individual to account for repeated measurements. Models were ranked by the difference from the top model in Akaike's Information Criterion corrected for small sample size (ΔAIC_c). K is the number of parameters, w_i is the model weight, and $-2\ln L$ is the log-likelihood multiplied by -2 .

Model	K	ΔAIC_c	w_i	$-2\ln L$
Bill size + Temp	4	0.00 ^a	0.31	661.16
Bill size	3	1.01	0.19	664.26
Bill size*Temp	5	1.64	0.14	660.68
Bill size + Temp + Wind	5	1.78	0.13	660.82
Bill size + Wind	4	3.04	0.07	664.18
Temp	3	3.37	0.06	666.62
Bill size*Temp + Wind	6	3.41	0.06	660.30
Intercept only	2	4.69	0.03	670.00
Temp + Wind	4	5.12	0.02	666.26
Wind	3	6.70	0.01	669.94

^a The AIC_c value of the top model = 669.38.

challenge for *M. m. atlantica*. In particular, singing behavior declined at hotter ambient temperatures. Although variation in song rate can have multiple causes, there is evidence that females assess song rate for mate selection (Gottlander 1987, Radesäter et al. 1987, Alatalo et al. 1990, Wasserman and Cigliano 1991), and thus song rate can be an important part of reproductive success for males. A reduction in song rate should allow for thermoregulatory behaviors, such as panting, adjusting body posture to facilitate heat loss, and moving to a shaded location, all of which have been observed in other taxa at high temperatures (Calder 1968, Ricklefs and Hainsworth 1968, Austin and Miller 1982, Carmi-Winkler et al. 1987, Williams 2001, Smit et al. 2013); however, it should also reduce opportunities for mate attraction and territory defense. Therefore, males that can maintain singing rates in hotter temperatures, presumably as a result of an increased capacity for thermoregulation due to a larger bill, are at an advantage in terms of reproductive opportunities.

An additional hypothesis is that larger bills allow greater foraging success and therefore more energy or time to contribute to breeding activities such as singing. The higher song rate of males with larger bills, independent of temperature, supports this hypothesis. However, vegetation communities in *M. m. atlantica*'s range are not dominated by plants with large or hard seeds (Duncan and Duncan 1987, Stalter and Lamont 1990), suggesting that larger bills would not provide a foraging advantage in this system. Further, no evidence has been found of a relationship between bill size and bite force among Song Sparrows in this population or between Atlantic and Eastern song sparrow subspecies (R. Danner personal

observation). If larger bills allow more efficient foraging, we would predict that birds with larger bills would forage less often than birds with smaller bills. The activity budget data presented in this paper do not support the prediction that song activity and bill size relationships are also related to foraging efficiency.

Further evidence of thermoregulatory challenges in this system were shown at higher ambient temperatures, when *M. m. atlantica* moved from open sand to elevated structures and reduced the amount of time spent foraging. *M. m. atlantica* also moved to cooler, shaded locations at higher temperatures. We hypothesize that these shifts reduced body heat gained through insolation and facilitated heat loss by a move away from the hot thermal layer above the sand to cooler (typically shaded) microhabitats. Taxa in other hot and water-limited environments also display reduced foraging activity and efficiency and increased thermoregulatory behaviors as ambient temperatures rise (Calder 1968, Goldstein 1984, Carmi-Winkler et al. 1987, Williams 2001, Tieleman and Williams 2002, du Plessis et al. 2012, Smit et al. 2013, Edwards et al. 2015), although movement away from hotter ground surface microclimates has not previously been documented.

Our study took place during a relatively uniformly hot portion of the summer. As a result, there was little variation in temperature across days, thus preventing us from definitively isolating the effects of temperature and time of day on behavior. Therefore, time of day could have caused or contributed to the observed activity patterns throughout the day.

In addition to thermal budgets, other factors can influence song production. Song activity has been associated with social status (Spencer et al. 2004, Botero et al. 2009), testosterone levels (reviewed by Catchpole and Slater 2003), breeding status (Garamszegi and Moller 2004), body condition (Galeotti et al. 1997), territory quality (Manica et al. 2014), food availability (Barnett and Briskie 2011), and diel rhythms (reviewed by Catchpole and Slater 2003). To control for these variables as much as possible, we synchronized our observations to occur within a short time window during the breeding season, and sampled multiple individuals in very similar habitat at various times of the day.

Because heat waves are expected to be more frequent and last longer as global warming continues (Meehl and Tebaldi 2004), we expect thermal challenges to behavior to increase in severity and to drive the evolution of larger bills for birds in thermally challenging environments. Heat waves have recently caused large-scale breeding failure in birds (Bolger et al. 2005), and mortality in birds (McKechnie and Wolf 2010), bats (Welbergen et al. 2008), and humans, though the role of behavior was not explicitly studied in these cases. Campbell-Tennant et al. (2015) showed that the bill sizes of 4 of 5 species of

Australian parrot have increased over the past 140 yr, but similar analyses have not been performed for other species.

Until recently, bill morphology was assumed to be solely a result of selection for foraging. Recent discoveries, however, show that bill morphology is also important for thermoregulation (Tattersall et al. 2009, Greenberg et al. 2012a, this study) and song performance (Podos et al. 2004). In addition, recent study has shown that external bill morphology reflects the morphology of internal structures, including the nasal conchae, which are respiratory structures important for maintaining heat and water balance, which suggests that internal and external structures evolve in tandem (R. Danner personal observation). Combined, these findings highlight the potentially complex nature of multiple selection pressures acting on the bill. Future studies should therefore examine the evolution of the bill with an integrative approach, focusing on both external and internal bill morphology at the nexus of selection for foraging, thermoregulation, and song production.

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Ethics statement: Our study adhered to the Institutional Animal Care and Use Committee permit #NZP 10-08 and U.S. Geological Survey banding permit #22665.

Author contributions: D.L. designed methods and provided logistical support for the data collection. R.D. conducted the data analysis. D.L. and R.D. both contributed to writing the manuscript.

LITERATURE CITED

- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In Second International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, September 2–8, 1971 (B. N. Petrov and F. Csáki, Editors). Akadémiai Kiadó, Budapest, Hungary. pp. 267–281.
- Alatalo, R. V., C. Glynn, and A. Lundberg (1990). Singing rate and female attraction in the Pied Flycatcher: An experiment. *Animal Behaviour* 39:601–603.
- Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Review* 1:108–140.
- Allen, R. G., I. A. Walter, R. L. Elliott, T. A. Howell, D. Ikenfisu, M. E. Jensen, and R. L. Snyder (Editors) (2005). The ASCE Standardized Reference Evapotranspiration Equation. ASCE Publications, Chicago, IL, USA.
- Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten (2002). Song Sparrow (*Melospiza melodia*). In *The Birds of North America Online* (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/704>
- Austin, G. T., and J. S. Miller (1982). Temperature-related behavior of some migrant birds in the desert. *Western North American Naturalist* 42:232–240.
- Barnett, C. A., and J. V. Briskie (2011). Strategic regulation of body mass and singing behavior in New Zealand robins. *Ethology* 117:28–36.
- Bartoń, K. (2014). MuMIn: Multi-model inference. R package version 1.12.1. <http://CRAN.R-project.org/package=MuMIn>
- Bates, D., M. Maechler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48. doi:10.18637/jss.v067.i01
- Berger, M., and J. S. Hart (1974). Physiology and energetics of flight. *Avian biology* 4:415–477.
- Bergmann, C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3:595–708.
- Bolger, D. T., M. A. Patten, and D. C. Bostock (2005). Avian reproductive failure in response to an extreme climatic event. *Oecologia* 142:398–406.
- Bolund, E., H. Schielzeth, and W. Forstmeier (2012). Singing activity stimulates partner reproductive investment. *Behavioral Ecology and Sociobiology* 66:975–984.
- Botero, C. A., R. J. Rossman, L. M. Caro, L. M. Stenzler, I. J. Lovette, S. R. de Kort, and S. L. Vehrencamp (2009). Syllable type consistency is related to age, social status and reproductive success in the Tropical Mockingbird. *Animal Behaviour* 77: 701–706.
- Boucher-Lalonde, V., A. Morin, and D. J. Currie (2014). A consistent occupancy–climate relationship across birds and mammals of the Americas. *Oikos* 123:1029–1036.
- Boyles, J. G., F. Seebacher, B. Smit, and A. E. McKechnie (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology* 51:676–690.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer, New York, NY, USA.
- Calder, W. A. (1968). The diurnal activity of the Roadrunner, *Geococcyx californianus*. *The Condor* 70:84–85.
- Campbell-Tennant, D. J. E., J. L. Gardner, M. R. Kearney, and M. R. E. Symonds (2015). Climate-related spatial and temporal variation in bill morphology over the past century in Australian parrots. *Journal of Biogeography* 42:1163–1175.
- Carmi-Winkler, N., A. A. Degen, and B. Pinshow (1987). Seasonal time-energy budgets of free-living Chukars in the Negev Desert. *The Condor* 89:594–601.
- Carrascal, L. M., J. A. Díaz, D. L. Huertas, and I. Mozetich (2001). Behavioral thermoregulation by treecreepers: Trade-off between saving energy and reducing crypsis. *Ecology* 82: 1642–1654.
- Catchpole, C. K., and P. J. B. Slater (2003). *Bird Song: Biological Themes and Variations*. Cambridge University Press, Cambridge, UK.
- Danner, R. M., and R. Greenberg (2015). A critical season approach to Allen's rule: Bill size declines with winter temperature in a cold temperate environment. *Journal of Biogeography* 42:114–120.

- Darnell, M. Z., and P. Munguia (2011). Thermoregulation as an alternate function of the sexually dimorphic fiddler crab claw. *The American Naturalist* 178:419–428.
- Darwin, C. (1859). *On the Origins of Species by Means of Natural Selection*. Murray, London, UK.
- Dawson, T. J., C. E. Blaney, A. J. Munn, A. Krockenberger, and S. K. Maloney (2000). Thermoregulation by kangaroos from mesic and arid habitats: Influence of temperature on routes of heat loss in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*). *Physiological and Biochemical Zoology* 73:374–381.
- Duncan, W. H., and M. B. Duncan (1987). *Seaside Plants of the Gulf and Atlantic Coasts*. Smithsonian Institution Press, Washington, DC, USA.
- du Plessis, K. L., R. O. Martin, P. A. R. Hockey, S. J. Cunningham, and A. R. Ridley (2012). The costs of keeping cool in a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology* 18:3063–3070.
- Edwards, E. K., N. J. Mitchell, and A. R. Ridley (2015). The impact of high temperatures on foraging behaviour and body condition in the Western Australian Magpie *Cracticus tibicen dorsalis*. *Ostrich* 86:137–144.
- Galeotti, P., N. Saino, R. Sacchi, and A. P. Møller (1997). Song correlates with social context, testosterone and body condition in male Barn Swallows. *Animal Behaviour* 53:687–700.
- Garamszegi, L. Z., and A. P. Møller (2004). Extrapair paternity and the evolution of bird song. *Behavioral Ecology* 15:508–519.
- Goldstein, D. (1984). The thermal environment and its constraint on activity of desert quail in summer. *The Auk* 101:542–550.
- Gottlander, K. (1987). Variation in the song rate of the male Pied Flycatcher *Ficedula hypoleuca*: Causes and consequences. *Animal Behaviour* 35:1037–1043.
- Grant, G. S. (1968). Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Systematic Zoology* 17:319–333.
- Grant, G. S. (1982). *Avian Incubation: Egg Temperature, Nest Humidity, and Behavioral Thermoregulation in a Hot Environment*. Ornithological Monographs 30.
- Greenberg, R., and R. M. Danner (2012). The influence of the California marine layer on bill size in a generalist songbird. *Evolution* 66:3825–3835.
- Greenberg, R., and R. M. Danner (2013). Climate, ecological release and bill dimorphism in an island songbird. *Biology Letters* 9:20130118. <http://dx.doi.org/10.1098/rsbl.2013.0118>
- Greenberg, R., V. Cadena, R. M. Danner, and G. Tattersall (2012a). Heat loss may explain bill size differences between birds occupying different habitats. *PLOS One* 7:e40933. doi:10.1371/journal.pone.0040933
- Greenberg, R., R. Danner, B. Olsen, and D. Luther (2012b). High summer temperature explains bill size variation in salt marsh sparrows. *Ecography* 35:146–152.
- Hasselquist, D., and S. Bensch (2008). Daily energy expenditure of singing Great Reed Warblers *Acrocephalus arundinaceus*. *Journal of Avian Biology* 39:384–388.
- Hill, R. W., and J. H. Veghte (1976). Jackrabbit ears: Surface temperatures and vascular responses. *Science* 194:436–438.
- Hoi-Leitner, M., H. Nechtelberger, and H. Hoi (1995). Song rate as a signal for nest site quality in Blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology* 37:399–405.
- Hudson, L. N., N. J. B. Isaac, and D. C. Reuman (2013). The relationship between body mass and field metabolic rate among individual birds and mammals. *Journal of Animal Ecology* 82:1009–1020.
- Kleiber, M. (1932). Body size and metabolism. *Hilgardia* 6:315–351.
- Luther, D. A., and R. Greenberg (2014). Contributing factors to bill morphology: Climate, habitat, and sex. *Ecology and Evolution* 4:699–705.
- Maloiy, G. M. O., J. M. Z. Kamau, A. Shkolnik, M. Meir, and R. Arieli (1982). Thermoregulation and metabolism in a small desert carnivore: The Fennec fox (*Fennecus zerda*) (Mammalia). *Journal of Zoology* 198:279–291.
- Manica, L. T., R. Maia, A. Dias, J. Podos, and R. H. Macedo (2014). Vocal output predicts territory quality in a Neotropical songbird. *Behavioural Processes* 109:21–26.
- McKechnie, A. E., and B. O. Wolf (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters* 6:253–256.
- McLachlan, A. (1991). Ecology of coastal dune fauna. *Journal of Arid Environments* 21:229–243.
- Meehl, G. A., and C. Tebaldi (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305:994–997.
- Miller, A. H. (1956). Ecologic factors that accelerate formation of races and species of terrestrial vertebrates. *Evolution* 10:262–277.
- Møller, A. P., N. Saino, G. Taramino, P. Galeotti, and S. Ferrario (1998). Paternity and multiple signalling: Effects of a secondary sexual character and song on paternity in the Barn Swallow. *The American Naturalist* 151:236–242.
- Nakagawa, S., and H. Schielzeth (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Oberweger, K., and F. Goller (2001). The metabolic cost of birdsong production. *Journal of Experimental Biology* 204:3379–3388.
- Pigot, A. L., I. P. F. Owens, and C. D. L. Orme (2010). The environmental limits to geographic range expansion in birds. *Ecology Letters* 13:705–715.
- Podos, J., S. K. Huber, and B. Taft (2004). Bird song: The interface of evolution and mechanism. *Annual Review of Ecology, Evolution, and Systematics* 2004:55–87.
- Radesäter, T., S. Jakobsson, N. Andbjør, A. Bylin, and K. Nyström (1987). Song rate and pair formation in the Willow Warbler, *Phylloscopus trochilus*. *Animal Behaviour* 35:1645–1651.
- R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ricklefs, R., and F. Hainsworth (1968). Temperature dependent behavior of the Cactus Wren. *Ecology* 49:227–233.
- Smit, B., C. T. Harding, P. A. R. Hockey, and A. E. McKechnie (2013). Adaptive thermoregulation during summer in two populations of an arid-zone passerine. *Ecology* 94:1142–1154.
- Snow, D. W. (1954). Trends in geographical variation in Palearctic members of the genus *Parus*. *Evolution* 8:19–28.
- Speakman, J. R., and E. Król (2010). Maximal heat dissipation capacity and hyperthermia risk: Neglected key factors in the ecology of endotherms. *Journal of Animal Ecology* 79:726–746.

- Spencer, K. A., K. L. Buchanan, A. R. Goldsmith, and C. K. Catchpole (2004). Developmental stress, social rank and song complexity in the European Starling (*Sturnus vulgaris*). *Proceedings of the Royal Society of London, Series B* 271: S121–S123.
- Stalter, R., and E. E. Lamont (1990). The vascular flora of Assateague Island, Virginia. *Bulletin of the Torrey Botanical Club* 117:48–56.
- Steen, I., and J. B. Steen (1965). The importance of the legs in the thermoregulation of birds. *Acta Physiologica Scandinavica* 63:285–291.
- Stitt, J. T. (1976). The regulation of respiratory evaporative heat loss in the rabbit. *Journal of Physiology* 258:157–171.
- Symonds, M. R., and G. J. Tattersall (2010). Geographical variation in bill size across bird species provides evidence for Allen's rule. *The American Naturalist* 176:188–197.
- Tattersall, G. J., D. V. Andrade, and A. S. Abe (2009). Heat exchange from the toucan bill reveals a controllable vascular thermal radiator. *Science* 325:468–470.
- Tieleman, B. I., and J. B. Williams (2002). Effects of food supplementation on behavioural decisions of hoopoe-larks in the Arabian Desert: Balancing water, energy and thermoregulation. *Animal Behaviour* 63:519–529.
- Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences USA* 106:19637–19643.
- Todd, W. E. (1930). Note on the Eastern Song Sparrows. *The Auk* 47:257–258.
- VanderWerf, E. A. (2012). Ecogeographic patterns of morphological variation in elepaos (*Chasiempis* spp.): Bergmann's, Allen's, and Gloger's rules in a microcosm. *Ornithological Monographs* 73:1–34.
- Ward, S., H. M. Lampe, and P. J. B. Slater (2004). Singing is not energetically demanding for Pied Flycatchers, *Ficedula hypoleuca*. *Behavioral Ecology* 15:477–484.
- Ward, S., J. R. Speakman, and P. J. B. Slater (2003). The energy cost of song in the canary, *Serinus canaria*. *Animal Behaviour* 66:893–902.
- Wasserman, F. E., and J. A. Cigliano (1991). Song output and stimulation of the female in White-throated Sparrows. *Behavioral Ecology and Sociobiology* 29:55–59.
- Weissenböck, N. M., C. M. Weiss, H. M. Schwammer, and H. Kratochvil (2010). Thermal windows on the body surface of African elephants (*Loxodonta africana*) studied by infrared thermography. *Journal of Thermal Biology* 35:182–188.
- Welbergen, J. A., S. M. Klose, N. Markus, and P. Eby (2008). Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society of London, Series B* 275:419–425.
- Williams, J. B. (2001). Energy expenditure and water flux of free-living Dune Larks in the Namib: A test of the reallocation hypothesis on a desert bird. *Functional Ecology* 15:175–185.
- Wolf, B. O., and G. E. Walsberg (1996). Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* 77:2228–2236.
- Yarborough, C. G. (1971). The influence of distribution and ecology on the thermoregulation of small birds. *Comparative Biochemistry and Physiology A* 39:235–266.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New York, NY, USA.