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A test of a corollary of Allen's rule suggests a role for population density

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Abstract:	A body of research by Russell Greenberg, Glenn Tattersall, and their colleagues has proposed a corollary of Allen's Rule: that in freshwater-limited environments, bill surface area increases with temperature. Increases in both population density and sexual dimorphism, however, could also explain increases in bill surface area. After controlling for the effects of a hybrid zone, we tested whether temperature or population density in the Saltmarsh Sparrow (*Ammospiza caudacuta*), a sexually monomorphic estuarine specialist, explained greater variance in bill surface area. This allowed us to examine multiple potential selective mechanisms underlying the Greenberg-Tattersall Corollary. We found that Saltmarsh Sparrows follow the general pattern of the Corollary (larger bills in warmer summer climates) but only after controlling for population density. The relationship between bill surface area and temperature varied inversely with population density. We discuss the relative abilities of sexual selection and ecological competition to explain these results.

ABSTRACT

A body of research by Russell Greenberg, Glenn Tattersall, and their colleagues has proposed a corollary of Allen's Rule: that in freshwater-limited environments, bill surface area increases with temperature. Increases in both population density and sexual dimorphism, however, could also explain increases in bill surface area. After controlling for the effects of a hybrid zone, we tested whether temperature or population density in the Saltmarsh Sparrow (*Ammospiza caudacuta*), a sexually monomorphic estuarine specialist, explained greater variance in bill surface area. This allowed us to examine multiple potential selective mechanisms underlying the Greenberg-Tattersall Corollary. We found that Saltmarsh Sparrows follow the general pattern of the Corollary (larger bills in warmer summer climates) but only after controlling for population density. The relationship between bill surface area and temperature varied inversely with population density. We discuss the relative abilities of sexual selection and ecological competition to explain these results.

Key words: Ammospiza caudacuta, *Ammospiza nelsoni*, competition, sexual selection, thermoregulation, character displacement

INTRODUCTION

Bird bills are evolutionarily labile and are known to evolve quickly for a variety of purposes. Traditionally, bird bills have been thought of primarily as adapted for ecological competition, specifically foraging efficiency (van Valen 1965, Selander 1966, Schluter et al. 1985, Freed et al. 1987, Benkman 1993, Grant and Grant 2006; reviewed by Rubega 2000). More recently, however, bills have been shown to be shaped by other selective forces, such as thermoregulation (reviewed by Tattersall et al. 2017). Birds can regulate blood flow to the bill through vasodilation and vasoconstriction, thereby increasing or decreasing heat lost to conduction and convection across the bill surface (Lucas and Stettenheim 1972). This process was demonstrated initially in waterfowl (Hagan and Heath 1980, Scott et al. 2008) and toucans (Tattersall et al. 2009), but has since been shown in songbirds (Greenberg et al. 2012a). Also, bill size correlates with temperature gradients across a wide diversity of bird orders (Symonds and Tattersall 2010). As such, it appears that bird bills may be yet another example of Allen's rule that the size of body appendages is correlated with temperature (Allen 1877).

In passerine songbirds in particular, vasomodification in the bill appears to be important in freshwater-limited environments and has been characterized by a body of research (Tattersall et al. 2009, 2017; Symonds and Tattersall 2010; Luther and Greenberg 2011, 2014; Greenberg and Danner 2012, 2013; Greenberg et al. 2012a, b; Luther and Danner 2016). Specifically, Russell S. Greenberg (1953-2013; Koenig and Marra 2013), Glenn Tattersall, and their colleagues have amassed evidence across diverse avian taxa showing a corollary pattern to Allen's Rule, whereby bill surface area is positively correlated with temperatures in freshwater-limited environments (hereafter the "Greenberg-Tattersall Corollary"). They hypothesized that this pattern is produced as a result of selection not only for thermoregulation, as is generally considered with Allen's rule, but for water conservation as well (but see Tattersall et al. 2017 for additional examples of large-billed birds in warm environments that are not water limited, and Gardner et al. 2016 for how humidity also impacts the effect of evapotranspiration and Allen's rule on bill size).

Bird bills are covered in keratinized tissue (Van Hemert et al. 2012), which is impermeable to water. As such, dilation of the bill vasculature allows for heat loss without evaporative water loss, which would otherwise occur through thermoregulatory mechanisms such as increased blood flow to the skin surface or panting (Wolf and Walsberg 1996). In a dune and salt-marsh specialist subspecies of the Song Sparrow *(Melospiza melodia atlantica*), individuals dissipate up to 33 percent more heat than their smaller-billed inland conspecifics (*M. m. melodia*) while reducing water loss by up to 7.7 percent (Greenberg et al. 2012a). A positive correlation between bill surface area and summer maximum temperatures has been observed in a variety of freshwater-limited ecosystems: tidal marshes (Greenberg et al. 2012b), mangrove swamps (Luther and Greenberg 2011, 2014), coastal dune communities (Greenberg et al. 2012a), marine-scrub islands (Greenberg and Danner 2012), and arid woodlands (Campbell-Tennant et al. 2015). Furthermore, this pattern of increased bill size does not appear, or is weaker, for related taxa in less water-limited environments (Greenberg and Olsen 2010) or where temperatures are too high to allow for effective conductive cooling (Greenberg and Danner 2012). Among five Australian parrot species, bill size increased over the last century concomitant with increases in temperature in all but one taxon. The one exception exists in the area with the highest rainfall among the five species (Campbell-Tennant et al. 2015), while the remainder can be found largely in areas that receive less than 30 cm of rain annually. While hypotheses regarding the importance of water conservation remain largely untested experimentally (but see Greenberg et al. 2012a), the pattern is compelling.

There is evidence, however, that natural selection on thermal and osmotic homeostasis may not be the only mechanism behind the Greenberg-Tattersall Corollary; population density may also contribute. Greenberg and Olsen (2010) show that in populations of both tidal marsh and oceanic island sparrows where bills are larger, population density is significantly higher than in inland populations with smaller bills. They further show that this increase in size is accompanied by increases in bill sexual dimorphism, and suggest that larger, dimorphic bills might result from an increase in conflict experienced by the more competitive sex under these conditions. This pattern of increased bill dimorphism in coastal passerellids (family Passerelidae, *sensu* Chesser et al. 2017) has since been shown a number of times (Greenberg and Olsen 2010, Greenberg and Danner 2013, Olsen et al. 2013, Luther and Greenberg 2014). The same is true for saltmarsh specialist rails compared to their closest freshwater relative (Perkins et al. 2009), and for toucans (Castro et al. 2003), which have been shown to use their bills as thermoregulatory organs (Tattersall et al. 2009). Interestingly, among North American passerellids, the only known non-coastal sparrow with a sexually dimorphic bill is the Black–throated Sparrow (*Amphispiza bilineata*), a desert scrub specialist of the arid southwestern US and Mexico (Greenberg and Olsen 2010) that also exhibits a suite of adaptations to highly limited freshwater sources (Smyth and Bartholomew 1966). In at least one passerellid taxon, however, it is the inland, freshwater subspecies that possesses greater bill size and dimorphism (Neto et al. 2013, 2017), although it is unclear how population density varies with bill size in this system.

Multiple authors have hypothesized that the thermoregulatory advantages of a larger bill allow males to sing more during the heat of the day and thereby compete more effectively for both territories and mates (Greenberg and Danner 2013, Olsen et al. 2013). Indeed, male Song Sparrows with larger bills in a beach-dune system sing more frequently than males with smaller bills (Luther and Danner 2016). While late-day singing can have advantages other than sexual competition in some songbirds (Gordinho et al. 2015), female Swamp Sparrows of a tidal-marsh subspecies (*M. georgiana nigrescens*) prefer the songs of large-billed conspecific males, while females in the more inland subspecies (*M. g. georgiana*) do not (Liu et al. 2008; Ballentine et al. 2013a, b). Together, this body of evidence suggests that larger male bills might be more advantageous than larger female bills in warmer freshwater-limited environments, or that the increases in population density found in some estuarine birds may drive both an increase in overall bill size and an increase in bill dimorphism.

Regardless, both sexual and natural selection and their interaction have been suggested as factors that shape bill-size evolution, but it is unclear how important or necessary any mechanism is to produce the pattern described by the Greenberg-Tattersall Corollary. Investigating exceptions to the broad patterns, however, could be illustrative. To date all of the intraspecific examinations of the Corollary have either been conducted only on males or only in taxa with sexual dimorphism. As a result, our understanding of the mechanisms producing larger bills in coastal climates is confounded with the observation of dimorphic bills in warmer climates with denser populations.

Here, however, we test for environmental correlates of bill size in the Saltmarsh Sparrow (*Ammospiza caudacuta*), which is the single saltmarsh specialist bird species known to lack bill sexual dimorphism (Greenberg and Olsen 2010). This may be unsurprising given that the mating system of the saltmarsh sparrow (i.e., "scramble competition" polygamy, where males neither defend territories nor mate-guard females: Post and Greenlaw 1982, Greenlaw and Post 2012) is also different from all saltmarsh taxa exhibiting sexual bill dimorphism. They do, however, still possess larger bills on average than their closest non-tidal-marsh relative (Greenlaw et al. 2018; Shriver et al. 2011), which is the convergent pattern across a large suite of coastal birds (Grenier and Greenberg 2005; Luther and Greenberg 2011). Further, the breeding range of the Saltmarsh Sparrow range is oriented roughly north-south along the northeastern United States (Greenlaw et al. 2018), spanning a linear, latitudinal cline of climatic conditions. Importantly, however, Saltmarsh Sparrows also possess variation in breeding density independent of the temperature cline, as density is highest in the range center (Wiest et al. 2016; Field et al. 2018). This system is therefore ideal for testing whether sexual dimorphism is a necessary condition to produce correlations between bill size and temperature and whether either the Greenberg-Tattersall Corollary or population density are sufficient to explain the convergent increases in bill size among coastal birds.

We tested three hypotheses regarding intraspecific bill size variation to explain why Saltmarsh Sparrows have larger bills than their nearest freshwater relative despite lacking sexual bill dimorphism: 1) bill size is driven by selection from higher temperatures in this freshwater-limited environment (i.e., the Greenberg-Tattersall Corollary); 2) bill size is driven by population density and not temperature, as suggested by Greenberg and Olsen (2010); and 3) bill size is driven by an interaction between temperature and density (i.e., thermoregulatory adaptation that produces the Greenberg-Tattersall Corollary is dependent on the competitive environment).

The results of these three tests have different implications for the viable mechanism(s) underlying the Greenberg-Tattersall Corollary. Support for the first hypothesis would indicate that bill dimorphism in coastal birds is not necessary to produce the Greenberg-Tattersall Corollary, as even a species without dimorphism shows a relation between bill size and temperature. Support for the second hypothesis would suggest that the increased bill sizes of coastal birds are not, in and of themselves, support for the Corollary, but are related to their increased population densities and not the increases in temperature. Further, the selective environment that produces bill dimorphism may be required to produce the reported relationships between temperature and bill size found in other taxa. Support for the third hypothesis would indicate that bill dimorphism is not necessary for the Corollary, similarly to the first hypothesis. Further, it would suggest that, while the competitive environment may be a prerequisite for a relationship between temperature and bill size, it is not due exclusively to the kinds of mate competition found within the socially monogamous, territory-defense mating systems that have been studied heretofore. Increases in population density could alter many forms of competition, but previous authors who have used bill dimorphism to explain the Corollary have all invoked male territory-defense behaviors (Greenberg and Danner 2013, Olsen et al. 2013, Luther and Danner 2016), which saltmarsh sparrows do not exhibit (Greenlaw et al. 2018). We tested these three hypotheses while controlling for the possible confounding effects of a known hybrid zone with the smaller-billed Nelson's Sparrow (*A. nelsoni*) at the northern edge of the breeding range (Hodgman et al. 2002, Shriver et al. 2005, Walsh et al. 2011, 2015a).

MATERIAL AND METHODS

Field sites & measurements

From 2010–2012, we captured adult Saltmarsh and Nelson's sparrows in 31 marshes across a latitudinal range that includes 66% of the estimated Saltmarsh Sparrow breeding birds

(Wiest et al. 2016) and the very southern end of the breeding range of the Atlantic subspecies of the Nelson's Sparrow (*A. nelsoni subvirgata*). Capture locations were in high-marsh habitat (variously dominated by *Spartina patens,* short-form *S. alterniflora, Distichlis spicata,* and *Juncus gerardii*) and provided replication both across the range and within watersheds to reflect local habitat heterogeneity.

At each site, we captured sparrows with mist nets and ringed birds with uniquely numbered aluminum leg rings issued by the United States Geological Survey and a site-specific color ring. We collected morphological measurements including mass (to the nearest 0.1 g), wing chord (to the nearest mm), nalospi (bill length to the nearest 0.1 mm, measured from the distal edge of the nares to the distal edge of the maxilla), and bill height and width at the distal end of the nares (to the nearest 0.1 mm). For adult birds of known sex, we used bill measurements from their first capture to calculate bill surface area, assuming a bill shape approximating an elliptical cone ([bill height + bill width]/4*nalospi*π; Greenberg et al. 2012b). We recorded sex, based on presence of brood patch or cloacal protuberance, excluding all juveniles and birds of unknown sex (which generally were only present early in the breeding season and may have been individuals in migration).

Because Saltmarsh Sparrows within the hybrid zone may be partially introgressed with their sister taxon, Nelson's Sparrow, we assigned species identity within the hybrid zone using a linear discriminant function of morphometric and plumage characteristics (Walsh et al. 2015b). Phenotypic data reliably differentiate between Saltmarsh (pure and back-crossed) and Nelson's (pure and back-crossed) individuals but are unable to differentiate between pure and back-crossed individuals within either species group, although first and second generation hybrids are rare (< 5%; Walsh et al. 2015b). Some Saltmarsh Sparrows within the hybrid zone may thus be expected to be at least partially introgressed with their sister taxon.

Statistical analysis

Body size index - To create a body size index, we conducted a principal component analysis for Saltmarsh Sparrows, using scaled and centered data with function *prcomp* in Program R version 3.02 (R Core Team 2014) based on wing chord and the cubed root of mass (to convert this measurement to its one-dimensional component). We then used the first principal component as an index of overall body size for all subsequent tests and also ran a simple linear model to look at the relationship between body size and latitude. We repeated this approach for Nelson's Sparrows to make a body size index for tests for character displacement described below. For every other test, "body size" refers to the index calculated for the Saltmarsh Sparrow group. We did not include tarsus measurements, a standard metric of bird body size, because, like the bill, bird legs are keratinized extremities that could also be under selection for increased surface area in high environmental temperatures (Tattersall et al. 2017).

Correlates of bill size variation and model selection - To test our three hypotheses concerning Saltmarsh Sparrow bill surface area variation, we created five linear mixed models with Program R (function *lmer* in the 'lme4' package; Bates et al. 2015). All models included body size (the principal component described above), sex, and an indicator variable describing whether or not a sampling site was within the hybrid zone as fixed effects and marsh identity (site) as a random variable to control for repeated measurements of populations. We defined marshes within a great-circle distance of 196 km of Yarmouth, Maine, USA (which corresponds to the Atlantic coastline from Petit Manan Point in Maine to Duxbury Bay in Massachusetts, USA) as within the sparrow hybrid zone, based on the estimated genetic introgression cline center and width across 29 genetic loci (Walsh et al. 2016a). We did not include an interaction term between body size and sex because preliminary data exploration with a linear model indicated that the allometric relationship was similar for both sexes (see Results). During model selection we then tested a null model with just these variables against four additional models with the fixed effects of A) latitude, B) population density, C) the additive effect of those two variables, and D) their interaction. We determined the relative support for each model using the second-order Akaike Information Criterion (AIC_C) and assumed that models with $\Delta AIC_C < 2.0$ had equivalent support (Akaike 1974, Hurvich and Tsai 1989, Burnham and Anderson 2002). *Post hoc* t-statistics and P-values were calculated in ‘lmerTest’ package using Satterthwaite’s method (Kuznetsova et al. 2017). We calculated marginal and conditional r^2 values using the *r.squaredGLMM* function in the ‘MuMIn’ package (Bartoń 2019).

We used latitude as a proxy for temperature, as the range of the Saltmarsh Sparrow is a narrow band of marsh that stretches roughly north to south and temperatures increase to the south. The correlation coefficient between latitude and average daily climate normals from 1981–2010 for US National Oceanic and Atmospheric Administration weather stations nearest to our bird sampling sites is -0.89. The 30-year climate normals for maximum daily temperatures (US National Oceanic and Atmospheric Administration) range from 24.1–29.3º C during July across our sampling region with an average of 26.5º C.

We calculated mean Saltmarsh Sparrow densities for each 0.10 degrees of latitude using sparrow density estimates from a separate study (Wiest et al. 2016). Abundance was initially estimated for marsh patches and calculated using bird detections during 5-min, passive point-count surveys conducted 2–3 times per year (2011–2012) from within 50 m of a fixed survey point. Abundance was then estimated using a general multinomial-Poisson mixture model that accounted for detection probability using time-to-detection methods (see Wiest et al. 2016 for further details). These abundance estimates were converted to bird density by dividing by marsh area, and were only included in the regional density estimates used in the present study when they were > 0.0 and when marsh patches were at least 25% high marsh (i.e., appropriate nesting habitat: Greenlaw et al. 2018). This allowed us to calculate an average population density among those populations with A) enough individuals to have a meaningful evolutionary influence on the regional metapopulation and B) to exclude small populations where bill size evolution is influenced more strongly by genetic drift. Before calculating regional (0.1 latitudinal degrees) estimates, we recalculated all patch density estimates as birds per ha of high marsh habitat as a more realistic estimate of the density within appropriate habitat.

Character displacement – Sympatry with the Nelson's Sparrow might alter any spatial gradients in Saltmarsh Sparrow bill size due to character displacement through ecological competition (Grant and Grant 2006), character displacement related to species reinforcement (Parsons et al. 1993, Saetre et al. 1997, Coyne and Orr 2004), the introgression of alleles from the smaller billed Nelson's Sparrow, or less predictable changes in the strength of mate competition due to the presence of available, but less preferred, interspecific mating opportunities. To investigate potential mechanisms for any effect of the zone of sympatry on bill size, we tested for character displacement between Saltmarsh and Nelson's sparrows. We used a single mixed model for both species to explain variation in bill surface area as a function of the three-way interaction (and the subordinate two-way interactions and additive effects) between hybrid zone position (i.e., sympatric or allopatric), species identity, and sex, while controlling for body size with the species-specific principal component (described above) as a fixed effect. This model tests whether bill size of Saltmarsh and Nelson's Sparrows are more or less different within the hybrid zone and whether the degree of sexual dimorphism differs inside the hybrid zone. While Nelson's sparrows also do not defend territories, and might therefore be expected to also not exhibit bill sexual dimorphism, similar to Saltmarsh Sparrows, we are aware of no tests for bill dimorphism in this taxon. *Post hoc*, we used Least Squares Means (function *ref.grid* in the 'lsmeans' package; Lenth and Herv 2015) to compare model predicted means among the treatment groups and the Tukey method for pairwise contrasts for eight multiple comparisons (function *contrast* in 'lsmeans' package: Lenth and Herv 2015) to test for differences among the groups.

RESULTS

We measured the bills of 1,593 sparrows (Nelson's = 251; Saltmarsh = 1,342) across 31 marshes that span both sides of the hybrid zone. We measured Saltmarsh Sparrow bills at 28 marshes (39.6º – 43.8ºN) and Nelson's Sparrows at 13 marshes (43.0º – 44.7ºN). We measured 21 allopatric Nelson's Sparrows in marshes north of the hybrid zone; 230 Nelson's and 634 Saltmarsh sparrows within the hybrid zone; and 708 allopatric Saltmarsh Sparrows south of the hybrid zone. The mean number of surveyed marsh patches used to compute each regional (tenth degree of latitude) density was 3.1 (range: 1 – 11). The median of the regional Saltmarsh Sparrow densities was 0.58 birds per ha of high marsh (range = 0.11 – 1.67). Nelson's Sparrow regional densities were generally higher (median = 1.84 birds per ha of high marsh; range = 0.25 – 5.01 birds per ha of high marsh).

Across the full Saltmarsh Sparrow range, body size predicted bill surface area similarly for both sexes ($t = 0.1$, $P = 0.90$; male Saltmarsh Sparrow $\beta \pm$ SE = 1.3 ± 0.2; female = 1.1 ±

0.2). Across all samples and sexes, bill surface area was 5.3 mm^2 larger for Saltmarsh (mean ± 95% CI = 70.8 ± 0.8 mm^2) vs. Nelson's (65.5 ± 0.9 mm^2) sparrows. The first principal component explained 69% and 66% of the variation in the body size measurements for Saltmarsh and Nelson's sparrows, respectively. This principal component was positively related to latitude ($F_{1,213} = 15.5$, $P < 0.0001$), although the relationship was weak ($r^2 = 0.02$). The raw pattern of bill measurements, uncorrected for body size, shows maximum bill surface areas near 42ºN (near the southern boundary of the hybrid zone and the peak in regional sparrow density: Field et al. 2018) and declines both to the south and north (Fig. 1).

Correlates of bill size variation – The top-ranked model (model weight > 0.999, marginal $r^2 = 0.20$, conditional $r^2 = 0.21$; Table 1) of bill surface area among Saltmarsh Sparrows included a positive relationship with body size, no effect of sex, increased bill size within the hybrid zone, and an interaction between latitude and bird density (Table 2). The interaction indicated that bill surface area was more negatively related to latitude when densities were low (Fig. 2). Further, the univariate relationship between bill size and density was negative, after controlling for this interaction (Table 1, Fig. 3). This model outperformed the next-ranked model (model weight < 0.001, $\Delta AIC_C = 22.0$), which included the additive effect of latitude and population density without their interaction, and the null model ($\Delta AIC_C = 26.5$; Table 1).

Character displacement & sexual dimorphism – Controlling for body size, there was no evidence for sexual dimorphism in bill size in Saltmarsh Sparrows either outside (estimate of the difference between males and females ± SE = 0.83 ± 0.45 mm^2, t = 1.8, $P = 0.59$) or inside (0.38 ± 0.46 mm^2, t = 0.8, $P = 0.99$) the hybrid zone (Fig. 4). Likewise, there was no sexual dimorphism in bill size among Nelson's Sparrows outside (4.1 ± 2.5 mm^2, t = 1.6, $P = 0.74$) or inside (0.91 ± 0.73 mm^2, t = 1.2, $P = 0.92$) the hybrid zone (Fig. 4).

Bill size was higher on average for both male (estimated mean difference ± SE = 2.1 ± 0.8 mm^2, t = 2.7, *P* = 0.04) and female (2.5 ± 0.8 mm^2, t = 3.1, *P* = 0.02) Saltmarsh Sparrows inside the hybrid zone relative to outside of it (Fig. 4). There was, however, no evidence for character displacement, as the difference between Saltmarsh and Nelson's sparrows in allopatry (estimated difference ± 95% CI = 7.5 ± 1.2 mm^2) was greater than the estimated difference of the two taxa in sympatry (5.1 ± 0.9 mm^2). Nelson's Sparrow bill size was the same for males (2.2 ± 1.7 mm^2, t = 1.3, *P* = 0.59) and larger for females (7.2 ± 2.5 mm^2, t = 2.8, *P* = 0.02) inside the hybrid zone relative to outside (Fig. 4). Regardless of species or sex, sparrow bill size was larger on average inside the hybrid zone (mean surface area ± 95% CI = 69.0 ± 0.9 mm^2) relative to outside of it (65.5 ± 1.7 mm^2).

DISCUSSION

Bill size in Saltmarsh Sparrows was best predicted by an interaction between latitude (a proxy for temperature) and regional bird density (a proxy for competition), after controlling for the effects of a hybrid zone with Nelson's Sparrows (in support of Hypothesis 3). We found a negative relationship between bill size and latitude (Fig. 2), indicating a similar relationship with temperature as has been reported in many other species (see Tattersall et al. 2017 for a list of over 50 species showing intraspecific correlations in bill size related to thermoregulation), but only after controlling for bird density (Fig. 3). Consequently, Saltmarsh Sparrows are an indirect point of support for the Greenberg-Tattersall Corollary, the positive correlation between bill surface area and summer temperatures (Tattersall et al. 2017) in freshwater-limited environments, but highlight that this pattern can be obscured by other selective gradients. Like other coastal sparrows, Saltmarsh Sparrows possess a larger bill than their nearest inland relative

(Grenier and Greenberg 2005, Shriver et al. 2011, Greenlaw et al. 2018), supporting the hypothesis that bill size is related to freshwater limitation. Unlike other coastal bird taxa, however, the effect of temperature on Saltmarsh Sparrow bill size is only apparent after regional bird density is controlled for, and raw bill size was smallest at the southern end of the range where temperatures and presumably water stress are greatest. Our results demonstrate for the first time that bird density can mask the effects of the Greenberg-Tattersall Corollary, and we hypothesize that competition may have a role to play in the pattern's production in this system and others.

The geographic pattern we report here (Fig. 1) eliminates the possibility that temperature alone is sufficient to produce the Corollary's predicted pattern in bill size in Saltmarsh Sparrows (contrary to Hypothesis 1). Our results also demonstrate that broad spatial relationships between bill morphology and temperature are possible outside of socially monogamous mating systems, and therefore do not require territorial defense. There was a strong correspondence between bill size and climate, but this relationship was mediated by population density in a negative fashion (Fig. 3). The overall higher population densities of multiple coastal birds are thus not likely responsible for their convergent increases in bill size (contrary to Hypothesis 2).

The case for sexual selection – Larger bills appear to supply an advantage under warmer temperatures for populations of any given density, but the strength of the relationship was steeper at lower densities (Fig. 2). There are a number of mechanisms that could explain this interaction with population density. First, density is a known mediating influence on the strength of sexual selection (Kokko and Rankin 2006). If larger bills allow males to compete more effectively for mates in warm conditions, as has been suggested by others (Greenberg and Danner 2013, Olsen et al. 2013, Luther and Danner 2016), the strength of this selective force would be expected to vary with the strength of mate competition. There are many scenarios where the strength of sexual selection for competitive traits would vary inversely with density (Kokko et al. 2012). For example, higher male densities may make female monopolization more difficult (Klug et al. 2010), or females may exhibit less mate discrimination when males are more common (Hutchinson 2005).

The precise behavioral mechanism for this in the non-territorial Saltmarsh Sparrow would be different than hypothesized for other tidal marsh songbirds, which defend territories with song. Mate competition in Saltmarsh Sparrows occurs both via copulatory chases of females, often by multiple males, and via female-solicited choice (Greenlaw and Post 2012), although the precise selection criteria are unclear. Males do spend considerable time singing, however, despite their lack of territories. Bills, therefore, could assist in thermoregulation during both copulatory chases and song displays, but more work is necessary to directly support either of these hypotheses. It seems reasonable to posit, however, that it would be harder for a small number of males to monopolize all forced and female-solicited copulations in a marsh with higher male densities.

Second, differences in the frequency of multiple paternity might cause males in dense populations to obtain less offspring for a given mating (i.e., the Bateman gradient is less steep in these populations: Bateman 1948). Saltmarsh Sparrows show extreme levels of multiple paternity, with every offspring within a nest often having a different sire (Hill et al. 2010, Maxwell 2018). Further, rates of multiple paternity in a given brood were positively correlated with population density in the single study that has tested this relationship. Hill et al. (2010) found that between 12% and 24% of the variation in multiple paternity was explained by the number of males in the vicinity of the nest. We hypothesize that sexual selection for larger bills may be greater in sparser populations, because males that mate with a single additional female there would be more likely to sire multiple offspring in a nest. The Bateman gradient would thus be steeper in these populations, and this would result in stronger sexual selection for competitive traits like bill size, if the thermoregulatory advantages it confers assists with chasing females or singing during high environmental temperatures.

Any complete hypothesis regarding sexual selection as a mechanism for increases in bill surface area, however, must explain selection on both sexes. Among the sexually dimorphic tidal marsh species, this is perhaps easier, as multiple studies across a large diversity of bird taxa have reported positive correlations between minimum winter temperatures and bill size (Snow 1954; Symonds and Tattersall 2010; VanderWerf 2012; Danner and Greenberg 2014; Friedman et al. 2017; Ryeland et al. 2017; but see Greenberg et al. 2011). In these cases, sexual dimorphism would result if selection on large bills during the summer was stronger for males than females (e.g., due to female mate choice or male-male competition). The equilibrium between selection for large bills in the summer and small bills in the winter would then settle at a larger bill surface area for males than females, resulting in sexual dimorphism. We found no bill dimorphism in either Saltmarsh or Nelson's sparrows, however, which interestingly are the only two species, to our knowledge, to lack this pattern among those tidal marsh birds tested. These are also the only two North American tidal marsh birds that do not defend exclusive territories (Greenlaw et al. 2018, Shriver et al. 2011) and participate instead in frequent and athletic copulatory chases (Greenlaw and Post 2012). If variation in sexual selection is responsible for the relationship between density and bill size in male Saltmarsh Sparrows, low-density populations must increase selection on female bill size in these same marshes. Otherwise, we would expect to see bill sexual dimorphism in this taxon as well, assuming that winter temperatures are selecting for smaller bills in both sexes similarly. We hypothesize that the mating advantages supplied to males by larger bills during copulatory chases (i.e., the ability to avoid thermoregulatory stress during energetically expensive activity in the heat of the day) apply equally well to the females being chased as to the males doing the chasing. The same sexual similarity would not be true in taxa where most mate choice (either direct or indirect) occurs through male song. Thus, we would expect to see larger bills both in species that defend territories by song and those that don't, but we would only expect bill dimorphism in the former. Further, if this is true, the flight endurance of Saltmarsh Sparrows should correlate with bill size under high temperatures; females with larger bills should be able to express mating preferences (by out-maneuvering males) better than smaller-billed females; and this relationship should be strongest in environments with high breeding season temperatures and low male densities. Future studies should test these predictions explicitly.

The case for ecological competition – Third, ecological competition might allow population density to modulate the net selection strength from thermoregulation. For example, if smaller bills are more advantageous for foraging in populations with higher intraspecific competition, this selective force would weaken the ability of temperature to select for larger bills. We would expect ecological competition, however, to covary with the ratio between population density and local resource abundance, not simply with density, as we found here. The same sparrow density in two different marshes could experience radically different levels of competition if resource abundance varied. Among-marsh variation in resource abundance is not well understood, however, and if it is minor, we might still detect a direction correlation between bill size and density.

Further, the lack of character displacement we report here does not suggest a strong role for ecological competition. Nelson's and Saltmarsh Sparrows, which have very similar diets (Shriver et al. 2011, Greenlaw et al. 2018), showed smaller differences in bill size between the species in sympatry than in allopatry. Further, ecological competition is not thought to be strong in marsh-nesting sparrows. Neither Saltmarsh nor Nelson's Sparrows defend exclusive space within the marsh, and therefore do not appear to exclude each other from preferred resources. Foraging occurs in close proximity within overlapping home ranges both for individuals of the same and of different species (Post and Greenlaw 1982, Shriver et al. 2011, Greenlaw et al. 2018), and their invertebrate food resources are thought to be abundant relative to bird foraging demand (Post and Greenlaw 2006) in this highly productive ecosystem (Tiner 2013).

Additionally, variation in bill morphology among other populations of tidal-marsh taxa does not support the presumption of foraging niche competition. In marshes with both Saltmarsh and Seaside Sparrows (*A. maritima*), the two species again have very similar diets with no evidence for niche partitioning (Post and Greenlaw 2006), despite differences in bill size (Grenier and Greenberg 2005, Post and Greenlaw 2009, Greenlaw et al. 2018). Bill size differences in another tidal-marsh specialist, the Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*), are also unrelated to diet, but are attributable to differences in female mate choice (Olsen et al. 2013).

The case for other alternatives – Fourth, our reported negative relationship between bill size and population density (Fig. 3) could be due to an indirect correlation with any other environmental variable or simply be an artifact of our sampling distribution. Population density is likely related to habitat quality, for instance, and many other environmental correlates may thus covary with population density. The center-peaked density distribution shown by this species (Wiest et al. 2016; Field et al. 2018) may also align with a number of additional, unmeasured environmental factors. In fact, a quadratic relationship with latitude explains slightly more variance in bill surface area than our top model with the interaction between latitude and sparrow density ($\Delta AIC_C = 2.7$), although it is unclear what latitude is predicting at this point. Selection on the bill from any environmental covariate of density could explain the statistical interaction we report here.

Our reported negative relationship between bill size and population density could also be an artifact of our latitudinal sampling distribution. Our low-density populations were all in the northern half of our sampling range (range = 42.1° – 43.7° N), while we sampled high-density populations in both the north and south (range = 39.6° – 43.5° N). The lower 25th percentile of sparrow densities spanned only 1.6° of latitude among our 4.2°-long sampling region, while the second through fourth quartiles covered more of the 7.0° breeding distribution (3.2°, 2.3°, and 3.9° latitude for 2nd through 4th quartiles, respectively). Thus, the influence of a small number of populations could drive this interaction. Regardless of whether the reported relationship between bill size and density is due to competition or some other driver, however, we show a positive correlation between bill surface area and temperature once density has been controlled for.

It is important to note that bill size is not subject to the selective forces of temperature during just the summer months. Selection outside of the breeding season can also be a dominant force in bill evolution (Schluter and Smith 1986, Grant and Grant 1993, Francis and Guralnick 2010). Multiple bird species show correlations between bill size and minimum winter, not maximum summer, temperatures (Symonds and Tattersall 2010, Danner and Greenberg 2015). Saltmarsh Sparrows, however, are migratory with high degrees of mixing between breeding and non-breeding populations. Ringed birds from single breeding populations have been resighted across the non-breeding range and vice versa (Borowske 2015; SHARP, unpublished data). It seems highly unlikely that selection during the non-breeding period would be able to produce the geographic clines we report here during the breeding season.

Conclusions – While not tested directly in our study, a link between bill size and male mating success could explain an array of bill size patterns observed in various coastal avian taxa: the patterns of female choice reported in some taxa (Olsen et al. 2013), the display behaviors of others (Luther and Danner 2016), the presence of sexual dimorphism across a number of socially monogamous mating systems (Greenberg and Olsen 2010), and the correlations between bill morphology and density that we report here. No other selective process for the Greenberg-Tattersall Corollary can singly explain all of these patterns. Taken together, our findings, and those of others working in similar water-limited environments, suggest that sexual selection is a strong hypothesis for producing intraspecific geographic patterns in bill size, and we suggest that future investigations measure sexual selection on bill size directly across populations with a range of climates and densities.

DECLARATIONS

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Author contributions

This research is based on the undergraduate thesis of J. L. Froehly, drawing from her experimental design, analysis, and writing. B. J. Olsen and K. J. Ruskin worked with J. L. Froehly to expand the analysis, and B. J. Olsen primarily wrote the current draft with input from

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Conflicts of Interest

None.

Permits

Appropriate animal care was ensured by the Institutional Animal Care and Use Committee of the University of Maine under approval A2011-04-02, University of New Hampshire under approvals 100605 and 130604, State University of New York College of Environmental Science and Forestry under approval 120101, University of Connecticut under approval A11-013, and the University of Delaware under approval AUP1157-2015-2.

Data archiving

Data for this project are archived on the SHARP website at https://www.tidalmarshbirds.org/?page_id=1871.

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TABLES

Table 1. Results from model selection to explain geographic variation in Saltmarsh Sparrow (*Ammospiza caudacuta*) bill surface area.

Model[1,2]	**ΔAIC$_C$**[3]	**fixed effects (*k*)**	**model weight (w_i)**
Latitude x Intraspecific Density	0	6	>0.999
Latitude + Intraspecific Density	22.0	5	< 0.001
Latitude	23.3	4	< 0.001
Intraspecific Density	26.3	4	< 0.001
Null	26.5	3	< 0.001

[1] All models (including the null model) include fixed effects for body size (the first principal component score of mass and wing chord), sex (male or female), an indicator variable describing whether or not the sampled population was within the zone of introgression with Nelson's Sparrow (*A. nelsoni*), and a random effect for marsh identity.

[2] All models with interaction terms also included the component additive terms

[3] AIC$_C$ for the top model was 6520.79.

Table 2. Parameter estimates, standard errors (SE), and post hoc t-scores and P-values for the top-ranked model of Saltmarsh Sparrow (*Ammospiza caudacuta*) bill size across the majority of its breeding range. Covariates include a principal component for body size, bird sex (female is the reference level), an indicator variable for whether or not birds were found within the hybrid zone with A. nelsoni (outside of the hybrid zone is the reference level), degrees north latitude, sparrow density averaged over the nearest tenth of a degree of latitude, and the interaction between latitude and density. All variables were scaled before parameterization.

Parameter	Estimate	SE	t	*P*
Body Size	0.81	0.22	3.75	0.0002
Sex	0.16	0.45	0.36	0.72
Hybrid Zone	4.51	1.32	3.40	0.002
Latitude	-1.55	0.79	-1.96	0.06
Density	-1.37	0.29	-4.60	0.0003
Latitude x Density	1.65	0.29	5.70	0.001

FIGURE CAPTIONS

Figure 1. Mean bill surface area (mm^2 ± standard error) for Saltmarsh Sparrow (*Ammospiza caudacutus,* filled circles) and Nelson's Sparrow (*A. nelsoni,* open circles) calculated for each 0.05 degrees of latitude with sampled individuals as a function of latitude (a proxy for temperature). Each point represents 30 individuals on average (range 1 – 231). This raw pattern was best predicted by the interaction between latitude and population density (Fig. 2, Table 1).

Figure 2. Predicted relationship between bill surface area (mm^2) and latitude for marshes with low (first quartile density; dotted line with shaded 95% confidence interval), medium (median density; solid line), and high (third quartile density; dashed line with shaded 95% confidence interval) densities of Saltmarsh Sparrow (*Ammospiza caudacuta*). Darker confidence interval shading indicates areas of overlap between the first and third quartile intervals. The confidence interval around the median density is omitted for visual clarity but lies in between the two other quartile intervals. Predicted values control for the effects of body size, sex, and position relative to the hybrid zone with Nelson's Sparrows (*A. nelsoni*).

Figure 3. Mean bill surface area (mm^2 ± SE) of Saltmarsh Sparrows (*Ammospiza caudacutus*), corrected for body size, in 25 marshes (2 – 121 sparrows per marsh, median = 11 sparrows). Symbol shape indicates whether marshes are outside (square) or inside (circle) of the hybrid zone with *A. nelsoni*. Sparrows were measured at 40º (open squares), 41º (filled squares), 42º (open circles), 43º (gray circles), and 44º (black circles) north latitude.

Figure 4. Least squares mean bill surface area (mm^2 ± 95% confidence intervals) for female (circles) and male (squares) Nelson's (*Ammodramus nelsoni*) and Saltmarsh (*A. caudacutus*) sparrows. Values in (a) were measured outside of the hybrid zone of the two species (Nelson's Sparrows in Washington County, Maine, USA; Saltmarsh Sparrows south of Cape Cod, Massachusetts, USA) and values in (b) were measured inside the hybrid zone.

Figure 1.

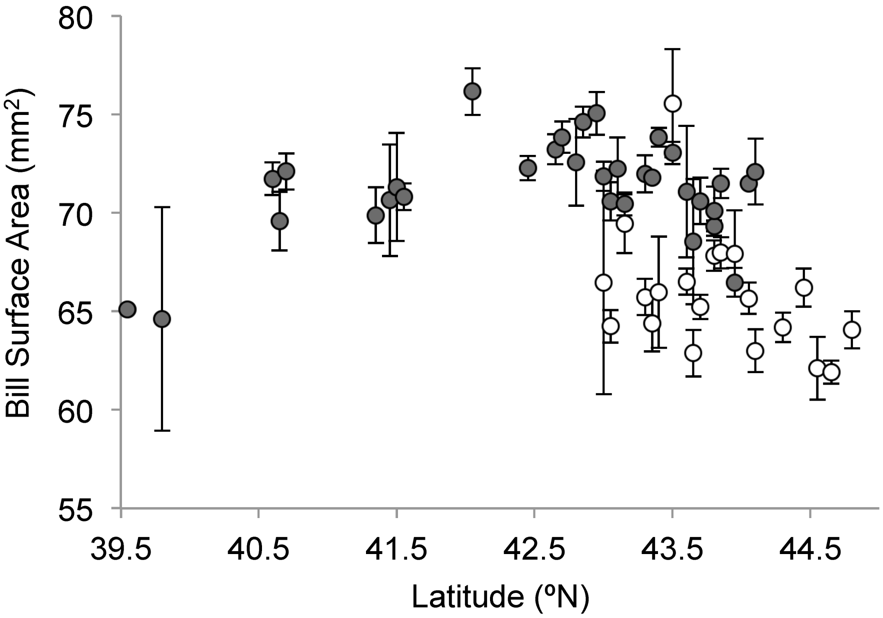
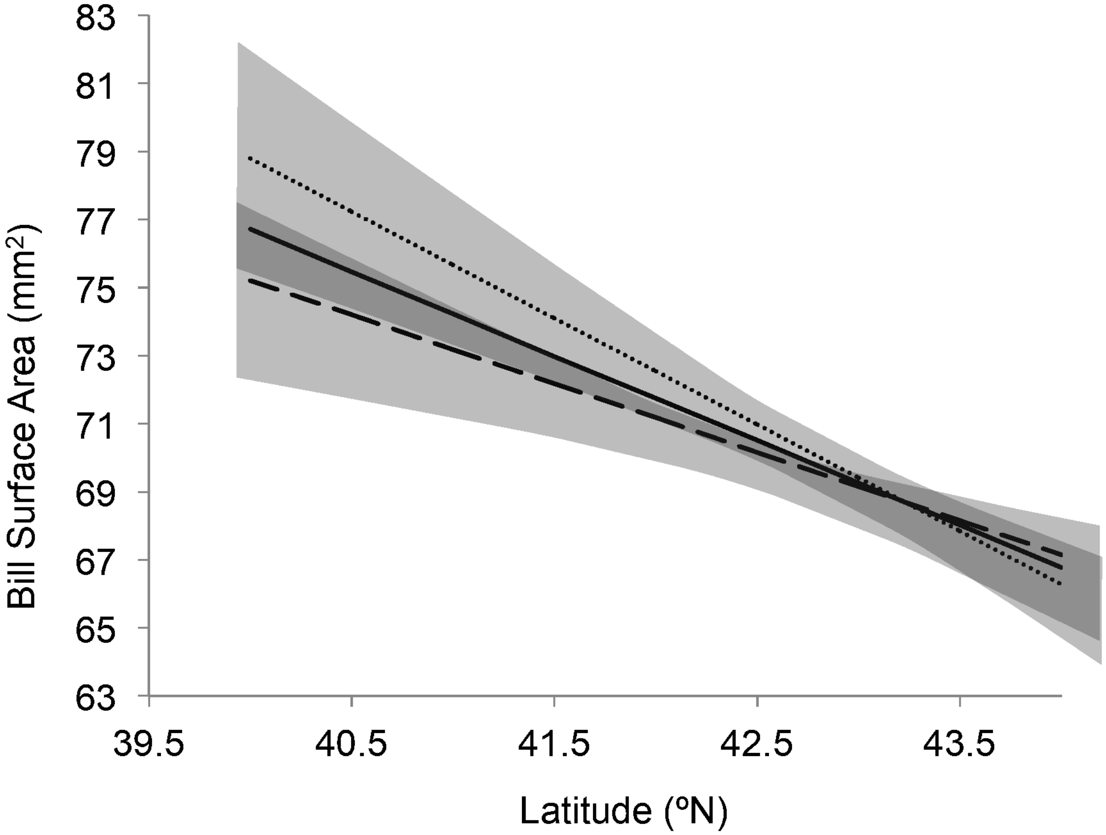

80
75
70
65
60
55
Bill Surface Area (mm^2)
39.5
40.5
41.5
42.5
43.5
44.5
Latitude (ºN)

Figure 2.



83
81
79
77
75
73
71
69
67
65
63
Bill Surface Area (mm^2)
39.5
40.5
41.5
42.5
43.5
Latitude (ºN)

Figure 3.

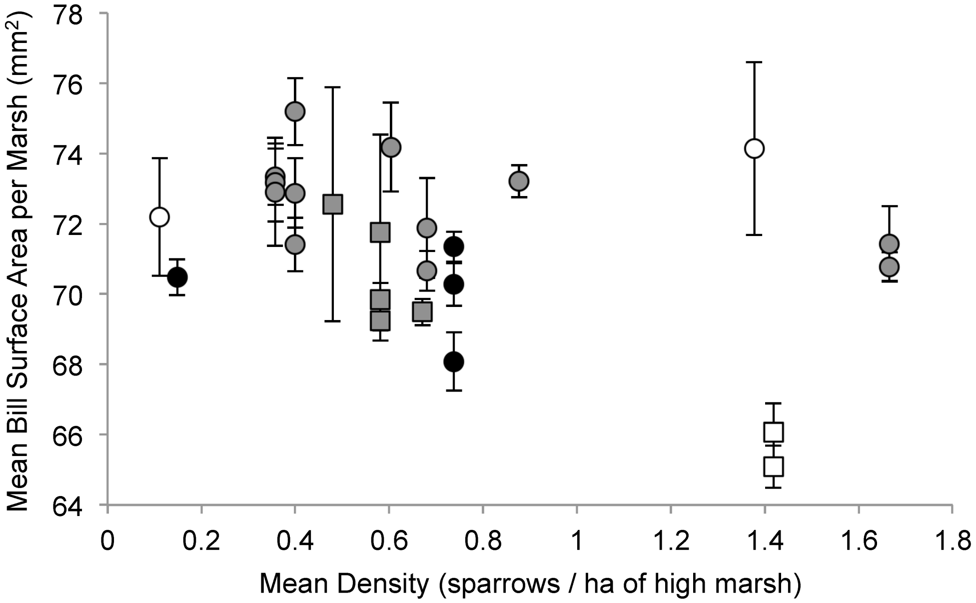

Mean Bill Surface Area per Marsh (mm^2)
78
76
74
72
70
68
66
64
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
Mean Density (sparrows / ha of high marsh)

Figure 4.