

Bill size and dimorphism in tidal-marsh sparrows: island-like processes in a continental habitat

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Abstract. Conditions favoring population divergence in trophic features, such as the low levels of species richness and interspecific competition found on islands, can be similar to conditions that increase their sexual dimorphism or overall variance. Male emberizid sparrows of tidal marshes have undergone parallel evolution of large bills. We tested for parallel increases between dimorphism and overall variation in bill size by comparing three groups totaling 30 sparrow subspecies: tidal-marsh sparrows, nontidal relatives of tidal-marsh taxa, and representative sparrow taxa. Bill size (and not other features) showed the following patterns in tidal-marsh sparrows compared to nontidal relatives or sparrows at large: (1) an increase; (2) a greater increase in males than females; (3) an increase in sexual dimorphism; and (4) greater variation in females. A high degree of sexual dimorphism in bill size is consistent with the hypothesis that low levels of interspecific and high levels of intraspecific competition select for intraspecific niche divergence. Alternatively, increased sexual selection in tidal-marsh sparrows, vis-à-vis high densities and hence increased male–male competition, may account for the differentially large increase in bill size in males. Relaxed natural selection due to high ecosystem productivity and low interspecific competition may explain why, in tidal-marsh sparrows, female bills have diverged less than males and show higher levels of variability at larger sizes. Both the niche divergence and sexual selection hypotheses depend upon processes, particularly increases in population density, that are similar to those often reported for island passerines. However, the low species diversity and increased intraspecific competition of salt marsh faunas is probably a result of abiotic constraints on colonization (tides and salinity) rather than the isolating distances of island biotas. Thus, both a shift in bill size and increases in its dimorphism and variability may be favored by high productivity and abiotic constraints.

Key words: dominance hypothesis; ecological divergence; Emberizidae; niche variation; salt marsh birds.

INTRODUCTION

Adaptive radiation, which leads to the rapid evolution of ecologically and morphologically diverse species within a single clade, usually occurs in environments where overall species diversity, and hence competition, is low (Darwin 1859). Although research on adaptive radiations focuses on the genesis of interspecific variation, the conditions that underlie their evolution can be similar to those that promote variation within populations as well, and the two processes need to be considered together (Bolnick and Doebeli 2003, Butler et al. 2007). Adaptive radiations begin with a single taxa colonizing newly available habitat (such as an island), which is characterized by both a different distribution of resources and reduced interspecific competition. In response, animal niches can change in two distinct ways: (1) Niches can shift to new resource-use optima; or (2) niches can broaden to encompass a broader range

of resources. The second of these options can result in three different phenomena: (A) Intraspecific subniches can arise for each sex; (B) broad niches can be occupied by all individuals, or (C) specialized subniches can form that are unrelated to sex. These ecological patterns may lead to divergence in morphological patterns. Niche shifts can result in directional selection on morphology to allow for increased foraging generalization (Robinson-Wolrath and Owens 2003); intraspecific subniches can result in polymorphisms in morphological traits, with the prime example being ecologically related sexual dimorphism (Selander 1966, Gosler and Caruthers 1994); and finally, relaxed selection (low interspecific competition and no new resource optima) can result in increased morphological variation (Van Valen 1965). Although considerable effort has been focused on determining under what conditions each of these three ecomorphological responses might occur, the interplay between these processes has rarely been considered in a single set of colonizing species (but see Dayan and Simberloff 1994, Butler et al. 2007).

In addition to the above resource-related processes, colonization of species-depauperate environments, such

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as islands, can lead to changes in morphology and morphological variation through altered social interactions. If populations build to high densities, then selection can favor the evolution of larger overall body size or an enlargement of characters critical in behavioral dominance (the “dominance hypothesis”; Robinson-Wolrath and Owens 2003, Scott et al. 2003). In addition, in species with well-defined sex roles, a higher incidence of intrasexual conflict in one sex (usually males) can also lead to increased sexual dimorphism (Stamps et al. 1997).

Avian bill size has been at the center of research on character displacement (Grant and Grant 2006) and adaptive radiation. Bird bills are also involved in some striking examples of ecologically based sexual dimorphism (Selander 1966, Temeles et al. 2000, Radford and du Plessis 2004). Finally, although contentious (Soulé and Stewart 1970), evidence for the niche variation hypotheses (where niche generalization is inversely related to interspecific competition) has come from studies of avian bill variability (Van Valen 1965).

Many of the studies cited above focused on island systems where low interspecific and high intraspecific competition are prevalent conditions. Attempts to find habitat-specific patterns for bill size dimorphism and variation embedded within continental avifaunas have generally not been successful (e.g., Willson 1969, Willson et al. 1975). Perhaps these large-scale analyses were not sufficiently focused on finding conditions similar to those on islands. Tidal marshes provide an excellent system to examine the initial ecological and evolutionary response to a newly emerging habitat. Tidal marshes are characterized by high primary productivity, a unique combination of benthic marine resources associated with regularly inundated substrates (Greenberg et al. 2006), and harsh physical conditions that may limit colonization (low climatic buffering, high salinity, tidal flooding). Further, tidal marshes are limited in extent, locally distributed, and ephemeral through recent evolutionary time, expanding and receding with the advance and decline of glacial ice sheets (Malamud-Roam et al. 2006). Tidal marshes north of the last glacial maximum were ice-bound until <15 000 years ago, and further south many of the estuarine marshes did not develop until the postglacial flooding of river mouths. Therefore, many vertebrate taxa associated with tidal marshes show evidence of a recent colonization of newly available habitat, where they are morphologically and physiologically distinct from inland relatives yet show little underlying genetic differentiation (Chan et al. 2006). In addition to these recent colonization events, it is likely that sparrows went through colonization/extinction cycles in parallel with the advance and retreat of glacial ice throughout the Pleistocene.

In North America, three different genera and six species of emberizid sparrows have colonized tidal-marsh habitats along the Atlantic, Pacific, and Gulf Coasts (Grenier and Greenberg 2005). Close examina-

tion of these taxa has led to the description of at least 10 different subspecies or subspecies groups, which probably reflect at least seven different tidal-marsh invasions. Two observations suggested that sparrows should be a focus of analysis of divergence and intraspecific variation in tidal marshes. First, the males of these taxa have evolved a parallel increase in relative bill size relative to males of their most likely sister taxa (Grenier and Greenberg 2005). Second, the salt marsh subspecies of Savannah Sparrow (*Passerculus sandwichensis* [Rising 1987]) and Swamp Sparrow (*Melospiza georgiana* [Olsen et al. 2008, 2009]) are known to be more dimorphic than their inland counterparts, suggesting that male divergence and sexual dimorphism might characterize tidal-marsh sparrows.

By comparing tidal-marsh and non-tidal-marsh sparrows overall, as well as tidal-marsh sparrows and their probable closest relatives in a pairwise fashion, we addressed the following questions in this study: (1) Have tidal-marsh sparrows diverged in overall morphology, and in particular, foraging-related structures such as bill size? (2) Does morphological variation within and between the sexes, particularly bill size, differ between tidal-marsh and non-tidal-marsh sparrows? The patterns uncovered by answering these questions form the basis of an integrated examination of the interplay of bill size divergence and intraspecific variation in tidal-marsh-colonizing species, and how these processes in a continental ecosystem compare to those reported from island systems.

METHODS

Classification of taxa

Taxa were classified into three groups (Appendix A): tidal-marsh taxa (10 subspecies or species of three genera of North American sparrows, *Passerculus*, *Melospiza*, and *Ammodramus*); the seven closest known relatives of the tidal-marsh taxa; and an outgroup of 13 sparrow species, representing every North American sparrow genus except those restricted to the Arctic or subtropics (see Appendix B for criteria for taxa inclusion in the above group).

Measurements and density estimates

Measurements were taken from museum study skins (1232 measured by R. Greenberg) and field studies (70 *Melospiza georgiana* measured by B. Olsen) totaling 1302 individuals and 30 taxa (see Appendix C for means and SE for all taxa). For each specimen or live bird, we measured (with calipers to the closest 0.01 mm) bill length, width, and depth at the anterior edge of the nares; tarsus; and unflattened wing chord. Tarsus length was measured from the middle of the intertarsal joint to the distal edge of the last scale above the hallux. Bill size was approximated as $1/8(\text{length} \times \text{width} \times \text{depth} \times \pi)$, based on the formula for a parabolic cone, and then transformed by taking the cube root, to more directly compare the magnitude of change to our linear

measurements of tarsus length and wing chord. We measured only adult birds collected or captured during the known breeding season for each taxon. In addition to measurements, we recorded date, location, and mass (if measured) from the specimen tag or field data sheets.

To examine patterns of dimorphism in core size, we obtained mean, sample size, and standard deviation of body mass for most of the taxa (and in most cases for both sexes) from a variety of sources (Appendix D), including museum specimen catalogues, studies cited in Birds of North America Accounts (*available online*)⁴ and Dunning (2006). To compare the magnitude of differences with linear measurements, we used the cube root of body mass (Amadon 1943). The degree of sexual dimorphism in all measurements was standardized across taxa using female means by taking (male mean – female mean)/female mean \times 100.

We surveyed the literature for maximum breeding densities for tidal-marsh sparrows and compared these values to the maximum value (excluding island data) cited in the Birds of North America (see footnote 4) accounts for all North American sparrow species for which the data are available. For most species the values are provided as pairs per hectare. The nonterritorial and promiscuous Saltmarsh Sparrow (*Ammodramus caudacutus*) values are for nesting females. However, at least in the Saltmarsh Sparrow breeding season, sex ratios of this species are highly skewed toward males ($\sim 2:1$; C. Elphick, *personal communication*); thus the female-nesting figure is a low estimate of male density.

Statistical analysis

The hypotheses that tidal-marsh sparrows are more dimorphic in bill size, relative bill size (bill size/tarsus length), tarsus length, and wing chord were tested using the following Multimodel in SAS PROC MIXED (Singer 1998), whereby random slope and intercept terms are ascribed at the taxon level. The following model was developed:

$$Y_{ij} = \gamma_{00} + \gamma_{01}(\text{tidal}) + \gamma_{02}(\text{tidal related}) + \gamma_{10}(\text{male}) \\ + \gamma_{11}(\text{tidal} \times \text{male}) + \gamma_{12}(\text{tidal related} \times \text{male}) \\ + \mu_{1j}(\text{male}) + \mu_{0j} + \varepsilon_{ij}$$

where the subscripts ij refer to the i th specimen of the j th taxon. The parameter γ is the mean or deviation from the mean of the particular morphological feature in question for the portion of the population defined by the subscripts (i.e., γ_{00} = global mean for females of the outgroup sparrows, γ_{11} = mean deviation from γ_{00} for male salt-marsh sparrows, and γ_{12} = mean deviation from γ_{00} for male inland sparrows). The parameter μ_{0j} is a unique error contribution for each taxon, allowing each taxon's intercept to vary from the mean intercept, and μ_{1j} = the unique error contribution of each taxon,

allowing each taxon to have its own slope. The parameter ε_{ij} = the random deviation of individual i in taxon j .

The tidal and tidal-marsh-related taxa are modeled based on an intercept vector consisting of values for outgroup females (γ_{00}). The two interaction terms (i.e., tidal-marsh \times male and tidal-marsh-related \times male) were examined for significant departure from the null hypotheses of no difference in sexual dimorphism between the outgroup and either tidal-marsh birds or tidal-marsh-related birds using a Likelihood Ratio Test.

Paired t tests based on taxon means were used to examine differences between tidal-marsh taxa and their closest inland relatives (see Appendix B for pairings). The proper statistical treatment of some of the taxa is unclear. The three San Francisco Bay subspecies of Song Sparrows (*Melospiza melodia*) show little genetic structure based on the analysis of microsatellite variation (Chan and Arcese 2003). Therefore, they each may not represent separate colonization events from the inland subspecies. A similar situation is found in the salt marsh Savannah Sparrows, where Large-billed (*Passerculus sandwichensis rostratus*) and Belding's (*P. s. beldingi*) Savannah Sparrows (Zink et al. 2005) cannot be separated from each other based on MtDNA. However, these two tidal-marsh subspecies groups each possess members that are morphologically distinct and display a different degree of sexual dimorphism, so pooling or averaging across these subspecies would obscure a potentially important source of variation. We have conducted the paired t tests using both a set of comparisons that average the mean measurements taken from the individual subspecies, and a set that treats them as independent for comparisons with inland taxa.

The relationship between the standard deviations and means of bill size was tested using an ANCOVA homogeneity of slopes model (StatSoft 2003) for tidal-marsh vs. all non-tidal-marsh taxa. All non-tidal-marsh taxa were included because the size range for tidal-marsh-related species was too small to compare across the size ranges found in tidal-marsh taxa.

Variation in the maximum reported breeding densities for the species groups were analyzed using ANOVA. The raw data were log transformed to eliminate significant heterogeneity of variance between the groups. Bonferroni's test was applied to determine group-specific differences.

RESULTS

Dimorphism in tidal-marsh, tidal-marsh-related, and outgroup taxa

The three main morphological measurements (bill size, tarsus, and wing chord) are correlated, but the linear relationship explains a relatively small portion of the variance in these variables (r^2 , bill size/tarsus = 0.40; bill size/wing = 0.25; tarsus/wing = 0.10). Therefore, we analyzed these variables separately to compare the

⁴ (<http://bna.birds.cornell.edu/bna/>)

relative degree of inter-taxon divergence and sexual dimorphism.

The mean percent dimorphism in bill size varied significantly among the three taxa groups, and the average dimorphism was substantially higher in tidal-marsh species than the other two groups (16.1% vs. 2.5%) (Fig. 1). The multilevel models (Appendix E) showed a highly significant difference in bill dimorphism between the tidal-marsh sparrows and the outgroup and no difference between tidal-marsh relatives and the outgroup. The same pattern was found when bill size was standardized by tarsus length, although tarsus length also showed significant between-group variation in the same direction as bill size (Appendix E). Although wing chord was sexually dimorphic throughout the sparrows (note the highly significant variation with “sex” in Appendix E), we detected no significant variation in dimorphism among the groups in wing chord.

Ninety percent of the tidal-marsh sparrow taxa showed significant dimorphism in bill size (males larger) when the sexes were compared within taxa using a *t* test. Only one other sparrow taxon showed a significant difference (Black-throated Sparrow, *Amphispiza bilineata*). Sixty percent of the tidal-marsh sparrows were significantly dimorphic in tarsus length, whereas only one of the tidal-marsh-related (Swamp Sparrow) and only one of the outgroup species (Green-tailed Towhee, *Pipilo chlorurus*) showed significant dimorphism in tarsus length. In contrast to tarsus and bill size, all of the tidal-marsh and tidal-marsh-related taxa and 61.5% of the outgroup taxa showed significant differences in wing length.

The percent dimorphism based on (body mass)^{1/3} tended to be low and did not vary significantly among the three groups of sparrows ($F_{2,23} = 1.4$, $P = 0.27$). The trend in body mass dimorphism showed a similar pattern to that found in tarsus and bill size, with mean percent dimorphism highest in the tidal-marsh group (mean \pm standard error = $2.0\% \pm 0.7\%$, $n = 8$), followed by the tidal-marsh-related species ($1.5\% \pm 0.4\%$, $n = 6$) and the representative sparrows ($0.9\% \pm 0.4\%$, $n = 13$). The paired comparison between tidal-marsh taxa and their closest relatives (six pairs available) was also not significant (Appendix D).

Magnitude of dimorphism in tidal-marsh vs. related taxa

Considering all 10 taxa of tidal-marsh sparrow, the average dimorphism in the cube root of bill size was $16.1\% \pm 3.4\%$. With a more conservative approach (averaging within the San Francisco Bay and salt marsh Savannah Sparrow groups) this value was $14.7\% \pm 2.3\%$. The average bill size dimorphism for the seven sister taxa was $2.7\% \pm 0.95\%$. The difference in the average magnitude of bill dimorphism was significant using either the complete ($t_9 = 4.4$, $P = 0.002$) or the more conservative data set ($t_6 = 3.0$, $P = 0.03$).

Tarsus length dimorphism also tended to be greater in tidal-marsh sparrows. Considering all 10 tidal-marsh

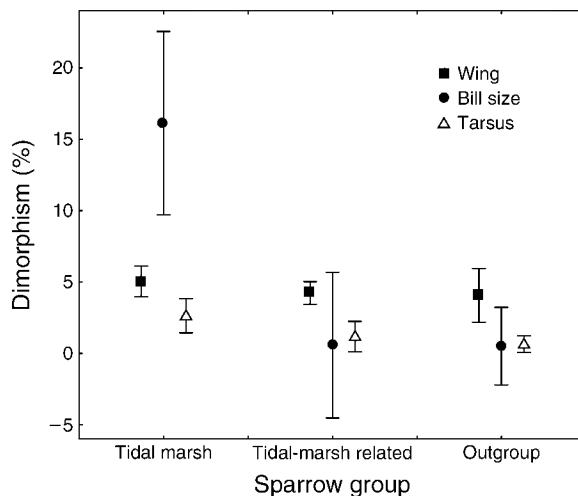


FIG. 1. Mean and SE for percent dimorphism [(male – female)/female] \times 100] for wing chord, bill size, and tarsus length for tidal-marsh ($n = 10$), tidal-marsh-related ($n = 7$), and outgroup ($n = 13$) sparrows. Bill size [(length \times width \times depth \times π]/8) was converted to a linear measurement by taking the cube root.

taxa, the average percent dimorphism was $2.58\% \pm 0.54\%$ compared to $0.89\% \pm 0.33\%$ in the related, non-tidal-marsh taxa ($t_9 = 2.3$, $P = 0.04$). However, the more conservative taxa list results in a nonsignificant difference in dimorphism between the salt marsh and related taxa ($2.31\% \pm 0.55\%$ vs. $1.27\% \pm 0.33\%$, $t_6 = 1.4$, $P = 0.20$). Average percent wing dimorphism was similar between tidal-marsh and tidal-marsh-related species ($4.06\% \pm 0.58\%$ vs. $3.78\% \pm 0.23\%$, $t_9 = 0.3$, $P = 0.75$ for the complete list and $4.24\% \pm 0.63\%$ vs. $3.99\% \pm 0.26\%$, $t_6 = 0.4$, $P = 0.70$ for the more conservative list).

Morphological divergence between tidal-marsh taxa and their close relatives

Tidal-marsh sparrows of both sexes had significantly larger bills than their inland relatives. This is true within each sex (male paired $t = 2.5$, $P = 0.02$ for complete and $t = 2.9$, $P = 0.03$ for conservative list; female paired $t = 2.4$, $P = 0.04$ for complete and $t = 2.41$, $P = 0.05$ for conservative list). Bill size divergence remained significant for both sexes when bill size was standardized by tarsus length (males, $t = 3.7$, $P = 0.005$; females, $t = 2.7$, $P = 0.04$ for conservative list). In contrast to bill size and relative bill size, tarsus length showed no significant differences between tidal-marsh and related taxa in either sex (male $t = 1.8$, $P = 0.11$ and female $t = 1.0$, $P = 0.33$ for complete, and male $t = 2.1$, $P = 0.07$; female $t = 1.2$, $P = 0.27$ for conservative list). Wing length also did not differ between tidal-marsh taxa and their relatives (male $t = 1.0$, $P = 0.36$ and female $t = 0.6$, $P = 0.55$ for complete, and male $t = 1.5$, $P = 0.18$ and female $t = 0.7$, $P = 0.51$ for the conservative list). Fig. 2 clearly shows the greater mean percentage of (bill size)^{1/3} divergence between tidal-marsh sparrows (of both sexes) and their

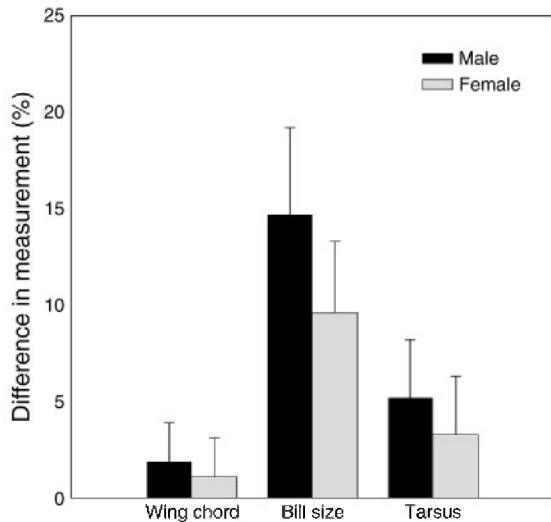


FIG. 2. Mean and standard error of the percentage difference in wing chord, (bill size)^{1/3}, and tarsus length between tidal-marsh and their closest known relative taxon $[(\text{tidal-marsh} - \text{tidal-marsh relative})/\text{tidal-marsh relative}] \times 100$.

non-tidal-marsh relatives when compared to tarsus or wing length. Female bill size ($9.6\% \pm 3.7\%$ larger than relative taxa), however, was significantly less divergent (paired t test, $t_9 = 3.5$, $P = 0.006$) than males ($14.7\% \pm 5.5\%$ larger than relative taxa).

Differences in variation in bill size

As expected, the taxon-specific variation in bill size increased with mean bill size across all groups of sparrows. However, the rate of this increase varied between tidal-marsh and non-tidal-marsh sparrows (Fig. 3A). The slope of the regression was over twice as great for the more dimorphic group (tidal, 0.14 ± 0.02 , $r^2 = 0.84$; nontidal, 0.06 ± 0.01 , $r^2 = 0.77$; ANCOVA for homogeneity of slopes, $F_{1,26} = 12.6$, $P = 0.001$). Additionally, we found a marked difference between the sexes in this relationship. When only male sparrows were considered (Fig. 3B), the slopes for the relationship were similar within tidal-marsh and non-tidal-marsh taxa (tidal, 0.7 ± 0.02 , $r^2 = 0.54$; nontidal, 0.9 ± 0.01 , $r^2 = 0.75$; $F_{1,26} = 0.2$, $P = 0.66$). In contrast, female tidal-marsh sparrows (Fig. 3C) produced a slope that was over five times steeper than non-tidal-marsh females (0.16 ± 0.01 , $r^2 = 0.75$, vs. 0.03 ± 0.01 , $r^2 = 0.51$, $F_{1,26} = 53.0$, $P < 0.0001$). The difference between the tidal-marsh and non-tidal-marsh relationships found in either females alone or in both sexes pooled remains highly significant when (1) the two non-tidal-marsh species with the largest bills are removed (females only, $F_{1,13} = 18.5$, $P = 0.0002$; both sexes pooled, $F_{1,24} = 16.9$, $P = 0.0004$), and (2) only tidal-marsh and tidal-marsh-related species are compared (females only, $F_{2,13} = 30.7$, $P < 0.0001$; sexes pooled, $F_{1,13} = 14.2$, $P = 0.002$).

Maximum breeding densities in tidal-marsh vs. non-tidal-marsh sparrows

Tidal-marsh sparrows consistently attain very high densities (Fig. 4, Appendix F), with Seaside Sparrow (*Ammodramus maritimus*), Belding's Savannah Sparrow, and Suisun Song Sparrow (*Melospiza melodia maxillaris*) occurring locally at densities exceeding 10 pairs/ha. Comparing the maximum densities reported for continental breeding populations, tidal-marsh taxa show a much higher mean value (16.9 ± 4.4 pairs or males/ha)

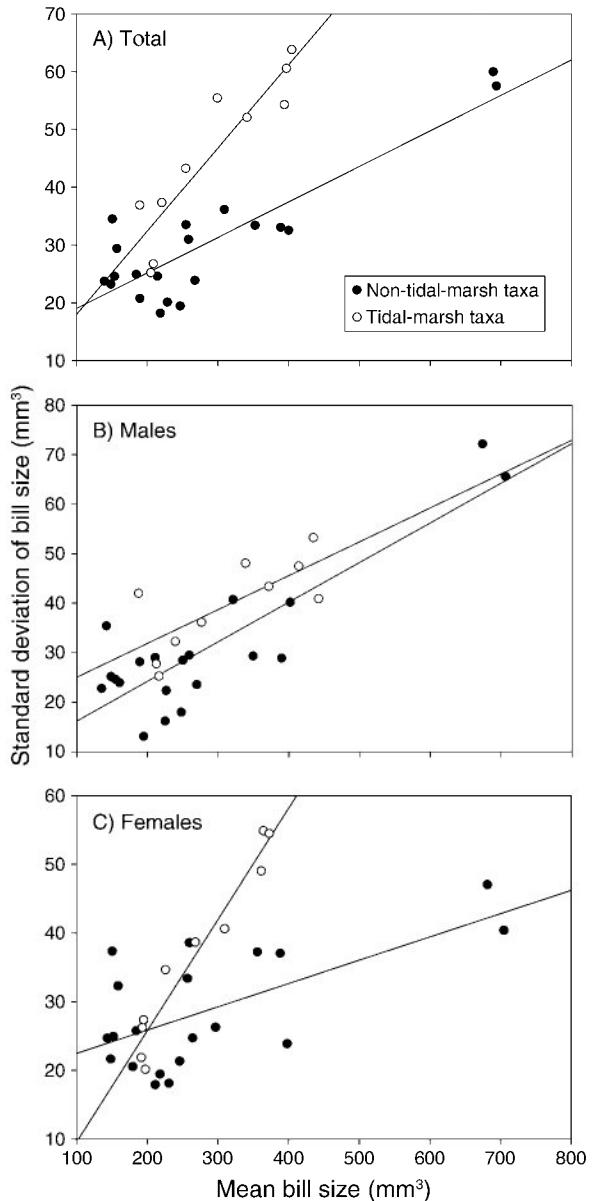


FIG. 3. Standard deviation of bill size plotted against mean bill size in tidal-marsh vs. all non-tidal-marsh sparrows (out-group and closely related pooled) for (A) all individuals, (B) males, and (C) females. Regression lines for tidal-marsh and non-tidal-marsh taxa are included.

than tidal-marsh-related (6.0 ± 3.8 pairs) or outgroup taxa (2.2 ± 0.57 pairs) (ANOVA on log-transformed data, $F_{2,33} = 17.4$, $P < 0.0001$). Tidal-marsh taxa had significantly higher densities than tidal-marsh-related ($P = 0.025$) or outgroup taxa ($P < 0.0001$) based on the Bonferroni's test. Island populations of both the Savannah Sparrow and Song Sparrow have been reported to be of comparable density to those of salt marshes (up to 40 and 20 pairs/ha, respectively).

DISCUSSION

Patterns in sexual dimorphism and divergence in tidal-marsh sparrows

Grenier and Greenberg (2005) demonstrated that the males of different tidal-marsh sparrow taxa have consistently larger bills than inland emberizids. We have extended this pattern of parallel evolution by documenting that females have significantly larger bills as well. Female tidal-marsh sparrows, however, showed a 35% smaller average increase over their non-tidal-marsh relatives than did males. Our analysis also confirms that absolute bill size and bill size/tarsus length, rather than overall body size, are the primary features that have diverged in tidal-marsh taxa.

The difference in the degree of divergence for each sex contributes to consistent sexual dimorphism in overall bill and relative bill size in tidal-marsh species. Sexual dimorphism in tarsus length is also strongly associated with tidal-marsh life, but wing chord and body mass show little or no association with the tidal-marsh ecosystem. These patterns lend support to the idea that the shift in food resources and/or competitive environment associated with the colonization of a novel continental habitat may have lead to a divergence in morphology and an increase in sexual dimorphism.

Additional insight into the underlying processes may be provided by the positive relationship between bill size variation and mean bill size across the different Emberizid groups. Overall, variability increases faster in tidal-marsh than non-tidal-marsh sparrows (Fig. 3A), and this pattern appears to be driven by differences between tidal and non-tidal-marsh females, since male variation within the tidal marsh tracks the non-tidal-marsh closely. One explanation for this pattern is that sexual selection on tidal-marsh males is the primary cause of bill divergence within the ecosystem, whereas female bill size divergence in the tidal marsh is due to genetic correlation with males. Female bill size may be under less intense selection, resulting in higher variation among females as bill size increases. If this is true, the high levels of variation in tidal-marsh bill sizes compared to non-tidal-marsh bills may support the niche variation hypothesis (Van Valen 1965); in the absence of sexual selection, the low interspecific competition that characterizes tidal marshes results in weak stabilizing selection on female bills. Relaxed selection on females in the tidal ecosystem is suggested not only by the increased rate of bill variation relative to

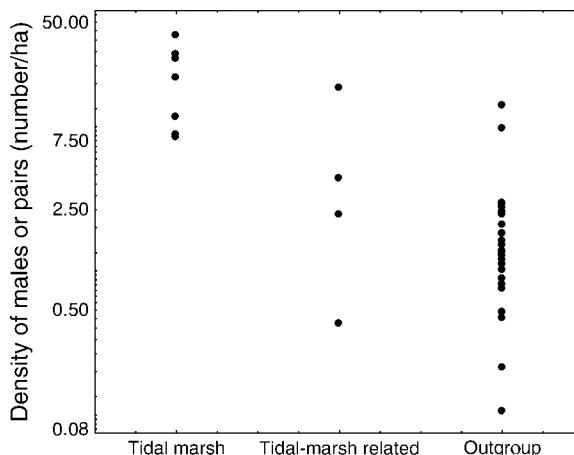


FIG. 4. Mean maximum reported breeding densities for North American sparrows classified by type (see Appendix F for taxon-specific data).

tidal-marsh males, but also by the higher increase in variance relative to both sexes of all other sparrows analyzed.

Divergence and dimorphism as trophic adaptations

The increase in bill size in island passerines has been used as evidence that the divergence is driven by foraging ecology (Grant 1965, Clegg and Owens 2002). Grenier and Greenberg (2005) hypothesized that adaptation to different resources was the driving force in the evolution of large bills in tidal-marsh sparrows. The larger bills of island birds have been attributed to an increase in diet generalization. This could also explain the trend in tidal-marsh sparrows, but specialization in diet (invertebrates) or foraging behavior (probing in tidal mud) are legitimate alternatives. At this point, however, there are no comparative data between tidal-marsh and non-tidal-marsh sparrows that either support or contradict this hypothesis. Similarly, the increase in sexual dimorphism among tidal-marsh birds could represent the type of intersexual niche segregation that has been proposed as a response to reduced interspecific and increased intraspecific competition in island species (e.g., *Anolis* [Butler et al. 2007]). Reduced competition within monogamous pairs could increase the efficiency of provisioning young (Gosler 1987). Finally, the increased dimorphism could be associated with an increased divergence in sexual roles, where the two sexes optimize different aspects of their life history. Once again, no specific data exist that have tested for relative niche segregation in tidal-marsh vs. non-tidal-marsh sparrows.

Sexual selection on male bill size

Despite the initial suppositions of many island and tidal-marsh studies linking increased bill size and dimorphism with trophic adaptations, the differences we found in male and female responses among tidal-marsh

taxa suggest that sexual selection might be an important, if not the primary, factor. Sexual selection could be operating through two different mechanisms: (1) a shift in mating systems in tidal-marsh birds affecting competition and access to females or female-preferred resources (Rising 1987), or (2) a general increase in conflict experienced by the more competitive sex due to an increase in population density (Stamps et al. 1997).

Shifts from monogamous to polygamous mating systems are often accompanied by increases in dimorphism in overall size or the size of particular features. Mating systems of some, but not all, tidal-marsh sparrows have been studied in depth and are generally unremarkable. The tidal-marsh Song Sparrows (Johnston 1956), the coastal plain Swamp Sparrow (*Melospiza georgiana nigrescens* [Olsen et al. 2008]), and the Seaside Sparrow (Post and Greenlaw 1994) are all socially monogamous, with few or no reports of polygamy. Extra-pair paternity has been detected at rates comparable to most temperate songbirds (Grenier 2004, Hill and Post 2005, Olsen et al. 2008). Only the Saltmarsh and Nelson's (*Ammodramus nelsoni*) Sparrows (sharp-tailed sparrows) have been reported to have polygynous or promiscuous mating systems (Greenlaw and Rising 1994), and these show no or moderate degrees of bill size dimorphism.

Tidal-marsh sparrows consistently attain very high densities (Fig. 4), and this at least makes the conflict-caused dimorphism argument plausible. In this case, males face intense competition for territories or, particularly in the case of sharp-tailed sparrows, access to females. Three environmental factors appear to contribute to increased density in tidal-marsh sparrows: (1) reduced interspecific competition; (2) high ecosystem productivity; and (3) limited nesting sites that avoid tidal flooding. In such a social environment, selection on features that enhance male resource holding potential should be under intense selection.

Sparrow bills are multipurpose tools, used for both fighting and singing as well as foraging and provisioning young. The relatively powerful bills of sparrows can be viewed as potential weapons in skirmishes, and their greater size and dimorphism in tidal-marsh sparrows might contribute to their ability to threaten and dominate these high-density situations. This possible route to larger bill size has been largely unexplored, but Willson (1972) presented some intriguing data suggesting that in interspecific dominance hierarchies of sparrows, bill size was a better predictor of success than body size.

Tidal marshes vs. islands: similar processes with different causes?

If the evolution of larger and more dimorphic bills is the result of increased intraspecific competition, then tidal-marsh sparrows are exhibiting patterns and processes that have been ascribed to island birds (Clegg and Owens 2002). It is reasonable to suspect similar processes

between the two scenarios. Indeed, island populations of Song and Savannah Sparrows show high densities that are comparable to tidal-marsh populations of the same genera. Similar to this study, Weatherhead (1980) found that island-breeding sparrows had lower dimorphism in mass but greater dimorphism in bill size than a mainland population. The low diversity of competitors and resulting density compensation found on islands is thought to be a result of low colonization probabilities and high extinction rates due to their isolation (MacArthur and Wilson 1967) and small size. Tidal-marsh faunas may similarly possess little species diversity, in part, because of high extinction rates due to their limited extent and, perhaps more importantly, the ephemerality of their distribution in the face of glacial cycles.

The low species richness of tidal-marsh passerines, however, is unlikely caused by geographical isolation, as is the case with islands. The filter for the successful colonization of tidal marshes is probably associated with the divergent environmental conditions, which demand physiological specializations and preclude generalist taxa, rather than isolation per se. In salt marsh plants, for example, the few species of grasses that have successfully colonized the marsh are differentiated by other wetland flora primarily by their tolerance of salinity. Under these physiologically challenging conditions, salt-tolerant plants (e.g., *Spartina*) often form expansive, single-species stands, whereas these species are outcompeted by a number of other wetland species under more brackish or freshwater conditions (Crain et al. 2004). Salinity could act as a similar filter for bird colonization, as specific behavioral and physiological adaptations (such as changes in renal structure and function) are found in salt marsh sparrows (Goldstein 2006). Once a sparrow species has crossed this (and perhaps other) physiological barriers, it is able to take advantage of the abundance of food resources found in the marsh with minimal competition from other species.

Tidal flow is another feature of salt marshes that can influence local sparrow density. Flooding renders much of the marsh area unavailable for successful reproduction, although these areas can still provide abundant food. The actual resource for competition may be access to safe nesting areas (Johnston 1956) rather than food, which may not be limiting in salt marsh sparrow populations (Post and Greenlaw 1982). Therefore, competition for nesting sites drives the increase in bill size and dimorphism, and abundant food with little trophic competition acts to relax natural selection on bill size.

Future field test

Ecomorphological analysis can only determine what ecological mechanisms are most consistent with observed patterns. The actual importance of different hypothesized mechanisms needs to be tested with data from the field. To further test the sexual selection hypothesis, future field studies of tidal-marsh and related taxa should

focus on comparing the two groups for the relative importance of territorial skirmishes and other forms of social conflict among males across a range of densities, the correlation between the ability to obtain high-quality territories and bill size variation, and the existence and degree of diet difference and foraging segregation between males and females. The relative intensity of selection on bill size in males and females can be estimated in the field by tracking the survival of cohorts with known bill sizes from fledging to recruitment into the breeding population. The niche divergence hypothesis can be examined further by establishing the existence and degree of dietary differences and foraging segregation between males and females, and by comparing the reproductive performance and dietary diversity of pairs with varying degrees of dimorphism (Gosler 1987).

CONCLUSIONS

Through a number of separate colonization events, tidal-marsh sparrows have diverged in consistent ways from their nontidal counterparts and sparrows in general. Divergence is most pronounced in bill size, which supports the existence of a shift in trophic adaptations to a new environment. This shift in bill size is much more pronounced in males than in females and is accompanied by an increase in sexual dimorphism. An increase in bill size dimorphism would support the idea that in a species-depauperate environment, intraspecific competition drives within-species niche divergence. Interestingly, across all North American tidal-marsh emberizids, variation increases with bill size at a much greater rate in females than males. This observation suggests that sexual selection on male bill size may be critical for the divergence of tidal-marsh sparrows. Tidal-marsh sparrows often breed at very high densities, which may select for features, such as bill size, that aid in intermale conflict. The reduced interspecific competition and high productivity of tidal marshes may relax natural selection on bill size, allowing for divergence in males and increased variability in females. In this way, divergence, sexual dimorphism, and morphological variability respond in interrelated ways to the ecological conditions in tidal marshes. Either the niche divergence or the sexual selection hypotheses are based on the assumption that increased intraspecific competition (either for food resources or territories) underlies the increase in sexual bill dimorphism. Reduced interspecific competition and high levels of intraspecific competition make tidal marshes a continental habitat that is reminiscent of island systems, but the driving forces behind the low colonization rates in tidal marshes are likely environmental constraints (such as salinity and tidal flow) rather than geographical isolation. In searching for other, similar continental systems, it might prove fruitful to investigate habitats where high productivity is paired with harsh abiotic influences (e.g., mangrove swamps, high-elevation riparian meadows, tundra).

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APPENDIX A

Taxa (by group), sampling location, and sample sizes of specimens measured (*Ecological Archives* E091-174-A1).

APPENDIX B

Justification for taxa included and the formation of tidal-marsh/non-tidal-marsh comparative pairs of taxa (*Ecological Archives* E091-174-A2).

APPENDIX C

Mean and standard deviation for measurements used in this study by taxa and sex (*Ecological Archives* E091-174-A3).

APPENDIX D

Mean, sample size and standard deviation with reference source for body mass values used in this study (*Ecological Archives* E091-174-A4).

APPENDIX E

Results of multilevel models for the effects of a sex × taxa group interaction on bill size, bill size/tarsus length, tarsus length, and wing chord (*Ecological Archives* E091-174-A5).

APPENDIX F

Maximum breeding densities (pairs or females/ha) reported for North American sparrows (*Ecological Archives* E091-174-A6).