A BIOGEOGRAPHIC PATTERN IN SPARROW BILL MORPHOLOGY: PARALLEL ADAPTATION TO TIDAL MARSHES

J. Letitia Grenier[1,2] and Russell Greenberg[3,4]
[1]*Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720*
[3]*Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C. 20008*
[4]*E-mail: antbird@erols.com*

Abstract.—The study of ecological convergence, the evolution of similar traits on multiple occasions in response to similar conditions, is a powerful method for developing and testing adaptive hypotheses. However, despite the great attention paid to geographic variation and the foraging ecology of birds, surprisingly few cases of convergent or parallel feeding adaptations have been adequately documented. In this study, we document a biogeographic pattern of parallel bill morphology across 10 sparrow taxa endemic to tidal marshes. All North American tidal marsh sparrows display parallel differentiation from close relatives in other habitats, suggesting that selection on bill morphology is strong. Relative to their body mass, tidal marsh sparrows have longer, thinner bills than their non-tidal marsh counterparts, which is likely an adaptation for consuming more invertebrates and fewer seeds, as well as for probing in sediment crevices to capture prey. Published data on tidal marsh food resources and diet of the relevant taxa support this hypothesis. This morphological differentiation is most pronounced between sister taxa with the greatest estimated divergence times, but is found even in taxa that show little or no structure in molecular genetic markers. We, therefore, speculate that tidal marsh ecosystems are likely settings for ecological speciation.

Key words.—Bill morphology, biogeographic rule, convergence, ecological speciation, Emberizidae, tidal marsh, trophic adaptation.

Relating patterns of morphological variation to specific environmental gradients has long been an important focus for the study of geographic variation in vertebrates, resulting in several biogeographic rules (e.g., Allen's, Bergmann's, and Gloger's rules; Zink and Remsen 1986). In addition, analysis of morphology has been employed to infer a number of other ecological relationships and evolutionary patterns (Leisler and Winkler 1985). Although such studies have usually tested for ways that ecologically related morphology varies within species assemblages, a few researchers have examined how species might, through convergent or parallel evolution, share similar morphological characteristics with unrelated taxa, as they respond in common to the challenges associated with colonizing a particular habitat. For example, Niemi (1985) was able to discern consistent morphological shifts associated with breeding in boreal fen habitats that were shared by birds in North America and northern Europe. Several other studies (Landmann and Winding 1995; Leisler and Winkler 2001; Korner-Nievergelt and Leisler 2004) have also detailed convergence in body size and the morphology of wing, claw, hind limb, flight apparatus, or digital pad among unrelated birds occupying habitats at high elevations or with specific dominant vegetation types. Such examples of habitat-specific convergence are still few. However, where selective forces associated with feeding are strong enough to select for particular traits across species, selection also may be important enough to promulgate ecological speciation (Schluter 2001).

Although relatively restricted in distribution to a narrow linear band or small estuarine pockets along coastlines, tidal marshes present both abundant food resources and numerous adaptive challenges to the terrestrial vertebrates that attempt to colonize them. The physical flux of tidal cycles and the chemical influence of salt combine to create a wetland ecosystem where the benthic environment has marine characteristics, yet the vegetative structure resembles that of terrestrial marsh habitats (Chabreck 1988). Abundant food resources in tidal marshes are related to exceptionally high primary productivity (Adam 1990), and the sharp environmental gradient from terrestrial to semimarine habitats likely favors local adaptation within the successfully colonizing taxa. However, the ephemeral nature of tidal marshes over geologic time and their restricted geographic distribution may have caused frequent extinction of marsh populations, inhibiting their differentiation from upland kin (Chapman 1976; Malamud-Roam et al. 2005). Therefore, the development of adaptation will be shaped by the opposing influences of natural selection and stochastic effects associated with small and unstable populations.

These considerations lead to the empirical question: How much adaptive differentiation characterizes vertebrates that have colonized tidal marshes? Although morphological differentiation has been described for at least 24 species of tidal marsh vertebrates (Greenberg and Maldonado 2005), evidence for geographic variation across the upland–tidal marsh gradient is well developed only in North American sparrows (Emberizidae). Ten species or distinctive subspecies have been described as endemic to tidal marshes (Fig. 1; Table 1; Greenberg and Maldonado 2005). Because these taxa have repeatedly colonized marshes along different North American coastlines, we examine whether the shifts in trophic morphology (bills) associated with tidal marsh residence have been consistent across taxa and around the continent over evolutionary time.

Bill morphology is an evolutionarily mutable feature in birds that is sensitive to selection following changes in foraging substrate or diet (Grant and Grant 2002). Furthermore,

[2] Present address: San Francisco Estuary Institute, 7770 Pardee Lane, Oakland, California 94621-1424; E-mail: letitia@sfei.org.
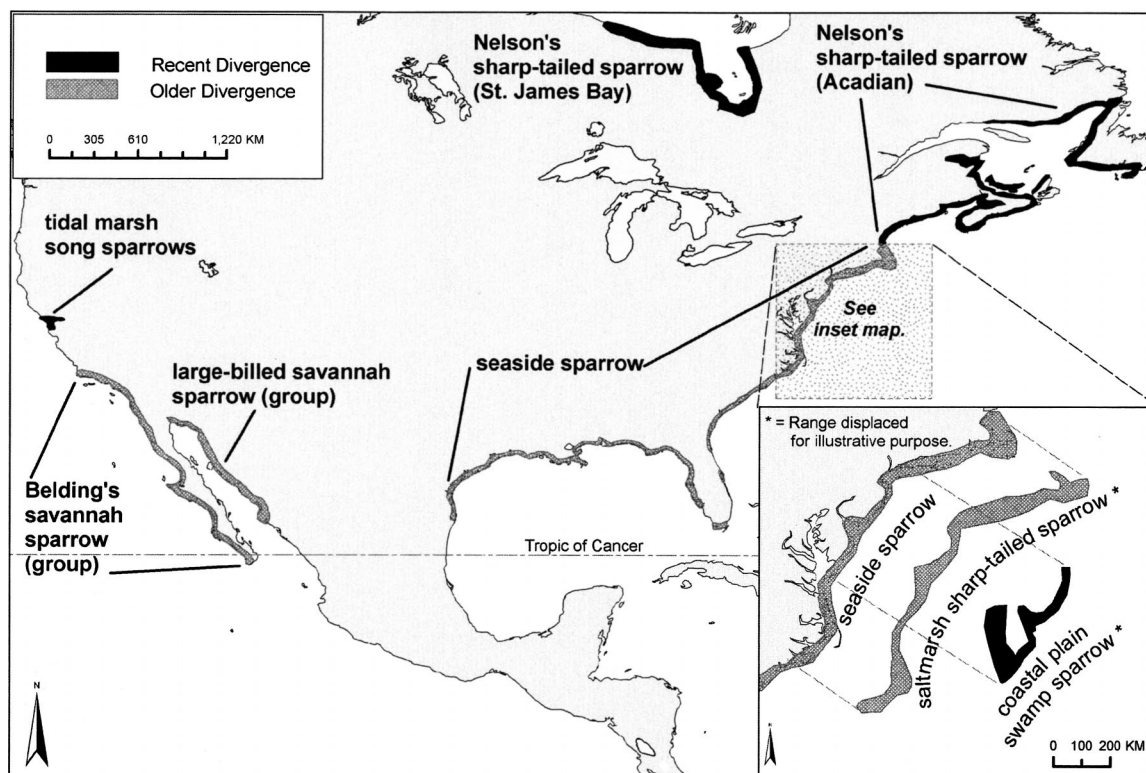
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FIG. 1. Breeding ranges and relative age of divergence of North American tidal marsh sparrow taxa. The Suisun, San Pablo, and Alameda song sparrows are endemic to Suisun, San Pablo, and South San Francisco Bays, respectively.

bird bills are arguably less constrained by other sources of selection than other morphological features, such as wings and legs (Benkman 1993; Peterson 1993). Greenberg and Droege (1990) noted that tidal marsh sparrows tend to have large bills in comparison to closely related non-tidal marsh taxa, and Murray (1969) hypothesized that larger bills in tidal marsh versus interior *Ammodramus* were due to dietary parallelism. In this study, we examine quantitatively the pattern of intra- and interspecific divergence in feeding-related bill morphology to test the hypothesis that populations colonizing tidal marshes have adapted repeatedly to the underlying environmental gradient. Furthermore, we use time-since-divergence estimates to examine the relationship between morphological divergence and duration of genetic isolation in tidal marsh taxa.

METHODS

We measured the 10 tidal marsh sparrow taxa and their closest putative non-tidal marsh relatives (Table 1). The analysis presented here was based on sampling the described and generally accepted subspecies of tidal marsh birds. The intent was to ensure sampling from areas within species ranges where geographic variation in bill size had been documented in the taxonomic literature, but our approach was not meant to imply that additional clinal variation does not exist. The determination of closest relatives was based primarily upon genetic studies (Table 1), with some modifications when data were unavailable, as follows. Because of the continuous distribution of marsh habitat from Suisun Bay to the California

Central Valley, we identified the Central Valley subspecies of song sparrow (*Melospiza melodia mailliardi*) to be the likely sister taxa to the Suisun song sparrow (*M. m. maxillaris*), although molecular data were not available for confirmation. The upland sister taxa of the salt marsh savannah sparrows (*Passerculus sandwichensis* spp.) have not been identified. Therefore, we chose sister taxa based on geography, as follows. We measured Belding's savannah sparrows from Southern California and northern Baja California (*P. s. beldingi*) and compared them to non-salt marsh populations from coastal California (*P. s. alaudinus*). The *P. s. beldingi* populations sampled were from the northern end of a morphological cline where bill sizes were the smallest relative to body size (Rising 2001), which may explain why this group was an outlier in our study relative to other tidal marsh sparrows with older divergence. We compared large-billed savannah sparrows (*P. s. rostratus*) from the Colorado River Delta and coastline to the southeast to specimens from the Great Basin (*P. s. nevadensis*).

We also measured 21 additional representative terrestrial species from the family Emberizidae to ascertain the relationship between bill morphology and body mass in sparrows in general. Phylogenetic independent contrasts (Felsenstein 1985) were not used because of the categorical nature of the habitat specialization variable. However, the additional taxa from the Emberizidae were chosen to minimize phylogenetic bias by including as many congeners and close relatives of the tidal marsh birds and their sister taxa as possible (e.g., *Ammodramus*, *Melospiza*, and *Passerella* spp.; Avise et al.

TABLE 1. Pairings of endemic tidal marsh sparrows and putative closest non-tidal marsh relatives. Divergence between pairs is classified as old (>500,000; old) or recent (<10,000 ybp; recent).

Tidal marsh taxon	Closest non-tidal marsh relative	Divergence	References
Passerculus sandwichensis beldingi (Belding's savannah sparrow)	*P. s. alaudinus* (Savannah sparrow)	old	Zink et al. 2005; see text
P. s. rostratus (Large-billed savannah sparrow)	*P. s. nevadensis* (Savannah sparrow)	old	Zink et al. 1991, 2005; see text
Ammodramus nelsoni subvirgatus (Acadian sharp-tailed sparrow)	*A. n. nelsoni* (Nelson's sharp-tailed sparrow)	recent	Rising and Avise 1994
A. n. alterus (St. James Bay sharp-tailed sparrow)	*A. n. nelsoni* (Nelson's sharp-tailed sparrow)	recent	Peters 1942; Rising and Avise 1994
A. caudacutus caudacutus (salt marsh sharp-tailed sparrow)	*A. leconteii* (LeConte's sparrow)	old	Zink and Avise 1990; Rising and Avise 1994
A. maritimus maritima (seaside sparrow)	*A. leconteii* (LeConte's sparrow)	old	Zink and Avise 1990
Melospiza melodia maxillaris (Suisun song sparrow)	*M. m. mailliardi* (Modesto song sparrow)	recent	see text
M. m. samuelis (San Pablo song sparrow)	*M. m. gouldii* (Marin song sparrow)	recent	Marshall 1948a; Chan and Arcese 2002
M. m. pusillula (Alameda song sparrow)	*M. m. heermanni* (Heermann's song sparrow)	recent	Marshall 1948a; Chan and Arcese 2002
M. georgiana nigrescens (coastal plain swamp sparrow)	*M. g. georgiana* (swamp sparrow)	recent	Greenberg et al. 1998

1980; Patten and Fugate 1998). The other additional sparrows were selected to represent the full diversity of bill and body sizes in the family (e.g., *Zonotrichia*, *Calcarius* spp.).

Bill morphology was analyzed using measurements from 10 male specimens from each taxon collected during the breeding season (National Museum of Natural History Collection, Washington, DC). By standardizing the time of year the specimens were collected, we minimized differences in bill length due to seasonal change; previous studies have found bill lengths to be relatively stable during the breeding season (Davis 1954; Johnson 1977; Morton and Morton 1987). We chose specimens that provided the widest geographic representation possible for each taxon, with the goal of representing the full diversity of morphology in each group. Bill depth, bill width, and culmen length were measured by R. Greenberg at or from the anterior edge of the nares using dial calipers. Bill depth and width were highly correlated ($r = 0.85$) and produced similar patterns, so we have presented only bill depth data. A mean body mass for each taxon was obtained from the literature (Marshall 1948a; Dunning 1992; Wheelwright and Rising 1993; Greenlaw and Rising 1994), the authors' unpublished data, or the Museum of Vertebrate Zoology, University of California, Berkeley, (MVZ) collections database. Body mass data for males were used for all tidal marsh taxa and their closest upland relatives, but only pooled mass data from both males and females were available for most of the other emberizids studied. To examine the pattern of covariation of body size with another morphological extremity less directly related to diet, we took measurements of tarsus length (after Pyle 1997). We restricted our measurements to five adult males collected during the breeding season (J. L. Grenier; MVZ) for each tidal marsh taxon and their non-tidal marsh pair. Although relatively short wings have been described for at least one tidal marsh taxon compared to conspecific non-tidal marsh populations (Rising 2001), we did not include wing length in this analysis.

Wing length should be investigated in future morphological studies of tidal marsh sparrows.

We examined how the degree of morphological divergence in bill length and body size of tidal marsh taxa varied with the estimated divergence time from closest non-tidal marsh sister taxa. With the exception of the San Francisco Bay song sparrows, estimated divergence time between tidal marsh taxa and closest non-tidal marsh relative was based on sequence divergence of mitochondrial DNA (mtDNA). Genetic structure (or lack thereof) of the song sparrows was inferred from F statistics of microsatellite loci (Chan and Arcese 2002). Divergence times were obtained using molecular clock estimates. Molecular clock studies calibrate rates of base pair substitutions with independent fossil or geological evidence. For songbirds, for example, the cytochrome *b* gene has been found to have a substitution rate of 1–3% per million years (Fleischer and McIntosh 2001), and we use 2%, a value used by many authors as a rough clock for estimating dates of cladogenesis (e.g., Avise and Walker 1998; Klicka and Zink 1999; García-Moreno 2004; Johnson and Cicero 2004; Lovette 2004). There were potential problems associated with applying a molecular clock beyond the taxa for which it was estimated, including rate heterogeneity across lineages, calibration error, and overestimation of divergence time due to ancestral polymorphism (Edwards and Beerli 2000; Arbogast et al. 2002; García-Moreno 2004). However, our classification of the timing of divergence in this analysis was sufficiently coarse to be robust to small sources of error. The tidal marsh taxa show a markedly bimodal distribution in estimated divergence times, with several taxa having no significant underlying genetic structure and the others having divergence times that range from 500,000 to 2 million years before present (ybp). We therefore classified divergence times as recent (<10,000 ybp) or older (>500,000 ybp) based on molecular data from six published phylogenies (Table 1). Furthermore, we assume that the mtDNA sequences are ef-
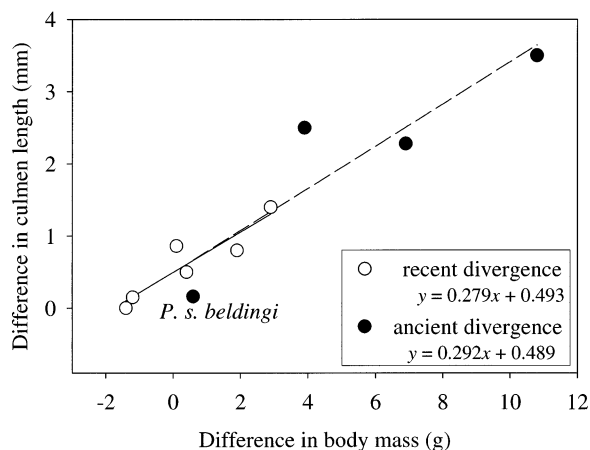
FIG. 2. Relationship between the difference in culmen length and the difference in body mass between sister taxa in different habitats. Differences were calculated as the mean for tidal marsh birds minus the mean for the upland relative. Lines are least-squares fit for paired taxa with older (dashed) and recent (solid) divergence times. Note that the *Passerculus sandwichensis beldingi* difference is much smaller than that of other older-diverged tidal marsh groups, possibly relating to a sampling artifact (see Methods).

fectively neutral with regard to natural selection, an assumption that was examined and found to be generally correct in the study of savannah sparrows by Zink et al. (2005). Certain substitutions in mildly deleterious haplotypes may be influenced by selection, but analyses thus far indicate that the effect of this selection, where it exists, on divergence estimates is probably minimal (Zink et al. 2005).

When conducting paired statistical tests, two upland taxa were used more than once as sister groups (Table 1). The differences calculated using the same sister taxa are nevertheless independent, because each tidal marsh taxon was free to evolve in either direction or not at all away from the ancestral form. Prior to using analysis of covariance to analyze morphological measurements with body mass or culmen length as a covariate, we tested the significance of the interaction term (heterogeneous slopes) and found it to be nonsignificant ($P > 0.05$). Mean values are reported ± 1 SE.

RESULTS

The 10 tidal marsh sparrow taxa examined had longer bills than their upland relatives (paired t-test, $t = 3.25$, df $= 9$, $P = 0.01$), averaging 9.5 ± 0.3 mm versus 8.5 ± 0.2 mm (Fig. 2), and their bills were also deeper (paired t-test, $t = 2.91$, df $= 9$, $P = 0.02$), 6.0 ± 0.2 mm versus 5.6 ± 0.3 mm. Body mass and tarsus length did not differ significantly (paired t-test, $P = 0.07$ and 0.27, respectively), but tidal marsh birds tended to be heavier than their sister taxa, averaging 19.7 ± 0.7 g versus 18.9 ± 0.9 g (Fig. 2).

Tidal marsh sparrows had longer bills (ANCOVA, $F_{1,15}$ intercept $= 5.8$, $P = 0.03$), even when controlling for the covariate of body mass (analyzed as the cube root of body mass to linearize the variable), which was also significant ($F_{1,15} = 25.1$, $P < 0.001$). If the subspecies *M. m. heermanni*, *M. m. mailliardi*, and *P. s. nevadensis* were omitted so that each upland species had only one taxon in the analysis, then the ANCOVA lost significance for habitat type ($P = 0.10$),

but the trend for tidal marsh birds to have longer bills remained. Although bills are deeper in tidal marsh, bill depth relative to length did not differ by habitat (ANCOVA, $F_{1,15}$ intercept $= 1.0$, $P = 0.34$) in this small dataset.

Because tidal marsh sparrows were generally larger than their relatives, a comparison of bill dimensions between birds of similar mass from different habitats was difficult. Therefore, to explore further the allometric relationship between bill dimensions and body mass, and to make a more direct comparison between similarly sized tidal marsh and upland taxa, we relaxed the requirement that non-tidal marsh species be sister taxa. We compared the bill dimensions of the 10 tidal marsh sparrows with 26 taxa from 24 species of emberizids and found a similar relationship: as body mass increased, bill length increased at a faster rate in tidal marsh birds than in non-tidal marsh birds (Fig. 3A). In this larger dataset, tidal marsh sparrows had relatively longer bills with respect to bill depth (Fig. 3B). The relationship of bill depth to the cube root of body mass was similar between tidal marsh and non-tidal marsh taxa (GLM; $F_{1,32}$ habitat $= 1.0$, $P = 0.33$; $F_{1,32}$ cube root of body mass $= 7.9$, $P = 0.008$; $F_{1,32}$ interaction $= 1.1$, $P = 0.30$).

The differences in bill length, body mass, and bill depth between tidal marsh sparrows and their closest relatives were significantly greater in pairs with older estimated divergence times than in those that diverged recently (Fig. 2; t-test; df $= 8$; $t = 1.5, 2.6, 2.6$: length, mass, depth, respectively; $P \leq 0.04$).

DISCUSSION

These analyses show a clear pattern of disproportionate increase in bill length relative to body mass and bill depth among sparrows that have invaded tidal marshes along the North American coast. Longer, thinner bills are associated with specific feeding adaptations in passerines. Bowman (1961) showed that in Galápagos finches, species with long, thin bills use them as forceps for probing for food. In the most extreme example, the warbler finch (*Certhidea olivacea*) has the most forcepslike bill and has a diet of 100% animal foods, as opposed to the other Galápagos finches, which all have a significant proportion of vegetable matter in the diet. Similarly, blackbirds (Icteridae) with longer, thinner bills have a greater proportion of animal foods in the diet than blackbirds with shorter, deeper bills (Beecher 1951). When seeds are not consumed, the force needed for cracking them, which is provided by short, deep bills (Bowman 1961), is no longer required, and bills can evolve toward a more efficient shape for capturing animal prey. This shape may be longer and thinner, because long, thin bills close relatively faster (Greenberg 1981) and provide the means to access invertebrates in crevices. Brandl et al. (1994) found that long, slender bills were correlated with a wider niche breadth in terms of taxonomic diversity of prey, and they attributed this relationship to probing in crevices to extract invertebrate taxa unavailable to birds with shorter bills.

The repeated biogeographic pattern described here is unusual, because it is likely to be based on trophic ecology rather than physiology (Dunbrack and Ramsay 1993; Laiolo and Rolando 2001; Yom-Tov et al. 2002). Several aspects of
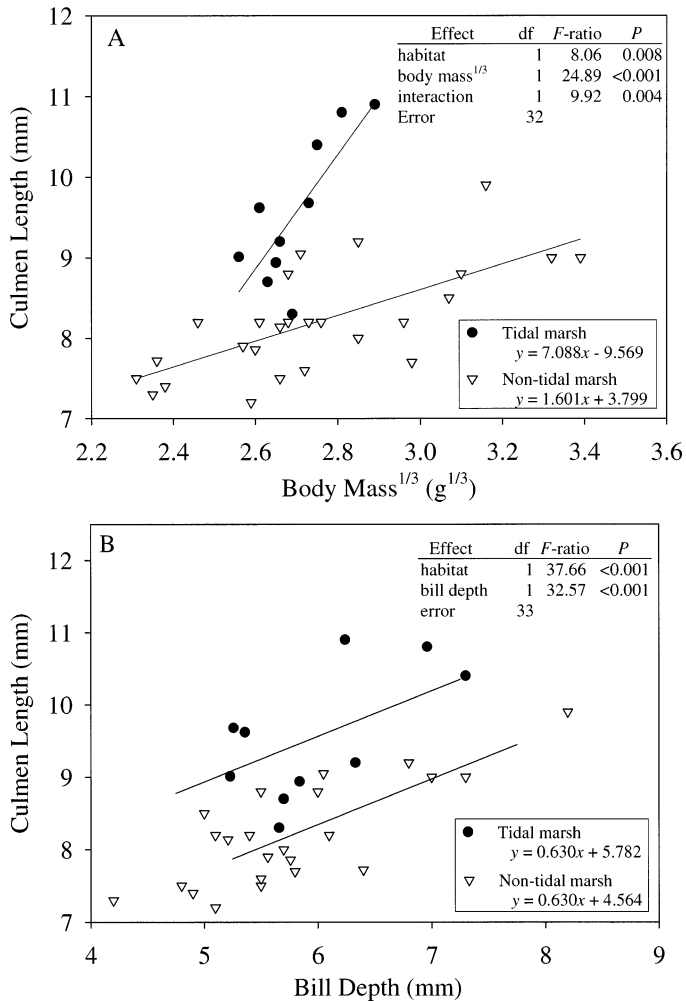
FIG. 3. Relationship between (A) culmen length and the cube root of body mass and (B) culmen length and bill depth for 36 taxa of Emberizidae. Tidal marsh birds have longer bills relative to body mass and bill depth. In order from least to greatest body mass, the tidal marsh taxa are *Ammodramus nelsoni alterus*, *A. n. subvirgatus*, *Melospiza georgiana nigrescens*, *M. melodia pusillula*, *M. m. samuelis*, *Passerculus sandwichensis beldingi*, *A. caudacutus caudacutus*, *M. m. maxillaris*, *P. s. rostratus*, and *A. maritimus maritima*; and the other taxa are *Spizella passerina*, *Emberiza pusilla*, *A. henslowii*, *A. leconteii*, *A. n. nelsoni*, *A. savannarum*, *M. lincolnii*, *A. bairdii*, *M. g. georgiana*, *P. s. alaudinus*, *Aimophila cassinii*, *A. ruficeps*, *Amphispiza belli*, *M. m. gouldii*, *S. arborea*, *Junco hyemalis*, *M. m. melodia*, *Calcarius mccownii*, *E. rustica*, *Zonotrichia albicollis*, *Pooecetes gramineus*, *Chondestes grammacus*, *Z. atricapilla*, *Passerella iliaca megarhyncha*, *P. i. iliaca*, and *Z. querula*.

the tidal marsh trophic environment suggest conditions that would favor selection for longer, thinner bills. Salt marshes have the lowest abundance and diversity of seeds in soil seed banks of wetland and grassland habitats in North America (Leck 1989). In contrast, benthic invertebrates are often present at high densities (Josselyn 1983; Adam 1990). The few studies of diets of tidal marsh sparrows indicate a consistently greater dependence on invertebrates than is found among their interior relatives (Wheelwright and Rising 1993; Greenlaw and Rising 1994; Post and Greenlaw 1994; Arcese et al. 2002; Grenier 2004). The dietary void created by decreased

consumption of seeds is filled by consumption of marine invertebrates, mainly crustaceans (amphipods and crabs) and mollusks (snails), widening the niche breadth compared to interior sparrows, which eat only terrestrial invertebrates and plant material. In addition, the longer, thinner bills of tidal marsh sparrows may allow greater access to invertebrates hiding in cracks and crevices in the sediment and vegetation (Post and Greenlaw 1994). As the sediment in the high marsh dries during neap tides, a network of cracks forms across its surface where crustaceans and other small invertebrates hide, probably to prevent desiccation and avoid predation (J. L. Grenier, pers. obs.).

Insight into the role of body mass with respect to these bill characters is provided by previous work on songbird allometry showing that body mass increases with bill depth. In African and North American finches, populations with greater predation pressure (i.e., ground dwelling and continental) have relatively larger body masses with respect to bill depth compared to populations with less predation pressure (i.e., arboreal and island; Schluter 1988; Benkman 1991). The similarity we found in the bill-depth-to-body-mass relationship between tidal marsh and other sparrows suggests that neither bill depth nor body mass is driving the observed differences in bill length in an allometric relationship. Therefore, we postulate that selection on bill length is driving the observed differences in bill morphology, and the trend for larger body size in tidal marsh sparrows is a consequence of the changes in bill depth. It is interesting to note that the tidal marsh birds with the largest bills have the smallest relative body size compared to upland sparrows, suggesting that the dense vegetation in tidal marshes may cause reduced predation pressure, and, therefore, less intense selection for large body size.

That the typical tidal marsh bill morphology is present even among the most recent colonists (*Melospiza*), which show little to no mitochondrial or microsatellite differentiation (Greenberg et al. 1998; Chan and Arcese 2002; R. Greenberg, unpubl. data), suggests that natural selection acts strongly on these characters. Alternatively, the differences might be a result of phenotypic plasticity in response to environmental conditions that differ between tidal marsh and interior habitats (James 1991). For example, James (1983) found that red-winged blackbirds (*Agelaius phoeniceus*) raised in more humid laboratory conditions had longer bills than those raised under drier conditions. The potential role of phenotypic plasticity as an alternative to adaptive change requires more experimental study. However, laboratory-reared coastal plain swamp sparrows fed a diet of baby cereal and lean ground beef (with supplements) and wild-reared birds fed a natural diet by their parents showed the same degree of bill-size differences from interior populations (Greenberg and Droege 1990).

Of particular interest is the pattern that the greatest divergence in morphology is found in taxa with the longest estimated divergence times. Assuming a genetic basis to this differentiation, this result suggests that bill size and shape continue to diverge over time. The colinearity of the least-squares fit lines for sister taxa with recent and older divergence times (Fig. 2) indicates that the same process of phenotypic diversification is occurring in both groups, regardless

of how long ago each pair bifurcated, suggesting that divergence to the tidal marsh phenotype is gradual. This finding contrasts with studies that have shown that bill size shows relatively high heritability and is subject to intense short-term selection, and, therefore, can evolve rapidly (Smith and Dhondt 1980; Boag and Grant 1981). Two possible explanations are: (1) specialization on occupying salt marshes and feeding on intertidal organisms may require additional adaptations to salinity, and these physiological responses may limit the rate of bill specialization; or (2) recent or current gene-flow (as indicated by lack of genetic structure) might slow the rate of adaptation in trophic characters.

The analysis of the relationship between morphological differentiation and divergence time depends strongly on the correct classification of taxa as ancient or recently derived. With no fossil evidence to elucidate the issue of tidal marsh sparrow divergence, we must explore more indirect evidence that might corroborate this classification scheme. Therefore, we note that the older taxa have a more southern distribution than the recent taxa (Fig. 1). Despite an overall latitudinal overlap in breeding distributions, the southern limit of the older taxa ranges from 23°N to 35°N, whereas that of the recent taxa is from 38°N to 51°N. Furthermore, the divergence times are bimodal, suggesting some taxa are the result of postglacial colonization whereas others have persisted through much or all or the Pleistocene. Tidal marshes in more northerly areas are probably quite recent, as some were under glacial ice and others occupy estuaries where conditions would not have favored tidal marsh formation during the glacial periods (Malamud-Roam et al. 2005). Conditions were probably adequate for tidal marsh formation along the Southern Atlantic, Gulf of Mexico, and Gulf of California coasts (Malamud-Roam et al. 2005). Therefore, we speculate that southern forms found refugia throughout the Pleistocene.

Our findings suggest that tidal marshes may be an appropriate ecotone in which to search for instances of ecological speciation (Smith et al. 1997), defined here as reproductive isolation as a result or byproduct of divergent selection. The physical, chemical, and trophic environments in tidal and non-tidal marshes are distinct, but the two habitats are often adjacent to one another as rivers grade into estuaries. Thus, individuals that colonize tidal marshes can exist in parapatry to conspecifics but across a sharp environmental gradient, as is the case for song sparrows in the San Francisco Bay area (Marshall 1948b) and the king and clapper rails (*Rallus elegans* and *R. longirostris*) of eastern North America. Both the sparrows and rails show distinct morphological differences despite little divergence in molecular markers (Chan and Arcese 2002; Chan et al. 2005), even though, in the case of the rails, the taxa are considered to be separate species. Furthermore, species richness is low in tidal marshes (Dunson and Travis 1994), which may allow colonists to take advantage of open niches and unexploited resources. For example, very few passerines are tidal marsh residents (R. Greenberg and J. Maldonado, unpubl. data). These conditions set the stage for the evolution of resource polymorphisms, which can then be maintained within a species or lead to speciation (Smith and Skulason 1996). For parapatric speciation to occur, assortative mating in correlation with the traits under selection is necessary (Rice and Hostert 1993). Assortative

mating by habitat is easy to imagine in the sparrows in question, because most species (song sparrows, savannah sparrows, and swamp sparrows) have territories that include space for both foraging and reproduction. For example, sparrows with bill morphologies appropriate for feeding in tidal marsh will set up territories in tidal marsh and, thus, will breed in tidal marsh. Previous authors have associated patterns of diversification with selection across ecological gradients (Smith et al. 1997; Schneider et al. 1999). Based on their findings, we predict that phenotypic differences across the tidal marsh–terrestrial transition, despite little to no detectable genetic differentiation, will be greater than differences between more genetically distant populations in the same terrestrial habitat.

More work on the ecology and evolution of tidal marsh sparrows is needed to understand in detail how their morphological differentiation relates to enhanced exploitation of food resources and to confirm that this parallel pattern has adaptive value. Studies of differentiation in genes under selection, gene flow, and assortative mating between adjacent upland and tidal marsh populations of *Melospiza* would help determine whether ecological speciation is occurring in this genus.

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