TROPHIC ADAPTATIONS IN SPARROWS AND OTHER VERTEBRATES OF TIDAL MARSHES

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Abstract. Tidal marshes present trophic challenges to terrestrial vertebrates in terms of both the abiotic (tidal flow and salinity) and biotic (vegetative structure and food resources) environments. Although primary productivity is high in tidal marshes, supporting an abundance of terrestrial and intertidal invertebrates, seeds, and fruit are far less abundant than in comparable interior habitats. In response to these food resources, terrestrial vertebrates in tidal marshes tend to be either herbivores or predators on invertebrates, including marine taxa. We examine the trophic adaptations of sparrows in the subfamily Emberizinae, the vertebrate group that shows the greatest amount of divergence associated with colonizing tidal marshes. Across several different evolutionary clades, tidal-marsh sparrows tend to be heavier and have significantly longer and narrower bills than their closest non-tidal-marsh relatives. The morphological divergence is greatest in taxa with longer associations with tidal marshes. We hypothesize that longer, narrower bills are an adaptation to greater year-round feeding on invertebrates, particularly benthic marine invertebrates, and a reduced dependence upon seeds. Tidal-marsh sparrows and a number of other terrestrial vertebrates share an additional indirect adaptation to foraging in tidal marshes. Most specialized taxa exhibit grayer and blacker dorsal coloration (particularly in brackish upper estuaries) than their closest non-tidal-marsh relatives. We propose that this consistent shift in dorsal coloration provides camouflage to terrestrial vertebrates foraging on exposed tidal sediments, which tend to be grayish to blackish in color due to the prevalence of iron sulfides, rather than the iron oxides common to more aerobic sediments in interior habitats.

Key Words: bill morphology, biogeographic rule, ecological speciation, tidal marsh, trophic adaptation.

ADAPTACIONES TROFICAS EN GORRIONES Y EN OTROS VERTEBRADOS DE MARISMAS DE MAREA

Resumen. Los marismas de marea presentan retos tróficos para vertebrados terrestres en términos ambientales, tanto abióticos (flujo de la marea y salinidad) y bióticos (estructura vegetativa y recursos alimenticios). A pesar de que la productividad primaria es alta en marismas de marea, soportar una abundancia de invertebrados terrestres e intermareales, semillas, y frutas son mucho menos abundantes que en habitats interiores comparables. En respuesta a estos recursos de alimento, vertebrados terrestres en marismas de marea tienden a ser ya sea herbívoros, o depredadores de invertebrados, incluida taxa marina. Examinamos las adaptaciones tróficas de gorriones en la subfamilia Emberizinae, el grupo vertebrado que muestra la mayor cantidad de divergencia asociada con la colonización de marismas de marea. A través de varias clades diferentes evolucionadas, los gorriones de marisma de marea tienden a ser mas fuertes y tienen significativamente picos mas largos y mas delgados, que sus parientes mas cercanos de marismas que no son de marea. La diferencia morfológica es mayor en taxa con asociaciones más amplias con marismas de marea. Hacemos una hipótesis de que picos más largos y más delgados son una adaptación a una alimentación de invertebrados durante todo el año, particularmente invertebrados bénticos marinos, y una dependencia reducida a semillas. Los gorriones de marisma de marea y un número más de otros vertebrados terrestres comparten una adaptación adicional indirecta al forrajeo de marismas de marea. La mayoría de la taxa especializada, exhibe una coloración dorsal más grisácea y negra (principalmente en estuarios salobres más altos) que sus parientes más cercanos que no son de marismas de marea. Proponemos que este consistente cambio en la coloración en el dorso, provee camuflaje a los vertebrados terrestres que forrajean en sedimentos expuestos por la marea, los cuales tienden a ser grisáceos a negros de color, debido a la prevalecencia de sulfuros de hierro, en lugar de óxidos de hierro, comunes en sedimentos mas aeróbicos en habitats del interior.

Tidal marshes present profound adaptive challenges to terrestrial vertebrates that attempt to colonize them. The physical influence of tidal cycles and the chemical influence of salinity combine to create a wetland ecosystem where the benthic environment has strong marine characteristics, yet the vegetative layers resemble freshwater marsh habitats (Chabreck 1988). The frequency of tidal inundation varies across marsh habitats by elevation, creating a gradient of floristically distinct zones (Eleuterius 1990, Faber 1996). At the lowest elevation, unvegetated tidal sloughs with periodically exposed mud offer another habitat absent from other wetlands.

Although tidal marshes can be quite productive, providing ample trophic opportunities to support dense vertebrate populations, these marshes are generally quite restricted in the

area they cover relative to interior habitats (Chapman 1977). Therefore, the population size of a terrestrial vertebrate inhabiting a tidal marsh is likely to be small compared to population size in upland habitats. Finally, most tidal marshes formed well after the receding of the ice during the last glaciation and, thus, were colonized by upland species over a relatively short span of time from an evolutionary perspective (Malamud-Roam et al., *this volume*). The influence of glaciation probably means that tidal-marsh taxa suffer from repeated episodes of local extinction or significant population bottlenecks.

The abundant food resources and sharp environmental gradient between marsh and upland favor local adaptation of tidal-marsh taxa, while the ephemeral nature of tidal-marsh habitats and their geographically restricted distribution inhibit differentiation. Thus, the empirical question remains: How much adaptive differentiation characterizes tidal-marsh vertebrates, and how do these adaptations develop?

PROPOSED TAXON CYCLE FOR TIDAL-MARSH VERTEBRATES

Trophic adaptation to tidal-marsh resources probably occurs in several stages, paralleling taxon cycles proposed for the evolution of biota in other systems (Ricklefs and Bermingham 2002). First, as estuaries form and tidal-marsh vegetation develops; animals that can withstand the physical challenges colonize the emerging marsh to take advantage of abundant food and few competitors. Second, the lack of competitors in tidal marshes allows for niche expansion and ensuing increased variation in trophic-related characters (e.g., diet, bill, legs, and feet). Third, if gene flow is reduced between tidal-marsh and non-tidal-marsh conspecifics, selection would drive adaptation to the novel tidal-marsh conditions. Initial diversification (from step 2) would provide the genetic variance for selection to act upon. Gene flow is likely to be reduced in situations where tidal-marsh populations are geographically isolated. Where populations are parapatric, assortative mating by habitat, which is easy to invoke for territorial passerines, may allow speciation to occur even in the face of relatively high levels of gene flow (Rice and Hostert 1993). In this case, diversifying selection for efficient exploitation of tidal marshes and upland foods may create resource polymorphisms in trophic-related characters (Skulason and Smith 1995). These polymorphisms could then evolve into genetically differentiated populations if assortative mating occurs (Smith et al. 1997). Where upland

and tidal-marsh populations were allopatric at the time of marsh colonization, directional selection may cause rapid divergence of the marsh populations. Possible examples of taxa that underwent speciation following differentiation resulting from adaptation to the marsh environment are the Clapper Rail (*Rallus longirostris*), Seaside Sparrow (*Ammodramus maritimus*), the Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*), the salt marsh harvest mouse (*Reithrodontomys raviventris*), and the salt marsh snake (*Nerodia clarkii*).

After a certain point, specialization for tidal marshes might hinder competitive ability in the habitat of origin, thus further reducing the possibility of gene flow and favoring the local adaptation to tidal-marsh conditions. Eventually, extreme specialization for saltmarshes might reduce competitive ability even in brackish marshes, allowing a second wave of invasions in brackish marshes by upland colonists.

THE COMPARATIVE APPROACH TO THE STUDY OF TIDAL-MARSH ADAPTATIONS

A time-honored approach to studying adaptation is examining patterns of phenotypic variation among unrelated taxa across a similar environmental gradient. The approach of relating geographic variation to causal explanations of adaptation in vertebrates has led to the development of a number of biogeographic rules that are both useful and controversial (Zink and Remsen 1986).

Differentiation of tidal-marsh taxa is prevalent in vertebrates along the Pacific and Atlantic coasts of North America, particularly among sparrows of the subfamily Emberizinae. Ten sparrow species or well-marked subspecies have been described as endemic to tidal marshes. Because emberizids have colonized tidal marshes at various times and along different coastlines, we focus mainly on the trophic adaptations of this particular group of vertebrates. However, we discuss other terrestrial-vertebrate taxa when comparisons are appropriate.

The mere correlation between geographic variation and occupancy of a particular habitat does not prove that tidal-marsh populations are responding adaptively to a selective gradient associated with that habitat. In order to use this comparative approach to develop an adaptive hypothesis for a particular character, we look for the following lines of evidence: (1) A similar pattern of phenotypic differentiation across unrelated taxa (convergence), (2) a testable explanation of how the convergence confers a fitness advantage, (3) a genetic basis for

the phenotypic differences, and (4) a correlation between the magnitude of divergence in a character and the extent of time a particular taxa has inhabited a particular ecosystem.

CONVERGENCE IN BILL DIFFERENTIATION IN TIDAL-MARSH PASSERINES

Bill morphology is an evolutionarily labile feature in birds that is sensitive to selection due to changes in foraging substrate or diet. Geographic variation in bill size and shape can be an adaptive response to differences in food resources between habitats (Bardwell et al. 2001). Bill shape relates to handling time and preferences for certain foods (Hrabar et al. 2002). Bowman (1961) used functional analysis and correlations to show that bill size and shape are intimately tied to the proportion and size of seeds and invertebrates in the diet. Boag and Grant (1981) quantified the selection intensity and corresponding change in bill depth when a drought caused a shift in the size of seeds available to the Galápagos Medium Ground-Finch (*Geospiza fortis*). While many of these studies focused on adaptations in bill depth for seed-eating, bill length has been related to speed of closure and, hence, the mobility of animal prey handled (Beecher 1962, Ashmole 1968, Greenberg 1981). Bill size and shape are also associated with the structures from which prey is captured (Bowman 1961). Thus, bill morphology is a likely trait to undergo adaptation to the trophic environment in tidal-marsh sparrows. Natural selection may also act upon leg and foot proportions, perhaps to improve foraging efficiency (Schluter and Smith 1986).

Murray (1969) found convergence in bill length of tidal-marsh *Ammodramus* taxa, and Greenberg and Droege (1990) showed that the pattern of longer and overall larger bills in tidal marshes compared to non-tidal-marsh relatives extends to other sparrow genera. The latter authors found that the overall volume of Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) bills in tidal marshes was significantly greater than the bill volume of the interior subspecies *M. g. georgiana* (Fig. 1). They provided a short review of the literature for Seaside Sparrows, sharp-tailed sparrows (*Ammodramus caudacutus* and *A. nelsoni*), Song Sparrows (*Melospiza melodia*), and Savannah Sparrows (*Passerculus sandwichensis*), pointing out that in each species the taxa found in tidal marshes have larger bills. Grenier and Greenberg (2005) extended this line of study by measuring museum specimens from 10 sparrow taxa endemic to tidal marshes, their closest upland relatives, and 20 other taxa in the family Emberizidae to determine the relationship between bill length, bill depth, and body mass in these groups. Tidal-marsh birds tended to be heavier and had significantly longer and deeper bills than their nearest kin outside of this habitat. Even when differences in body size between the two groups were factored out, tidal-marsh sparrows had longer bills (Fig. 2). Tidal-marsh sparrows had relatively longer bills with respect to bill depth as well. The authors also compared tarsus length between tidal-marsh birds and sister taxa, but found no significant differences.

These studies provide support for a new biogeographic rule (albeit one of limited taxonomic scope)—songbirds resident in tidal marshes have longer, narrower bills than interior relatives. The basis of this rule is a trophic adaptation, which stands in contrast to other established biogeographic rules (e.g., Allen's and Bergman's) with physiological premises.

HYPOTHESIZED FUNCTION OF DIFFERENTIATED BILLS

Based on our understanding of tidal-marsh food resources and the functional morphology of passerine bills, we hypothesize that the differentiation in bill size and shape is an adaptation for increased consumption of animal foods, particularly marine invertebrates, and
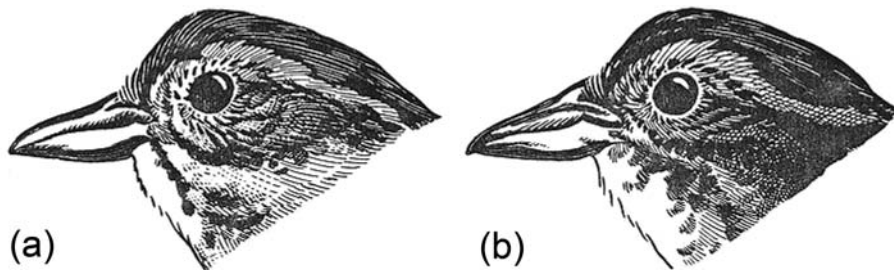

FIGURE 1. From Greenberg and Droege (1990). Line drawings of typical adult male *Melospiza georgiana georgiana* (a) and *M. g. nigrescens* (b). Note the longer bill and darker crown plumage of *nigrescens*.
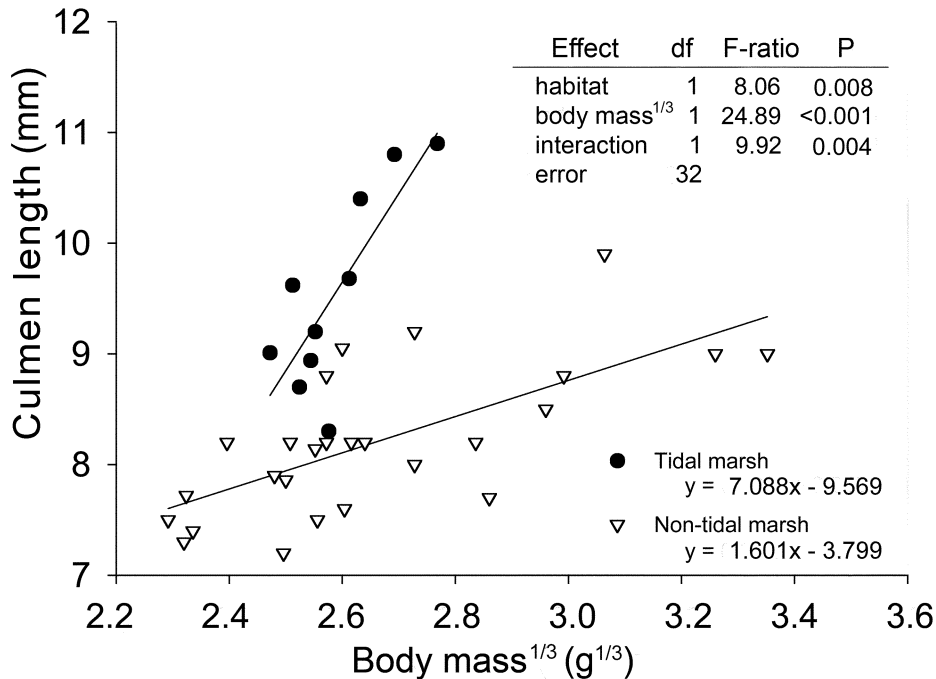
FIGURE 2. From Grenier and Greenberg (2005). Relationship between culmen length and body mass for 36 taxa in Emberizidae. Tidal-marsh birds have longer bills relative to body mass, and bill length increases more quickly with body mass in tidal-marsh taxa.

a concomitant decrease in eating seeds. Short, deep bills are used for cracking large, hard seeds, while bird species with purely animal diets have long, thin bills (Beecher 1951).

These bills designed for carnivory are often used as forceps to probe for and capture invertebrates in crevices under bark (Bowman 1961). Various researchers have proposed that tidal-marsh sparrows use their long bills to probe for invertebrates in the sediment (Post and Greenlaw 1994, Allison 1995). In marshes fringing northern San Francisco Bay, amphipods (*Traskorchestia traskiana*) likely form a large part of the diet for the San Pablo Song Sparrow (*Melospiza melodia samuelis*; Grenier 2004). S. Obrebski and G. H. Irwin (unpubl. data) found that these amphipods burrow into the substrate among the roots of the pickleweed (*Salicornia virginica*) or in cracks in the substrate during neap-tide periods, probably to avoid desiccation. Long bills may be valuable for extracting invertebrates such as amphipods from cracks that form when the high marsh has not been inundated for some time. A study of forest passerines (Brandl et al. 1994), concluded that species with longer, less-deep bills consumed a broader phylogenetic spectrum of prey taxa, because they were able to extract new prey types from under bark. Similarly, tidal-marsh

sparrows consume a broader diversity of prey than their upland kin by eating marine invertebrates, possibly by the same mechanism of being able to extract them from crevices.

As well as being useful for probing, long, thin bills may be an adaptation to handle more mobile prey. Functional mechanics analysis indicates that the tips of longer bills can be moved more quickly (Beecher 1962), and ecologists have surmised, therefore, that longer bills may close more rapidly on prey (Ashmole 1968), making them more efficient for capturing active prey (Greenberg 1981). Invertebrates are more active than seeds, so the modified bills of tidal-marsh sparrows may be adapted for efficiently capturing animal prey throughout the year.

TROPHIC OPPORTUNITIES AND CHALLENGES IN TIDAL MARSHES

Relatively few species of terrestrial vertebrates reside in tidal marshes, despite the rich food resources they offer (Chabreck 1988), suggesting that adaptation is required before tidal marshes can be exploited successfully. The greatest challenge for terrestrial vertebrates invading tidal marshes is probably the high salt content of the food and water in these areas (Sabat 2000). Inability to adapt to hyper-saline conditions may

exclude most songbird families from tidal-marsh residence. Salt tolerance, which mainly relates to adaptations for processing the food after it is eaten, is well documented for certain saltmarsh sparrows and the salt marsh harvest mouse (Goldstein, *this volume*; Fisler 1965).

Tidal marshes support an abundant invertebrate community that includes marine taxa, such as crustaceans, polychaetes, and mollusks, as well as terrestrial arthropods, mainly spiders and insects (Daiber 1982). In a study of the relationship between invertebrate abundance and avian foraging, Clarke et al. (1984) excluded birds from pools and the area around them in a Massachusetts saltmarshes in July and August, with little effect on the abundance of invertebrates in the exclosures. These data suggest that invertebrate resources are extremely abundant at certain times of year relative to the needs of avian predators, implying bottom-up rather than top-down control of food resources.

The low plant-species diversity and the high degree to which perennial plants rely upon vegetative propagation results in a limited diversity and abundance of seeds (Leck 1989) and no animal-dispersed fruits (Mitsch and Gosselink 2000) in tidal marshes. Based on studies on both North American coasts, Leck (1989) reported that few species were present in saltmarsh-soil seed banks (13–17 species) and seed abundance was low (700–900 seeds/m²) compared to freshwater marshes and grasslands (30–40 species, 1,000–3,000 seeds/m²). Furthermore, regular tidal scouring of the substrate limits seed accumulation (Adam 1990). However, saltmarsh plants are highly productive (Mitsch and Gosselink 2000), so food resources are abundant for herbivorous animals.

PATTERNS IN THE DIET OF TIDAL-MARSH SPARROWS

A comparison of diet by Greenlaw and Rising (1994) between the closely related Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*), which breeds in the interior of the continent as well as in tidal marshes, and the Saltmarsh Sharp-tailed Sparrow, which breeds exclusively in tidal marshes, exemplifies how the feeding niche differs in the tidal marsh habitat. Stomach contents from Nelson's Sharp-tailed Sparrows breeding in wet areas of New Brunswick and North Dakota, and migrating along the East Coast of the US showed that these birds eat mainly insects (78% of relative total volume, N = 15) and spiders (14%) from May–August, with seeds becoming very important post-breeding (73%, N = 11), and some mollusks consumed during fall migration in

coastal marshes (19%, N = 7). Nelson's Sharp-tailed Sparrow takes a wide variety of insects, suggesting little specialization on particular prey. The winter diet is not known. Contents of Saltmarsh Sharp-tailed Sparrow stomachs indicated a different trend in seasonal diet. Although insects were important, the proportion was lower in the breeding season (44%, N = 20) and stayed about the same in the fall (36%, N =12). However, plant matter, which was absent from the breeding diet, made up only 30% of fall foods. A major addition to the diet (amphipods, 24% in both seasons) replaced summer insects and fall seeds for these tidal-marsh sparrows (Greenlaw and Rising 1994).

The Seaside Sparrow, an obligate tidal-marsh species, consumes a diet similar to that of its close relative, the Saltmarsh Sharp-tailed Sparrow (Post and Greenlaw 1982). Also a generalist, the Seaside Sparrow eats insects, spiders, amphipods, mollusks, crabs, and marine worms during the breeding season and adds seeds as a major food source during winter (Martin et al. 1961). Martin et al. (1961) took a small sample (N = 6) of stomachs from New Jersey late in the breeding season and found a heavy reliance on marine invertebrates—36% crab and 24% snails by volume.

Fewer data on Swamp Sparrow diet have been published than for the other tidal-marsh songbirds. Like the upland Sharp-tailed Sparrows, inland Swamp Sparrows (*Melospiza georgiana georgiana* and *M. g. ericrypta*) consume mainly insects during breeding and seeds during fall and winter (Mowbray 1997). However, the proportion of animal matter in the inland Swamp Sparrow diet is relatively higher year-round (Mowbray 1997). The diet of the tidal-marsh subspecies has not been studied, but Greenberg and Droege (1990) suggest that these populations may consume marine invertebrates as a major food source.

The detailed summary of Savannah Sparrow diets by Wheelwright and Rising (1993) shows that this species follows the same pattern. The subspecies outside of tidal marshes consume insects, spiders, mollusks, seeds, and fruit, with insects predominating during breeding and seeds and fruit more important during the off-season. A survey of 1,098 stomachs of breeding Savannah Sparrows from 31 localities across North America showed that crustaceans, which were present in 2% of the stomachs from upland locales, were found in 30% of the tidal marsh stomachs (predominantly fiddler crabs [*Uca*]). Mollusks were also more frequent in the stomachs of saltmarsh birds, and insects were less common than in the upland samples (Wheelwright and Rising 1993).

The breeding season diet of non-tidal-marsh Song Sparrows is dominated by a wide variety of insects with the addition of a few other invertebrates and seeds, and seeds become the main food source in fall and winter (Arcese et al. 2002). Aldrich (1984) found that tidal-marsh Song Sparrows eat more animal matter than upland conspecifics, and this result was confirmed by a stable-isotope study that showed that San Pablo Song Sparrows from a tidal marsh in northern San Francisco Bay assimilated little, if any, plant matter during the breeding season (Grenier 2004). Behavioral data from the same study indicated that San Pablo Song Sparrows fed heavily in areas where the abundant invertebrate biomass was marine snails and amphipods, and sparrows frequently carried amphipods to nestlings. Comparing the stomach contents of 233 Song Sparrows from a variety of habitats around San Francisco Bay, Marshall (1948a) found that the fall diet of saltmarsh birds continued to be mainly animals with the addition of some *Grindelia* seeds and *Spartina* flowers, while brackish marsh and terrestrial populations consume mainly seeds supplemented by insects.

In summary, tidal-marsh sparrows and their close relatives are generalists that consume both animal matter and seeds. However, tidal-marsh birds tend to eat a greater proportion of invertebrates and a correspondingly lesser proportion of seeds than their inland relatives. This difference may be most pronounced in autumn and winter. Tidal-marsh sparrows also consume more marine invertebrates and fewer insects and spiders than upland sparrows.

TROPHIC PATTERNS IN OTHER TIDAL-MARSH VERTEBRATES

Beyond sparrows, few studies have focused on trophic specialization in tidal-marsh vertebrates. As discussed in detail for sparrows, the available data suggest that other birds in tidal marshes reduce consumption of seeds in favor of increased use of invertebrates, including intertidal taxa. Clapper Rails, which dwell in saltmarshes, and King Rails (*Rallus elegans*), which prefer brackish to freshwater marshes, both feed predominantly on animal matter, particularly crustaceans. However, King Rails (as well as freshwater populations of the Yuma Clapper Rail [*R. l. yumanensis*]) eat much larger quantities of insects and seeds than do Clapper Rails, particularly in the autumn and winter (Meanley 1992). Meanwhile, saltmarsh Clapper Rails eat primarily crabs and snails (Eddleman and Conway 1998). A study of the fall diet of Soras (*Porzana carolina*) in Connecticut showed

that in freshwater marshes, birds consumed large quantities of seeds, whereas birds in salt-marshes fed almost entirely on invertebrates (Webster 1964). Similarly, the stomach contents of diamondback terrapins (*Malaclemys terrapin*), the only turtle specialized on saltmarshes, consist almost exclusively of marine mollusks (Ernst and Barbour 1989).

Given that tidal marshes show strong similarity in vegetation to inland marshes and other habitats, we would expect species that are restricted to the vegetation layer to show less pronounced diet shifts than those that use the marine substrate. Few data are available to test this prediction, but a small amount of information seems to support the idea. Marsh Wrens (*Cistothorus palustris*) provide a good example of a species that forages almost entirely from reed, grass, and shrub layers of the tidal marsh. The detailed study of diet by Kale (1965) for the subspecies in *Spartina* marshes in Georgia shows that Marsh Wrens consume primarily insects and spiders, but a small portion of stomach samples contained invertebrates, such as crabs and amphipods, as well as snails associated with the marine substrate. A comparison with studies of interior populations (Beal 1907, Welter 1935) in New York state and California suggest interesting differences between tidal- and freshwater -marsh populations that should be explored. Kale (1965) found that ants and spiders were larger components of the breeding season diet of the Marsh Wrens in salt-marshes than freshwater marshes, where the diet was dominated by Orthoptera, Odonata, and Lepidoptera.

Specialized forms of tidal-marsh mammals are restricted to a few rodents. Rodent granivores give way to herbivores in tidal marshes. Common tidal-marsh rodents include muskrats (*Ondatra zibethicus*), California voles (*Microtus californicus*), and meadow voles (*M. pennsylvanicus*) which are predominantly herbivorous (Thaeler 1961, Willner et al. 1980, Batzli 1986). Consistent with the dominance of herbivory in saltmarsh mammals, the salt marsh harvest mouse, which is endemic to tidal marshes, consumes considerably more plant material than does its closest relative, the western harvest mouse (*Reithrodontomys megalotis*) in uplands (Fisler 1965). Fisler (1965) demonstrated that the salt marsh harvest mouse has a substantially longer digestive tract than the upland species, which is likely an adaptation for digesting a greater proportion of plant material in the diet. Absent among rodents commonly found in tidal marshes are granivorous and frugivorous species (Greenberg and Maldonado, *this volume*).

Carnivory is also prevalent in small mammals in tidal marshes. Shrews, a common component of tidal-marsh faunas, are specialists on invertebrates, and indirect evidence suggests that at least one specialized tidal-marsh subspecies of the ornate shrew (*Sorex ornatus sinuosus*; Hays and Lidicker 2000) feeds on amphipods. The restriction in diet guilds to herbivores and carnivores may result from filtering of colonizing species (e.g., shrews are more likely to colonize marshes because they are carnivores), or it may result from niche shifts. Marsh rice rats (*Oryzomys palustris*), common in tidal marshes of the southeastern US (Daiber 1982, Wolf 1982) are known to depend heavily on invertebrates, particularly from the benthic substrate (Sharp 1967). Comparison of stomach contents between rats in tidal marsh and the immediately adjacent uplands (Kruchek 2004) showed that tidal-marsh rice rats consume far more invertebrates and less plant material than those in the adjacent old fields. Even in the grass-specialized herbivore, the California vole, stable-isotope analysis of the spring pelage of an individual captured in saltmarsh revealed a diet based completely on animal foods (Grenier 2004).

DORSAL COLOR SPECIALIZATION FOR FORAGING IN TIDAL MARSHES

Another less apparent feeding-related adaptation to a new habitat is cryptic coloration to reduce predation risk while foraging. Tidal-marsh sparrows and their close relatives in the upland forage mainly along the sediment and in low foliage, obtaining food from near to or on the ground (Wheelwright and Rising 1993, Greenlaw and Rising 1994, Post and Greenlaw 1994, Mowbray 1997, Arcese et al. 2002). Often they are observed foraging on the exposed surface of tidal channels and sloughs. Thus, dorsal coloration that matches the background color of the sediment may be important for reducing the risk of predation. For tidal-marsh sparrows, the periodic exposure by the tide of unvegetated sediment provides both a novel foraging substrate and a new predation risk, so selection for cryptic dorsal plumage is plausible.

Grinnell (1913) noted that tidal-marsh vertebrates tend to be darker than their upland relatives, and Greenberg and Droege (1990) reviewed this phenomenon, noting that the trend is sometimes more toward grayer hues rather than darker coloration. Saltmarsh melanism is clearly expressed within the tidal-marsh sparrows. Seaside Sparrows can be distinguished from other sparrow species in the field by their dark olive-gray dorsal coloration (Sibley 2000), and the recently extirpated Dusky

Seaside Sparrow (*Ammodramus maritimus nigrescens*) exhibited distinctly melanistic plumage. Saltmarsh Sharp-tailed Sparrows are more heavily streaked with fewer white markings dorsally than Nelson's Sharp-tailed Sparrows, and *Ammodramus nelsoni subvirgatus* in tidal marshes of the Canadian maritime provinces are grayer than conspecifics from interior prairies (Ridgway and Friedmann 1901, Greenlaw and Rising 1994). The streaking of Belding's Savannah Sparrow is heavier and darker than typical Savannah Sparrows, but the large-billed subspecies are distinctly pale, although grayish in tone (Ridgway and Friedmann 1901, Wheelwright and Rising 1993). A quantitative study of variation in Song Sparrow dorsal plumage (Marshall 1948b), found upland *Melospiza melodia gouldii* to be reddish-brown, while tidal-marsh subspecies *maxillaris*, *samuelis* and *pusillula* were blackish-brown, blackish-olive, and yellowish-gray, respectively. Swamp Sparrows in tidal marshes also lose their colorful rusty tones dorsally, and rusty crown and nape plumage is replaced with black feathers (Greenberg and Droege 1990).

Saltmarsh melanism, or the tendency to be grayer or blacker, has been reported for several other birds as well (Table 1). The weaker plumage differentiation in Marsh Wrens is not surprising given that foraging in this species is more associated with water edge and vegetation rather than open sediment (Kroodsma and Verner 1997). In addition to these avian examples, saltmarsh melanism has been observed in various small mammals, namely cinereus shrew (*Sorex cinereus*), ornate shrew (*S. ornatus*), vagrant shrew (*S. vagrans*), California vole, meadow vole, and western harvest mouse (Grinnell 1913, Jackson 1928, Green 1932, Von Bloeker 1932, Rudd 1955, Hall and Kelson 1959, Thaeler 1961, Fisler 1965, Woods et al. 1982), and in one tidal-marsh snake (*Nerodia sipedon williamengelsi*; Conant et al. 1998)

It was long ago hypothesized (Grinnell 1913, Von Bloeker 1932) that the blackest forms of tidal-marsh species were found in brackish upper estuaries (such as Suisun Bay in the San Francisco estuary). This hypothesis is borne out by the following melanistic vertebrate taxa: Coastal Plain Swamp Sparrow, Suisun Song Sparrow (*Melospiza melodia maxillaris*), Dusky Seaside Sparrow, Suisun shrew (*Sorex ornatus sinuosis*), and tidal-marsh populations of the California vole.

The blacker and grayer dorsal coloration of tidal-marsh vertebrates may be an adaptation for blending in against the sediment background to reduce the risk of predation while foraging in the open. Relative to reddish sediment in

TABLE 1. COMPARISON OF PLUMAGE COLORATION OF TIDAL-MARSH-BIRD TAXA WITH THEIR CLOSEST NON-TIDAL-MARSH RELATIVES.

Tidal-marsh taxon	Taxon for comparison	Coloration in tidal marsh
Clapper Rail (East Coast; *Rallus longirostris crepitans* group)	King Rail (*Rallus elegans*)	Grayer.
Clapper Rail (West Coast; *R. l. obsoletus* group)	King Rail	Somewhat grayer.
Marsh Wren (*Cistothorus palustris griseus*) and other tidal-marsh populations	Marsh Wren, non-tidal marsh populations	Only *griseus* (southern Atlantic coast) is distinctly grayer.
Suisun Song Sparrow (*Melospiza melodia maxillaries*)	Modesto Song Sparrow (*M. m. mailliardi*)	Grayer with blacker markings.
Alameda Song Sparrow (*M. m. pusillula*)	Heermann's Song Sparrow (*M. m. heermanni*)	Grayer.
San Pablo Song Sparrow (*M. m. samuelis*)	Marin Song Sparrow (*M. m gouldii*)	Grayer.
Coastal Plain Swamp Sparrow (*M. georgiana nigrescens*)	Southern Swamp Sparrow (*M. g. georgiana*)	Grayer with blacker markings.
Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi* group)	Savannah Sparrow (*P. sandwichensis*): interior subspecies	Grayer with blacker markings.
Large-billed Savannah Sparrow (*P. s. rostratus* group)	Savannah Sparrow (*P. sandwichensis*): interior subspecies	Grayer.
Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*)	Nelson's Sharp-tailed Sparrow (*A. nelsoni*)	Grayer.
Acadian and James Bay Sharp-tailed sparrows (*A. n. subvirgatus* and *A. n. alterus*)	Nelson's Sharp-tailed Sparrow (*A. n. nelsoni*)	Grayer wings, less contrasting back.

terrestrial habitats, tidal marsh mud is grayer. This phenomenon occurs because sea water is rich in sulfates, and, in the anoxic conditions of tidal sediment, iron is reduced anaerobically to grayish iron sulfides rather than to the reddish iron oxides of aerobic soils (Mitsch and Gosselink 2000). The blacker coloration of birds and mammals in brackish marshes may be a result of background matching to blacker sediments. Upper estuary mud may have a greater quantity of dark organic materials relative to saltmarsh sediments, due to the closer proximity of riverine inputs (Odum 1988).

The Alameda Song Sparrow (*Melospiza melodia pusillula*) and the large-billed Savannah Sparrow group (*Passerculus sandwichensis rostratus* and related subspecies) are partial exceptions to the general trend of tidal-marsh melanism. Although both are relatively pale, they have grayish dorsal coloration, which is consistent with other tidal-marsh forms. Both sparrows inhabit the most saline and arid marshes of their respective regions. This correlation suggests background matching to a paler color for camouflage in drier, saltier marshes.

ENVIRONMENTAL AND GENETIC CONTRIBUTIONS TO TIDAL-MARSH ADAPTATIONS

Both environment and genes likely play a role in determining bill morphology. James (1983) found a surprisingly large environmental influence on bill shape in Red-winged Blackbirds (*Agelaius phoeniceus*) by cross fostering nestlings between geographic areas with morphologically distinct populations. Other studies show that bill size and shape are largely heritable (Boag and Grant 1981, Forstmeier et al. 2001). Given that Smith and Zach (1979) found Song Sparrow bill traits to be significantly heritable, we proceed with the assumption that the bill morphology of tidal-marsh sparrows is determined mainly by genetics. While heritability of bill morphology would make this trait potentially sensitive to selection, low heritability does not rule out the possibility that differentiation at the subspecies and species levels is genetically based (Merilä and Sheldon 2001).

The heritability of plumage coloration is not a simple question, because different feather colors are controlled by different mechanisms. A gene was recently identified that likely controls melanin deposition in Bananaquits (*Coereba flava*; Theron et al. 2001), and this gene or a number of other loci identified in poultry may contribute to increased melanin expression in tidal-marsh songbirds. Greenberg and Droege (1990) raised 11 Coastal Plain Swamp Sparrow nestlings taken from the wild at 4–6 d old in the lab under standardized conditions. When measured after the postjuvenal molt, these birds were similar in both dorsal color and bill size to adult Coastal Plain Swamp Sparrows and distinct from inland Swamp Sparrows. Although more experiments are required, this result suggests that bill

morphology and plumage color have large heritable components in tidal-marsh sparrows.

EVIDENCE FOR A TAXON CYCLE IN TIDAL-MARSH SPARROWS

Generally only one or two sparrow species can be found breeding in the same tidal marsh. The exception occurs along the mid-Atlantic seaboard, primarily Chesapeake and Delaware bays. In these estuaries, three species cohabit tidal marshes—two saltmarsh specialists, Seaside Sparrow and Saltmarsh Sharp-tailed Sparrow, joined by the Coastal Plain Swamp Sparrow. Genetic data suggest a very recent colonization of the brackish upper estuary by Swamp Sparrows (Greenberg et al. 1998) in contrast to a much longer association with tidal marshes in the other species indicated by a deep divergence from upland relatives (Zink and Avise 1990). We suggest that coastal marshes existed along the gently sloping continental shelf of the eastern seaboard throughout the Pleistocene, allowing the more specialized *Ammodramus* sparrows to persist in saltmarshes (Malamud-Roam et al., *this volume*). The more recent development of estuarine marshes (Malamud-Roam et al., *this volume*) may have allowed Swamp Sparrows from small inland populations, which were expanding as the most recent continental glaciers receded (Greenberg et al. 1998), to colonize these brackish areas that were less suited to the adaptations of Seaside and sharp-tailed sparrows.

Support for this idea that adaptive specialization for the tidal-marsh environment accrues over evolutionary time is provided by the correlation between morphological divergence and genetic divergence in tidal-marsh sparrows (Fig 3; Grenier and Greenberg 2005). The four tidal-marsh sparrows with ancient divergence times from their upland counterparts (>200,000 yr BP) exhibited significantly more extreme bill elongation than recently diverged groups (<10,000 yr BP). We suspect that divergence will increase in the younger taxa as enough time passes for beneficial mutations to accumulate and be selected. The type of tidal-marsh habitat each taxon inhabits is not a confounding factor in this analysis; saltmarsh specialists are found in both the ancient (Seaside Sparrow, Savannah Sparrow, Saltmarsh Sharp-tailed Sparrow) and recent (San Pablo Song Sparrow and Alameda Song Sparrow [*Melospiza melodia pusillula*]) divergence groups. Brackish-marsh specialists are found only in the recent divergence group, either in sympatry with other tidal-marsh sparrows (Coastal Plain Swamp Sparrow), which fits with the proposed taxon cycle, or in relatively young marshes only a
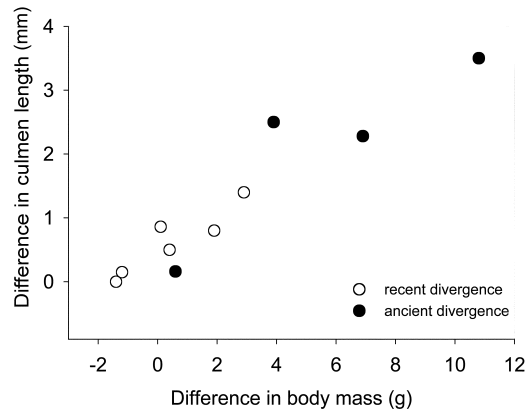

FIGURE 3. From Grenier and Greenberg (2005). Relationship between the difference in culmen length and the difference in body mass between sister taxa in different habitats. Differences are the mean for tidal-marsh birds minus the mean for the upland relative. Divergence is classified as either recent (<10,000 ybp) or ancient (>200,000 ybp).

few thousand years old (Suisun Song Sparrow; Atwater et al. 1979).

FUTURE RESEARCH

Although the patterns that we have discussed are compelling, rigorous field studies are required to empirically test if they reflect adaptation to tidal marshes. In variable environments like tidal marshes, natural selection acts in concentrated bursts to carve the evolutionary paths of populations (Benkman 1993), and for trophic adaptations the episodes of selective change are probably related to resource scarcity (Boag and Grant 1981, Schluter and Smith 1986). Therefore, studies are needed that track the distribution of feeding-related traits in a tidal-marsh population concurrent with the survival and reproductive success of individuals and the abundance of resources. Tidal-marsh passerines may be tractable systems for attempting this type of real-time measurement of natural selection, because populations are often dense enough to provide large sample sizes. More knowledge of the trophic ecology of tidal-marsh songbirds, particularly when and how they experience resource scarcity, would be a first step. Also, a better understanding of saltmarsh food resources, particularly invertebrate and seed distribution and abundance, is needed. Finally, cross-fostering experiments between upland and tidal-marsh subspecies would shed light on the importance of environment in creating the patterns we have reviewed.

REGIONAL STUDIES

Clapper Rail (*Rallus longirostris*) with fiddler crab (*Uca pugnax*)
Drawing by Julie Zickefoose