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TIDAL MARSHES: HOME FOR THE FEW AND THE HIGHLY SELECTED

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WHY STUDY TIDAL MARSHES?

Tidal marshes consist of grass or small shrub-dominated wetlands that experience regular tidal inundation. In subtropical and tropical regions, marshes give way to mangrove swamps dominated by a small number of salt-tolerant tree species. Tidal marshes can be fresh, brackish, saline, or hyper-saline with respect to salt concentrations in sea water. In this volume we focus on marshes (not mangroves [*Rhizophora, Avicennia,* and *Laguncularia*]) that are brackish to saline (5–35 ppt salt concentration). Tidal saltmarshes are widely distributed along most continental coastlines (Chapman 1977). Although found along thousands of kilometers of shorelines, the aerial extent of tidal marsh is quite small. We estimate that, excluding arctic marshes and tropical salt flats, tidal marshes cover ≈45,000 km^2 which, to put this in perspective, would cover a land area merely twice the size of the state of New Jersey. To place this figure further in an ecological context, the total area of another threatened ecosystem, tropical rain forest, is approximately 14,000,000 km^2 or >300 times greater than the amount of tidal marsh even after deforestation). Although the area covered by tidal marsh is small, this ecosystem forms a true ecotone between the ocean and land, and therefore plays a key role in both marine and terrestrial ecological processes. In the parlance of modern conservation biology, the tidal-marsh ecosystem provides numerous critical ecological services, including protecting shorelines from erosion, providing nursery areas for fish, crabs and other marine organisms, and improving water quality for estuaries.

Tidal saltmarshes are primarily associated with the large estuaries of mid-latitudes, in North America, Eurasia, and southern South America, with some in Australia and South Africa. Tidal marshes are highly productive yet, in some ways, inhospitable to birds and other vertebrates. Surrounded by a highly diverse source fauna from the interior of the continental land mass, relatively few species cross the threshold of the maximum high-tide line and colonize intertidal wetlands. In this volume, we discuss myriad approaches to understanding which species have colonized the landward side, how they have evolved to meet the adaptive challenges of tidal marsh ecosystems, and in what ways we can act to conserve these small but unique tidal marsh faunas.

Studies of tidal-marsh faunas have significance far beyond understanding the vagaries of this particular habitat. Tidal marshes, with their abrupt selective gradients and relatively simple biotic assemblages, provide a living laboratory for the study of evolutionary processes. The following are just a few of the major conceptually defined fields within biology that have focused on tidal marshes as a model system: (1) evolutionary biologists seeking to investigate systems where morphological changes may have evolved in the face of recent colonization and current gene flow between saltmarsh and inland populations, (2) ecologists interested in how life history and behavior may shift in the face of a local, but strongly divergent environment, (3) physiological ecologists, wishing to see how different organisms cope with the abiotic factors governing successful colonization of saltmarshes, (4) biogeographers interested in patterns of diversity in endemism in this habitat along different coasts and in different continents, and (5) conservation biologists, because of the disproportionately high frequency of endangered and threatened taxa that are endemic to tidal marshes.

Many of us have spent years in tidal marshes in pursuit of our particular study species. We came together for this project because we began to think beyond our particular study species and study marsh, slough, or estuary. It became apparent to us that tidal marsh vertebrates face a number of severe environmental threats that might best be understood by gaining a more global and less local estuary-centric perspective. Furthermore, although tidal marshes provide a laboratory for studying local ecological differentiation, the mechanisms and ultimate factors shaping this local divergence can best be understood by studying common adaptive challenges and their solutions in a more comparative manner. As we contacted vertebrate zoologists working around the globe, it became apparent that few tidal-marsh researchers think beyond their particular coastline. We believed that if we could provide the catalyst for a more holistic and global thinking about tidal marsh vertebrates, that would be an important step forward.

In October 2002, we held a symposium at Patuxent National Wildlife Research Center to bring researchers together from different coasts and marshes. But we took one step further. Both during the organization of the symposium and the subsequent preparation of this volume, we made a concerted effort to go beyond our ornithological roots and to pull together research from other vertebrate groups, as well as more process-oriented tidal-marsh ecologists. Including other classes of terrestrial vertebrates has opened our collective eyes and we appreciate the cooperation of the editors of *Studies in Avian Biology* to allow so much non-avian material in our publication.

Tidal marshes are among the most productive ecosystems in the world, with high levels of primary production created by vascular plants, phytoplankton, and algal mats on the substrate (Adam 1990, Mitsch and Gosselink 2000). Abundant plant and animal food resources are available through both the terrestrial vegetation and the marine food chains associated with tidal channels. It is small wonder that saltmarshes often support high abundances of the species that live there.

On the other hand, the fauna and flora associated with salt and brackish marshes are depauperate. Our attention is drawn to tidal-marsh systems not primarily for the diversity of birds and other terrestrial vertebrates, but for the high proportion of endemic taxa (subspecies or species with endemic subspecies). In the course of preparing this volume, we have identified 25 species of mammals, reptiles, and breeding birds that are either wholly restricted or have recognized subspecies that are restricted to tidal marshes (Table 1).

Tidal marshes present enormous adaptive challenges to animals attempting to colonize them. The vegetation is often quite distinct from adjacent upland or freshwater marsh habitats. Perhaps more severe are the challenges from the physical environment (Dunson and Travis 1994). In particular, animals must cope with the salinity of the water, the retained salinity in the food supply, the regular ebb and flow of tides, and the less predictable storm surges. Less obvious differences include basic geochemical processes, which, among other things can alter the dominant coloration of the substrate. How these challenges shape individual physiological, morphological and behavioral adaptations has often been the focus of excellent research, but efforts to integrate the effect of these environmental factors are far fewer.

The availability of tidal-marsh habitat as a setting for evolution and adaptation by colonizing terrestrial vertebrate species has varied greatly throughout the Pleistocene (Malamud-Roam et al., *this volume*). Perhaps because of this, the current fauna is a mosaic of species with old and very recent associations with this habitat (Chan et al., *this volume*). In North America, the fauna consists of repeated invasions from species in a few select genera of which sparrows (*Ammodramus* and *Melospiza*), shrews (*Sorex*), voles (*Microtus*), and water snakes (*Nerodia*) are the most frequently involved. On the other hand, tidal marshes are inhabited by a few ancient taxa, such as the diamondback terrapin (*Maloclemys terrapin*), that have evolved in estuarine habitats since the Tertiary. A plethora of recent work on molecular phylogenies of these species allows us to examine the pattern and time of invasions by new taxa. Furthermore, we can examine the nature of adaptation of taxa with older and more recent associations with tidal marshes (Grenier and Greenberg, *this volume*).

Because of this high level of differentiation of tidal marsh taxa, the restricted distribution of this habitat, and its location in some of the most heavily settled areas of the world, it is not surprising that many populations are very small and have shown rapid declines. Tidal marsh vertebrates face the continuing challenges of fragmentation, ditching and impoundment, reduction in area, pollution, and the establishment of invasive species (Daiber 1982). In addition, sea-level rise will not only influence the extent and zonation of tidal marshes (Erwin et al. 1994, *this volume*), but the salinity and perhaps the frequency of storm surges as well.

Given the enormous pressures on delicate coastal ecosystems, it should not be a surprise that the 25 species and the close to 50 subspecies that they represent are disproportionately endangered, threatened, or otherwise of heightened conservation concern (Table 1). One saltmarsh subspecies of ornate shrew from Baja California (*Sorex ornatus juncensis*) may already be extinct. Federally endangered taxa include the salt marsh harvest mouse (*Reithrodontomys raviventris*), three western subspecies of the Clapper Rail (*Rallus longirostris*), and the Florida meadow vole (*Microtus pennsylvanicus dukecampbelli).* The Atlantic Coast subspecies of the salt marsh water snake (*Nerodia clarkia taeniatus*) is listed as threatened by the USDI Fish and Wildlife Service. Although only seasonally associated with saltmarshes, the Orange-bellied Parrot (*Neophema chrysogaster*) of Australia and the Saunder's Gull (*Larus saunderi*) of Asia, may be added to the global list of species that may depend upon saltmarshes. Many of the other subspecies listed in Table 1 are on various state and regional lists for threatened or vulnerable species.

TABLE 1. VERTEBRATE TAXA RESTRICTED TO TIDAL MARSHES.

Species	Subspecies	Distribution	Status
Diamondback terrapin (*Malaclemys terrapin*)	*terrapin* *centrata* *tequesta* *rhizophorarum* *macrospilota* *pileata* *littoralis*	Atlantic coast of North America	Endangered in Massachusetts, threatened in Rhode Island, species of special concern in six other states.
Gulf saltmarsh snake (*Nerodia clarkii*)	*clarkii* *taeniata*	Gulf of Mexico and Atlantic coast of Florida	*taeniata* is threatened.
Carolina water snake (*Natrix sipedon*)	*williamengelsi*	Carolina coast of North America	State species of concern.
Northern brown snake (*Storeria dekayi*)	*limnetes*	Gulf of Mexico, North America	
Black Rail (*Laterallus jamaicensis*) [a]	*jamaicensis* *coturniculus*	Atlantic, Gulf of Mexico, and Pacific coasts of North America	Species of conservation concern (USDI Fish and Wildlife Service 2002).
Clapper Rail (*Rallus longirostrus*)	*obsoletus* group *crepitans* group	Atlantic, Gulf of Mexico, and Pacific coasts of North America	Populations in California are endangered.
Willet (*Catoptrophorus semipalmatus*)	*semipalmatus*	Atlantic coast of North America	None
Common Yellowthroat (*Geothlypis trichas*)	*sinuosa*	San Francisco Bay	State species of concern.
Marsh Wren (*Cistothorus palustris*)	*palustris* *waynei* *griseus* *marianae*	Atlantic coast of North America	*C. p. griseus* and *C. p. marianae* subspecies of conservation concern in Florida.
Song Sparrow (*Melospiza melodia*)	*samuelis* *pusillula* *maxillaris*	San Francisco Bay	State of California subspecies of concern.
Swamp Sparrow (*Melospiza georgiana*)	*nigrescens*	Mid-Atlantic North American coast	Maryland subspecies of concern.
Savanna Sparrow (*Passerculus sandwichensis*)	*rostrata* group *beldingi* group	Western Mexico and Southern and Baja California	Threatened in California.
Seaside Sparrow (*Ammodramus maritimus*)	Atlantic Coast group Gulf Coast group	Atlantic and Gulf of Mexico coasts	One subspecies endangered (*A. m. mirabilis*), one subspecies extinct (*A. m. nigrescens*). Species of national conservation concern (USDI Fish and Wildlife Service 2002).
Salt Marsh Sharp-tailed Sparrow (*Ammodramus caudacutus*)	*caudacutus* *diversus*	Atlantic coast of North America (non-breeding)	Species of national conservation concern (USDI Fish and Wildlife Service 2002).
Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*)	*subvirgatus* *alterus*	Atlantic and Gulf of Mexico coast of North America (non-breeding)	Species of national conservation concern (USDI Fish and Wildlife Service 2002).

TABLE 1. CONTINUED.

Species	Subspecies	Distribution	Status
Slender-billed Thornbill (*Acanthiza iradelei*)	*rosinae*	South coast of Australia	None
Masked shrew (*Sorex cinereus*)	*nigriculus*	Tidal marshes at mouth of Tuckahoe river, Cape May, New Jersey	None
Ornate shrew (*Sorex ornatus*)	*sinuosus* *salarius* *salicornicus* *juncensis*	San Pablo Bay, Monterey Bay, Los Angeles Bay, El Socorro marsh, Baja California.	State of California subspecies of concern. Extinct?
Wandering shrew (*Sorex vagrans*)	*halicoetes*	South arm of San Francisco Bay	State of California subspecies of concern.
Louisiana swamp rabbit (*Sylvilagus aquaticus*)	*littoralis*	Gulf coast	
Salt marsh harvest mouse (*Reithrodontomys raviventris*)	*raviventris* *halicoetes*	San Francisco Bay	Both California and federal endangered species.
Western harvest mouse (*Reithrodontomys megalotis*)	*distichlis* *limicola*	Monterey Bay, Los Angeles Bay	No status. State of California subspecies of concern.
California vole (*Microtus californicus*)	*paludicola* *sanpabloenis* *halophilus* *stephensi*	San Francisco Bay, San Pablo Bay, Monterey Bay, Los Angeles coast	Subspecies *sanpabloenis* and *stephensi* are California subspecies of concern.
Meadow vole (*Microtus pennsylvanicus*)	*dukecampbelli* *nigrans*	Gulf Coast, Waccasassa Bay in Levy County, and Suwannee National Wildlife Refuge, Florida; East coast Chesapeake Bay Area	Federally endangered.
White-tailed deer (*Odocoileus virginianus*)	*mcilhennyi*	Gulf coast	None

[a] Black Rail is included, although small populations of both North American subspecies can be found in inland freshwater marshes (Eddleman et al. 1994).

THREATS TO TIDAL SALTMARSHES

As we have suggested, the threats to the already local and restricted saltmarsh taxa are a bellwether of the overall threats to the integrity of salt marsh ecosystems. The following represents some of the major environmental issues facing the small amount of remaining tidal marsh.

DEVELOPMENT

Coastal areas along protected temperate shorelines are prime areas for human habitation. By the end of the last century, 37% of the world's population was found within 100 km of the coast (Cohen et al. 1997). At the same time, 42% of the U.S. population lived in coastal counties along the Pacific, Atlantic, and Gulf of Mexico (NOAA http://spo.nos.noaa.gov/projects/population/population.html). The impact of human populations around major navigable estuaries where most tidal marsh is found is undoubtedly higher than random sections of coastline. In particular, the filling and development of the shoreline of tidal estuaries such as the San Francisco and Chesapeake bays and the Rio Plata has led to the direct loss of large areas of saltmarsh. The loss of >80% of the original wetlands around San Francisco Bay is of particular concern (Takekawa et al., chapter 11, *this volume*), since its three major embayments support more endemic tidal marsh taxa than any other single coastal locality.

GRAZING AND AGRICULTURE

Marshes are often populated by palatable and nutritious forage plants and hence have been directly grazed or grasses have been harvested for hay. Harvesting salt hay for forage and mulch was an important industry in marshes along the east coast of North America in the 18th and 19th centuries (Dreyer and Niering 1995). Although no longer a common practice in North American tidal marshes, the use of coastal wetlands to support livestock still occurs in the maritime provinces of Canada and is common in Europe and parts of South America.

Apart from grazing and haying over the course of human history, large and unknown areas of tidal marsh have been diked and converted to agricultural use, such as the low countries of Northern Europe (Bos et al. 2002), areas of rice farming in Korea and China, and salt production.

A more profound change than the addition of grazing livestock to many marsh systems is the loss of large grazing animals towards the end of the Pleistocene (Levin et al. 2002). We know from studies of reintroduced horses, that tidal marsh grasses—particularly smooth cordgrass (*Spartina alterniflora*)—are highly palatable and preferred forage (Furbish and Albano 1994). In many marshes the largest vertebrate herbivores have shifted from ungulates to microtine and cricitid rodents. Nowadays, the most important herbivores in some marshes may be snails and snail populations are controlled by crabs (Sillman and Bertness 2002). But in the Tertiary and Pleistocene, large mammals might have been keystone herbivores in tidal marsh systems. It would be fair to say that the ecological and evolutionary impact of the loss of such herbivores is not fully understood (G. Chmura, pers. comm.)

Ditching, Channel Development, and Changes in Hydrology

Tidal marshes have borne the brunt of an array of management activities that either directly or indirectly affect their functioning. Barriers to or canalization of tidal flow can disrupt natural cycles of inundation. The reduction of tidal flow has been implicated in major vegetation changes in tidal marshes in Southern California (Zedler et al. 2001). Water management projects for creating shipping navigation channels have had a particularly large impact on the coastal marshes of the Mississippi Delta (Mitsch and Gosselink (2000). On the other hand, upstream impoundment of water may reduce the input of freshwater and induce salt water incursions into freshwater systems. Shifts towards higher salinity over the past 150 yr have been documented for the marshes of the Meadowlands in the Hudson River estuary (Sipple 1971). On an even larger scale, the balance between fresh-water flow and salt-water intrusion has been the subject of considerable interest in the estuaries of the Suisun Bay and lower Sacramento-San Joaquin deltas of the San Francisco Bay area (Goman 2001). The California Water Project has doubtlessly influenced this, but early Holocene shifts in plant composition suggest natural variation in the pattern of salt water incursion has been profound.

On a micro-scale, saltmarshes have been variously ditched for insect control (Daiber 1986) and opened with large water impoundments to provide habitat for insect control and to provide habitat for waterfowl (Erwin et al. 1994, Wolfe 1996). In some areas, human engineering of water distribution and vegetation in marshes has all but replaced the natural engineering of wildlife—particularly the muskrat (*Ondatra zibethicus*; Errington 1961).

Marsh Burning

Lightning fires can be an important source of natural disturbance to coastal marshes, occurring at particularly high frequencies along the southern Atlantic and Gulf coasts (Nyman and Chabreck 1995). The frequency of marsh burning has increased due to human activities, including the purposeful use of fire as a management tool to increase food for waterfowl and trappable wildlife. However, the effect of such management on non-target organisms and ecosystem function is just beginning to be evaluated (Mitchell et al*., this volume*).

Invasive Species

Coastal ecosystems have been on the receiving end of human-caused introductions that have resulted in species invading and changing tidal marshes. The most critical invasions have consisted of dominant tidal-marsh plants, because as they take over marshlands, they change the face of the habitat. Species of *Spartina* have been prone to establishing themselves on foreign shores (West Coast of the US, China, parts of Northern Europe, New Zealand, and Tasmania). Even along its native shoreline, smooth cordgrass is spreading as a result of nitrification and other environmental changes (Bertness et al 2002). The common reed *(Phragmites australis),* a native species, has spread in the high marshes of eastern North America, often creating large barren monocultures (Benoit and Askins 1999).

We have focused on how invasions of dominant plant species change the basic habitat structure and productivity in many, as yet poorly understood, ways. Major changes have occurred in the benthic fauna of major North American estuaries (Cohen and Carlton 1998) and the effect this has had on the feeding ecology of tidal marsh vertebrates has not been well documented. Vertebrate species themselves are often invasive, and the tidal-marsh fauna itself has been dramatically changed through human introductions. Species of *Rattus* and the house mouse (*Mus musculus*) are now distributed in marshes around the world. The rats, in particular, are known to be important nest predators and are hypothesized to have a negative impact on endangered taxa, such as the Clapper Rail. Other predator populations, including red fox (*Vulpes vulpes*) and Virginia opossum (*Didelphis virginiana*), have spread through human introductions and activities. The nutria (*Myocastor coypus*) has spread throughout the southeastern US resulting in severe levels of grazing damage. Although we know of no introduced breeding bird species, a variety of reptiles have colonized mangroves and subtropical saltmarshes of Florida.

Toxins, Pollutants, and Agricultural Run-off

Estuaries receive run-off from agricultural fields and urban development spread over large watersheds. Tidal marshes are often sprayed directly with pesticides, a practice that will probably increase under the threat of emergent mosquito-borne diseases, such as West Nile virus. In addition, tidal marshes that fringe estuaries also bear the brunt of any oil or chemical spills into the marine environment that drift into the shores. The effects of pollution are both acute and long term; the latter including the effects of increased nutrient loads into the tidal-marsh ecosystem and the former comprised of the toxic effects of chemicals to the vegetation and wildlife (Clark et al. 1992). The impact on dominant vegetation of increased nitrogen inputs into tidal marshes has been documented, at least for marshes along the Atlantic Coast of North America (Bertness et al. 2002).

Increase in Carbon Dioxide, Sea-level Rise, Changes in Salinity, and Global Warming

Sea level is rising in response to global increases in atmospheric temperatures. If, on a local scale, coastline accretion does not keep pace with this rise, then the leading edge of coastal marshes will become permanently inundated and lost as wildlife habitat. Over time, high marsh becomes middle and then low marsh with increasing sea levels. New high marsh forms after major disturbance of upland communities allows marsh invasion. Depending upon the shape of the estuarine basin and the land use on the lands above the maximum high-tide line, the possibility of upland expansion may be curtailed along many coastlines. Estimates for coastal wetland loss as a result of sea-level rise range from 0.5–1.5% per year.

Global warming may result in other, less obvious impacts on coastal marsh systems. Perhaps of equal concern as the loss of marshland is the change in salinity resulting from salt-water intrusion into brackish-marsh systems. The actual warming itself may favor the spread of lower latitude species into higher latitude coastlines. Warmer conditions may also favor the increase in the seasonal activity of mosquitoes and other disease-transmitting insects and help the spread of associated diseases. Finally, increases in atmospheric carbon dioxide (CO_2) have a demonstrable impact on the productivity and transpiration of salt-marsh plants. These effects vary between species and may shift the mix of tidal marsh dominants. Already it has been demonstrated that increases in CO_2 favor the spread of C^3 versus C^4 plants (Arp et al. 1993).

WHAT THIS VOLUME IS ABOUT

In this volume, the authors collectively provide a sweeping view of what we know about vertebrates—primarily terrestrial vertebrates—in the highly threatened tidal-marsh systems. The contents provide a broad view of tidal-marsh biogeography, more focused discussions of adaptations of different taxa to the challenges of tidal-marsh life, and a comprehensive account of the major conservation and management issues facing marshes and their wildlife. The following provides a brief guide to the narrative trail we explore.

Biogeography

We examine what is known—from both direct evidence and inference—about the changes in the quantity and distribution of tidal marshes from the Tertiary to recent times, with a focus on the San Francisco Bay estuaries, home of the greatest single concentration of endemic vertebrate species and subspecies. Having set the historical stage, we examine the distribution of tidal marshes and their vertebrate biota throughout the world. The disparate distributional literature for mammals and birds, and as much as possible, reptiles and amphibians has been sifted through to determine which species of these taxa occupy tidal marshes along different coasts and on different continents. Emphasis is placed on the distribution of differentiated taxa (subspecies and species) that occupy tidal marshes in different regions. Distributional patterns are synthesized and some preliminary hypotheses to explain the distributions are proposed. In addition, some of the features that characterize successful colonists of tidal marshes are explored.

In recent years, molecular phylogenies of groups that feature tidal-marsh taxa have been developed and the genetic structure of tidal marsh taxa has been detailed as well. This new information allows us to begin to estimate the length of historical association of various taxa and how this has affected adaptation to tidal marshes.

Adaptation to Tidal Marshes

Tidal marshes present myriad adaptive opportunities and challenges to the few species that colonize them. In a series of chapters, adaptation to tidal marsh life is explored from a variety of perspectives. Focusing on nesting biology of birds, we explore the role of tidal cycles and flooding events in shaping this central feature of avian ecology. Adaptations to saline environments are examined by focusing on the physiology of salinity tolerance in sparrows, a group that is not generally known for its maritime distribution. In the course of focusing in on sparrow adaptations, we review the different behavioral, physiological and morphological adaptations of vertebrates in brackish to salty environments. The volume further explores shared adaptations to the tropic opportunities with emphasis on the bill morphology of sparrows and background matching coloration of a suite of terrestrial species. Finally, we examine shifts in communication, demography and social organization that accompany successful occupation of tidal marshes.

Conservation Biology: Anthropogenic Environmental Impacts on Tidal Marshes of the Previous and Next Century

Tidal marshes have already been reduced in area, fragmented, ditched, and altered by the damming of streams and rerouting of water sources. To place the environmental issues facing saltmarsh vertebrates in context, we will provide regional reviews of four North American tidal-marsh areas—Northeast, Southeast, San Francisco Bay, and southern California—that together present the range of conservation issues. Two chapters address species specific approaches to evaluating both local- and landscape-level effects of habitat change. We finally turn to more synthetic treatments of environmental issues outlined above with chapters focusing on sea-level rise, invasive species, toxins (focusing on Clapper Rails), and the effect of active salt-marsh management, including burning, open-water management, and mosquito-control efforts.

If nothing else is accomplished, we hope that we will bring greater attention to the conservation of the tidal-marsh endemics. The first step towards a more concerted conservation effort is a systematic source of information on the population status and long-term trends of saltmarsh vertebrate populations. To catalyze this, we provide a collaborative chapter outlining approaches to the long-term monitoring of tidal-marsh birds. Future collaborations should focus on establishing similar systems for mammals and, in some areas, snakes and turtles. Such monitoring programs are only a first step. We hope they will provide the backbone to an active research program on tidal-marsh vertebrates.

We end the volume with a menu of exciting and important areas for both applied and basic research. By following these research leads, we will achieve the ability to better manage and protect the healthy, restore the degraded, and reestablish the lost marshlands, while achieving a greater understanding of how animals adapt to this unique environment.

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BIOGEOGRAPHY AND EVOLUTION OF TIDAL-MARSH FAUNAS

Bay-capped Wren-spinetail (*Spartonoica maluroides*)
Drawing by Julie Zickefoose