Tidal Marshes: A Global Perspective on the Evolution and Conservation of Their Terrestrial Vertebrates

RUSSELL GREENBERG, JESUS MALDONADO, SAM DROEGE, AND M. V. MCDONALD

Globally, tidal marshes are found in small pockets or narrow bands totaling only approximately 45,000 square kilometers. The combination of salinity, low floristic and structural complexity, and regular tidal inundation, as well as unpredictable catastrophic flooding, provides a unique selective environment that shapes local adaptations, including those that are morphological, physiological, demographic, and behavioral. Although tidal marshes support a low diversity of nonaquatic vertebrate species, a high proportion of these inhabitants, at least along North American coastlines, are restricted to or have subspecies restricted to tidal marshes. Tidal marshes and their endemic fauna face broad threats from a variety of human-caused environmental changes. Future research should focus on global inventories, intercontinental comparative work, and investigation to determine why almost all presently described endemic taxa appear to be found in North America.

Keywords: salt marsh, ecophysiology, ecotypic variation, coastal ecosystems, wetlands

Some habitats attract biological research because they support a high diversity of organisms. Other habitats are relatively depauperate, but in part because of their simple composition, they allow researchers to study the processes that determine the mode and tempo of evolutionary differentiation. In comparison with other temperate ecosystems, tidal marshes support relatively few species of terrestrial vertebrates, but a high proportion of those either are endemic or have subspecies restricted to tidal marsh habitat (Greenberg and Maldonado forthcoming). The tidal marsh ecosystem is thus an excellent natural laboratory for studying the mechanisms of local differentiation, because it offers a sharp environmental gradient between upland and marine systems over which selection can act and gene flow can occur (Mitsch and Gosselink 2000). Studies of tidal marsh ecosystems have led to important insights into fundamental issues of ecology, such as energy and nutrient flow (Teal 1962), the role of competition and facilitation in the formation of vegetation zones (Bertness 1992), and the top-down control of herbivory (Sillman and Bertness 2002). We suggest that tidal marshes are also an ideal system for investigating a central question of evolutionary ecology: What forces promote and deter the development of local adaptation and, ultimately, the evolution of endemic taxa?

Factors that are thought to influence the degree of local differentiation, and hence endemism, in continental habitats include (a) selective gradients generated by abiotic stressors, shifts in resources at lower trophic levels, and opportunities for the development of mutualisms; (b) the composition of source faunas in nearby habitats; (c) the degree of isolation from source habitats (both now and in the past); (d) the amount of habitat; and (e) the stability of habitat composition, location, and extent through time (Lomolino et al. 2006). In this article, we will undertake a qualitative review of these factors in generating and deterring local differentiation and endemism in coastal salt marshes.

Russell Greenberg (e-mail: greenbergr@si.edu) is director of the Smithsonian Migratory Bird Center at the National Zoological Park, Washington, DC 20008. He studies the ecology and evolution of migratory birds and vertebrates of coastal wetlands. Jesus Maldonado is with the Smithsonian Genetics Program at the National Zoological Park, where he studies the evolutionary genetics of mammals. Sam Droege develops biodiversity monitoring programs at the US Geological Service Patuxent Wildlife Research Center, Laurel, MD 20774. M. V. McDonald is at the Department of Zoology of the University of Central Arkansas, Conway, AR 72035, where she studies the communication and behavior of songbirds. © 2006 American Institute of Biological Sciences.

Tidal marshes are found along the low-energy coastlines of mid- to high-latitude regions of the major continents (except Antarctica), and lie at the ecotone between terrestrial, freshwater, and marine systems. Tidal marshes epitomize the aforementioned conflicting forces that shape local faunal diversification; tidal marshes are highly productive (Adam 1990), provide an abundance of trophic resources, and yet are limited in extent, simple in structure, and physically harsh for animals attempting to colonize them.

Furthermore, the high productivity does not result in a uniformly high abundance of food resources used by terrestrial vertebrates. Seed abundance is low compared with the levels in grassland, old field, or freshwater marsh (Leck 1989), and the abundance and diversity of herbivores feeding on terrestrial plants (grasses, forbs, and shrubs) is substantially lower than in freshwater marshes (Odum 1988), but the abundance of detritivores and benthic invertebrates is relatively high compared with that of grassland, scrub, or freshwater marsh.

Although individual tidal marsh systems have received considerable attention from the standpoint of research into ecosystem function, factors controlling plant distributions, and conservation issues (Adam 1990), few attempts have been made to take a geographically broad look at patterns of diversity and endemism in this globally distributed ecosystem. How tidal marsh organisms have responded to this habitat, from both an evolutionary and an ecological perspective, should be a good indicator of that habitat's distinctive biological features.

Here we focus on vertebrates from terrestrial or freshwater marsh environments that have colonized tidal marshes. We focus on species or subspecies that reproduce in tidal marshes, excluding migrants and temporary nonbreeding visitors; we consider only those taxa that have ranges primarily in coastal estuarine systems, including species that depend on the marsh vegetation and the underlying substrate of the tidal marsh habitats. Therefore, for most of this discussion we exclude many taxa that are common in tidal marshes but do not have morphologically distinct forms that are largely restricted to coastal habitats. We also exclude primarily aquatic species that may enter or feed in the channels and lagoons within tidal marshes, including fish, and fish-eating or otherwise aquatically foraging birds, mammals, and turtles, as well as strictly aerial-feeding taxa such as swallows, swifts, and bats. We assess the extent, geographic pattern, and nature of local adaptation to tidal marsh conditions and discuss the conservation status of endemic taxa in the context of the environmental threats to their populations and habitat.

Global distribution of tidal marshes
We focus our attention on tidal marshes, which are areas of predominantly graminoid or herbaceous vegetation found in the intertidal zone of temperate estuaries. Despite their global distribution, tidal marshes are quite limited in the total surface area that they cover. Nonarctic tidal marshes cover approximately 45,000 square kilometers (km^2), an area slightly larger than the country of Denmark (table 1). In subtropical estuaries, tidal marsh gives way to mangrove swamp covering an area of approximately 170,000 km^2 (Valiela et al. 2001).

Tidal marshes occur where coastlines are protected, either within estuaries, in deltas, or behind barrier islands, so that sediment deposits can support the colonization by plant life (which further facilitates marsh accretion). Tidal marshes are largely supplanted by mangrove swamps in subtropical to tropical waters, and salt marsh vegetation is restricted to the harshest hypersaline pans adjacent to the mangrove areas. Although many of the ecological characteristics of tidal marsh are shared with mangrove areas, the latter are both tropical and forestlike, and we will make only passing comparisons of the two.

The distribution of tidal marshes was reviewed by Chapman (1977), and the map based on his work is the one used most often to portray coastal marsh distribution (figure 1). However, we accumulated a more quantitative depiction of the distribution of tidal marshes (table 1), which shows that by far the greatest concentration is found along the South Atlantic and Gulf coasts of North America, followed by China. Other areas having more local concentrations of tidal marsh include coastal estuaries in Argentina, Brazil, Uruguay, the San Francisco Bay, and, at least historically, the coasts of the North and Baltic seas of Europe.

Tidal marshes range from fresh to hypersaline, with salinities sometimes exceeding those of seawater (Odum 1988). Tidal marshes are generally dominated by one to a few species of halophytic grasses or forbs. The diversity of plants is generally lowest at the lower elevations of a marsh, and tends to increase (to a point) as one moves away from the equator along a coastline (Chapman 1977). Along coastlines in more humid areas, the dominant lower marsh cover plants are the salt-adapted grasses in the genus *Spartina*. In more arid areas, succulents in the family Chenopodiacea (e.g., *Salicornia, Suaeda,* and *Sarcocornia*) become the important cover plants. Marshes along the Pacific Rim, including those bordering California, China, and Japan, are dominated by plants in these genera. The lower marsh zone in Europe is often entirely bare of vegetation (Mitsch and Gosselink 2000). Upper marshes, with lower salinity, are more floristically diverse (Odum 1988), often comprising a mixture of grasses, rushes, herbs, and shrubs. However, in some regions, the brackish upper marshes are dominated by *Phragmites,* forming single-species stands either as a native species (China, Europe, Middle East) or as an aggressive invasive (East Coast of North America).

Changes in marsh distribution in evolutionary time
When considering patterns of differentiation of taxa, it is critical to develop a good understanding of the changes in habitat availability throughout evolutionary time. Most of the differentiation in vertebrate forms in tidal marshes is at the level of subspecies, and therefore we expect Pleistocene events to have had the greatest impact on evolutionary processes influencing tidal marsh vertebrates. Almost no stratigraphic data exist for determining the location and extent of tidal marshes throughout the Pleistocene, and relatively few data

Table 1. The approximate surface area and dominant vegetation for tidal marshes, by coastline.

Continent	Coastline	Extension (square kilometers)	Dominant vegetation
North America	North Atlantic	500	*Spartina, Phragmites*
	South Atlantic, Gulf Coast	15,000	*Spartina, Juncus*
	Pacific	440	*Salicornia, Spartina*
Eastern South America	Atlantic	2300	*Spartina, Juncus*
Europe	All	1400	*Salicornia, Spartina*, grasses
Asia (Japan, Korea, China)	Pacific	25,000	Chenopods, *Phragmites*
Australia, New Zealand, Tasmania[a]	Southern (temperate)	772	*Sarcocornia*, other chenopod shrubs
South Africa	Southern	70	*Sarcocornia, Spartina*, grasses

a. There are more extensive salt marshes in tropical Australia, but these are high, level flats above mangroves—often hypersaline and with large salt flats and sparse vegetation—and are not counted in the total area.

Source: Greenberg and Maldonado (forthcoming).

are available for the Holocene (Malamud-Roam et al. forthcoming). However, indirect evidence based on the geomorphology of coastlines, on estimates of climatic conditions, and on probable sediment loads suggests that tidal marshes have been very dynamic throughout the advance and retreat of the glaciers. Analysis of important individual estuarine systems, such as the San Francisco Bay (Malamud-Roam et al. forthcoming), the Chesapeake Bay (Colman and Mixon 1988), and the estuary of the Río de la Plata (Lopez-Laborde 1997), show that these coastal features and their marshes are postglacial formations associated with rising sea levels, increasing sediment loads in rivers, and warming temperatures. In North America, many northern marshes were covered by glaciers; along more southerly coastlines, it is likely that refugia for marshes were located along shorelines protected by depositional barrier islands. Tidal marshes expanded and contracted during numerous periods in the Pleistocene, migrating north and south with changes in water temperature.

Global and local patterns of diversity and endemism

Although the open waters within tidal marshes are often used by visiting waterfowl, waders, and aquatic mammals, relatively few terrestrial species are resident or reproduce in vegetated portions of these marshes. Tidal marshes on major coastlines support 11 to 21 species of breeding birds and 13 to 26 species of mammals (Greenberg and Maldonado forthcoming). A surprisingly large number of amphibian and reptile species have been found occasionally within the boundaries of tidal marshes, but most are found in fresh to slightly brackish microenvironments, and only a few species of snakes, turtles, and crocodilians can be considered common residents of salt marshes (Neill 1958).

On the basis of extensive literature searches, we have identified 25 terrestrial vertebrate species that either are endemic to tidal marshes or have recognized subspecies restricted primarily to marshes (table 2). These include turtles, snakes, shrews, small rodents, emberizid sparrows, and rails. Only five species are en-

tirely restricted to coastal wetlands, including the seaside sparrow (*Ammodramus maritimus*), the saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*), and the salt marsh harvest mouse (*Reithrodontomys raviventris*). Tidal marshes and their faunas have been affected by human activity for so long that it may be difficult to reconstruct their prehuman diversity and endemism. This would be particularly true for areas with long histories of agriculture, such as Europe and China, and for the extinct megafauna that may have grazed the marshes up to the late Pleistocene (Levin et al. 2002).

Although no global review of diversity and endemism in the vertebrates of mangrove swamps has been published, the few taxon- and region-specific accounts suggest a pattern similar to that of tidal marshes: relatively few species, particularly for residents that reproduce within the mangrove habitat. As in tidal marshes, the few species comprise a relatively large number of endemic species or subspecies (Lefebvre
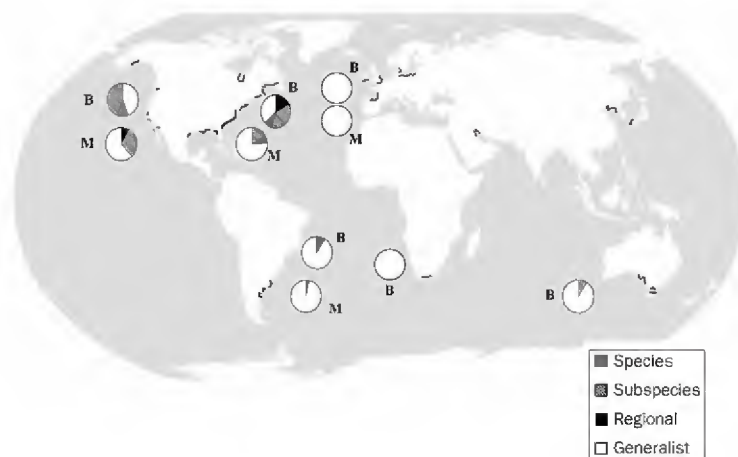

Figure 1. The global distribution of tidal marsh. Pie charts indicate the proportion of species in different categories of local differentiation in tidal marshes: (1) no differentiation, (2) species with populations regionally restricted to tidal marshes, (3) species with subspecies restricted to tidal marshes, and (4) species restricted to tidal marshes. Abbreviations: M, mammals; B, birds. Source: Greenberg and Maldonado (forthcoming); modified from Chapman (1977).

Table 2. Distribution, status, and year of description for vertebrate taxa restricted to tidal marshes.

Species	Year taxon was described	Subspecies	Distribution	Status
Diamondback terrapin (*Malaclemys terrapin*)	1793 1802 1955 1904 1865 1904	*terrapin centrata tequesta macrospilota pileata littoralis*	Atlantic coast of North America	Endangered in Massachusetts, threatened in Rhode Island, species of special concern in six other states
Gulf salt marsh snake (*Nerodia fasciata*)	1853 1895	*clarki taeniata*	Gulf Coast of North America, Atlantic coast of Florida	Ssp. *taeniata* is federally threatened
Carolina water snake (*Nerodia sipedon*)	1973	*williamengelsi*	Carolina coast of North America	State species of concern
Northern brown snake (*Storeria dekayi*)	1961	*limnetes*	Gulf Coast of North America	None
Black rail (*Laterallus jamaicensis*)	1789 1874	*jamaicensis coturniculus*	Atlantic, Gulf, and Pacific coasts of North America	Species of conservation concern (USFWS 2002)
Clapper rail (*Rallus longirostris*)	1872 1789	*obsoletus* group *crepitans* group	Atlantic, Gulf, and Pacific coasts of North America	Populations in California are federally endangered
Willet (*Catoptrophorus semipalmatus*)	1789	*semipalmatus*	Atlantic coast of North America	None
Common yellowthroat (*Geothlypis trichas*)	1901	*sinuosa*	San Francisco Bay	State species of concern
Marsh wren (*Cistothorus palustris*)	1810 1932 1892 1888	*palustris waynei griseus marianae*	Atlantic coast of North America	Ssp. *griseus* and *marianae* are subspecies of conservation concern in Florida
Song sparrow (*Melospiza melodia*)	1858 1899 1909	*samuelis pusillula maxillaris*	San Francisco Bay	California subspecies of concern
Swamp sparrow (*Melospiza georgiana*)	1951	*nigrescens*	Mid-Atlantic North American coast	Maryland subspecies of concern
Savanna sparrow (*Passerculus sandwichensis*)	1852 1867	*rostrata* group *beldingi* group	Western Mexico (*rostrata* group), Southern and Baja California (*beldingi* group)	Endangered in California
Seaside sparrow (*Ammodramus maritimus*)	1811 1811	Atlantic coast group Gulf Coast group	Atlantic and Gulf coasts	Ssp. *mirabilis* endangered; ssp. *nigrescens*) is of national conservation concern (USFWS 2002)
Saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*)	1788 1901	*caudacutus diversus*	Atlantic coast of North America (nonbreeding)	Species of national conservation concern (USFWS 2002)
Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*)	1887 1938	*subvirgatus alterus*	Atlantic and Gulf coasts of North America (nonbreeding)	Species of national conservation concern (USFWS 20002)
Slender-billed thornbill (*Acanthiza iredalei*)	1913	*rosinae*	Southern coast of Australia	None
Masked shrew (*Sorex cinereus*)	1932	*nigriculus*	Tidal marshes at the mouth of Tuckahoe river, Cape May, New Jersey	None
Ornate shrew (*Sorex ornatus*)	1913 1939 1932 1909	*sinuosus salarius salicornicus juncensis*	San Pablo Bay (ssp. *sinuosus*), Monterey Bay (ssp. *salarius*), Los Angeles Bay (ssp. *salicornicus*), El Socorro marsh, Baja California, Mexico (ssp. *juncensis*)	Ssp. *juncensis* is thought to be extinct; the other S. *ornatus* ssp. are California subspecies of concern
Wandering shrew (*Sorex vagrans*)	1928	*halicoetes*	Southern arm of San Francisco Bay	California subspecies of concern
Louisiana swamp rabbit (*Sylvilagus aquaticus*)	1909	*littoralis*	Gulf Coast	None
Salt marsh harvest mouse (*Reithrodontomys raviventris*)	1908 1909	*raviventris halicoetes*	San Francisco Bay	California and federal endangered species
Western harvest mouse (*Reithrodontomys megalotis*)	1937 1932	*distichlis limicola*	Monterey Bay (ssp. *distichlis*), Los Angeles Bay (ssp. *limicola*)	Ssp. *distichlis* has no status; ssp. *limicola* is a California subspecies of concern
California vole (*Microtus californicus*)	1935 1961 1937 1932	*paludicola sanpabloensis halophilus stephensi*	San Francisco Bay (ssp. *paludicola*), San Pablo Bay (ssp. *sanpabloensis*), Monterey Bay (ssp. *halophilus*), Los Angeles coast (ssp. *stephensi*)	Ssp. *sanpabloensis* and *stephensi* are California subspecies of concern
Meadow vole (*Microtus pennsylvanicus*)	1982 1897	*dukecampbelli nigrans*	Gulf Coast, Waccasassa Bay in Levy County, Suwannee National Wildlife Refuge, Florida (ssp. *dukecampbelli*), East Coast, Chesapeake Bay area (ssp. *nigrans*)	Endangered
White-tailed deer (*Odocoileus virginianus*)	1928	*mcilhennyi*	Gulf Coast	None

and Poulin 2000). The salinity, tidal flooding, and low plant diversity probably produce this pattern as well.

Perhaps the most striking feature of the listed endemic tidal marsh taxa is that they are largely restricted to North America (table 2). Fifteen are species (or subspecies) restricted to the Atlantic or Gulf coasts, and eight are found along the Pacific coast of North America. The only avian taxon outside of North America known to be mostly restricted to coastal salt marshes is a subspecies of the slender-billed thornbill (*Acanthiza iredalei rosinae*) in southern Australia. Other candidates for having subspecies restricted to tidal salt marsh include two bird species in South America: the bay-capped wren-spinetail (*Spartonoica maluroides*), a warbler-sized member of the largely South American ovenbird family (Furnariidae), and the dot-winged crake (*Porzana spiloptera*; Isacch et al. 2004). We have found no recognized species or subspecies of mammal or reptile restricted to tidal marshes outside North America.

Some of the regional difference in the number of described tidal marsh taxa may be an artifact of the resolution of taxonomic studies. However, tidal marsh taxa have been well documented for a long time. The first endemic species was described in 1788, and the first subspecies in 1789 (table 2), with a mean year of initial description for species and subspecies of 1830 and 1879, respectively. The salt marsh harvest mouse, the most recently recognized endemic tidal marsh species, was described in 1908, and the Carolina water snake (*Nerodia sipedon williamengelsi*), the most recent subspecies, was documented in 1973. Therefore, lack of taxonomic knowledge seems to be a particularly unlikely explanation for such well-known regions as Europe and Australia, but it is a possible factor in the lack of endemic subspecies described for the South American and East Asian coastlines.

A species–area relationship may help explain the preponderance of endemism in eastern North America: This area has the greatest extent of tidal marsh in the world, with the possible exception of China. However, the frequency of endemism along the western coast of North America cannot be easily explained by mere abundance of habitat, as this region currently has relatively little tidal marsh. Another factor could be the historical distribution of tidal marsh refugia during the glacial maxima. In this case, the Gulf of Mexico and the Gulf of California may have provided habitat that allowed endemic forms to persist when marshes receded from more northerly areas. Finally, ecological factors operating within North American marshes, or the presence of taxa that are prone to successful marsh colonization, may contribute to the unusual degree of endemism. At this time, however, no single, comprehensive theory can fully explain the phenomenon of North American tidal marsh endemism.

Genetic divergence of endemic populations

Comparative analysis of the temporal pattern of divergence for codistributed species can provide insights into the biogeographic history of a region (Avise 1994). This broader perspective provides a major advance over single-taxon approaches, in that it has the potential to be predictive for suites of species that have responded similarly to historical changes in habitat distribution (Riddle et al. 2000). In this way, patterns of genetic divergence may provide insight into how and when endemic taxa evolved within tidal marsh systems (Chan et al. forthcoming).

Studies of molecular markers, primarily mitochondrial DNA (mtDNA), have been conducted on almost half the endemic taxa of tidal marsh vertebrates (Chan et al. forthcoming). Given that there are far fewer endemic species than endemic subspecies, it is not surprising that, as a whole, endemic taxa show only weak divergence from their nontidal relatives (figure 2). A few species show deep evolutionary divergence, with sequence divergence values of 1% to 3% between the tidal marsh taxa and the closest known nontidal marsh relative (figure 2). Using a rough estimate of 500,000 years per 1% divergence (Avise and Nelson 1989), this would place the timing of divergence at the early to mid Pleistocene. Although the sample size is too small for formal analysis, the tendency is for the older taxa (seaside sparrow, savanna sparrow, diamondback terrapin, saltmarsh snake) to have southern distributions, which suggests that southern refugia along the Gulf and Mexican coastlines may have played a role in reducing the probability of extinction (Greenberg and Maldonado forthcoming). More frequent are species that show little or no significant change in genetic structure associated with tidal marsh occupancy. A good example of this is the trio of song sparrow subspecies found in the three estuaries of San Francisco Bay, each of which shows insignificant or very low F_{st} (fixation index) values (overall $F_{st} = 0.0217$, $P < 0.001$) for microsatellite DNA loci when analyzed with nearby upland subspecies (Chan et al. forthcoming). These results suggest that endemism may
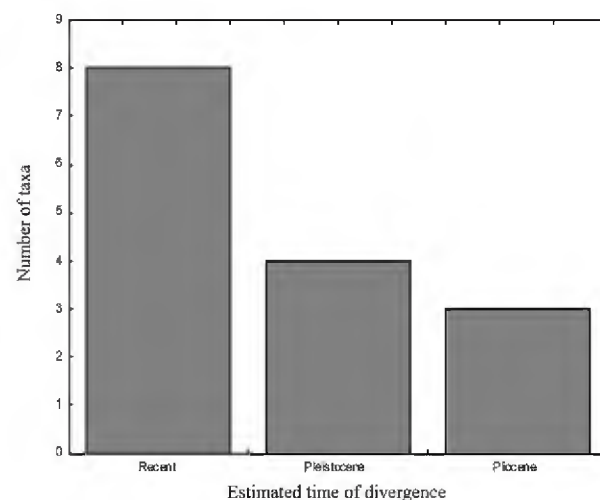

Figure 2. The number of taxa that probably diverged from their closest living relatives during the recent post-Pleistocene, Pleistocene, and late Tertiary periods, based on estimates from nucleotide substitutions in published genetic analyses (Chan et al. forthcoming).

not be strongly associated with long-term marsh stability, because much of the divergence is relatively recent.

Local adaptation to tidal marsh life

The rapid divergence in a number of salt marsh forms suggests a sharp environmental gradient that shapes local adaptation.

Environmental challenges of tidal marshes.
As most tidal marshes are frequently inundated with salt water, one of the fundamental adaptive challenges for successful colonization is the ability to tolerate salty fluids or to find alternative water sources. Food resources in tidal marshes differ from those of terrestrial or freshwater ecosystems, having a more diverse soil or benthic marine invertebrate component (Odum 1988, Mitsch and Gosselink 2000) and a low abundance and diversity of seeds in the soil seed bank (Leck 1989). Herbivory on grasses and shrubs is considerably lower than in freshwater marshes, and so the abundance and diversity of invertebrates may be more concentrated in the substratum.

Tidal marshes also have substrates distinct from upland or freshwater habitats. As a result of the anaerobic conditions and the high sulfur content of seawater (Odum 1988), tidal salt marshes are underlain by acid sulfate soils that have a characteristically gray or blackish coloration, sometimes with a greenish algal surface. Furthermore, animals often forage on temporarily exposed intertidal mud along sloughs and tidal pools, rendering them vulnerable to aerial predators.

Adaptation to salinity.
Adaptations to salinity vary in their complexity (Dunson and Travis 1994), and one of the simplest adaptations is behavioral avoidance. For example, meadow voles (*Microtus pennsylvanicus*) of tidal marshes cannot tolerate ingesting salty water, and satisfy their water needs by consuming dew and precipitation and selectively eating grasses with low salt content (Getz 1965). Similarly, coastal plain swamp sparrows (*Melospiza georgiana nigrescens*), which have relatively recently colonized tidal marshes, show some renal adaptations but no significant ability to survive while ingesting seawater. As a result, these sparrows are restricted to marshes with salinities of less than 10 to 15 parts per thousand. Other forms of behavioral adaptation are seen in tidal marsh snakes and turtles that show a reduced tendency to drink when placed in salt water compared with closely related freshwater taxa (Pettus 1958, Dunson and Travis 1994).

One of the simplest morphological and physiological adaptations to salinity is found in estuarine snakes and turtles whose integuments are less permeable to water than those of their freshwater counterparts, helping to minimize osmotic water loss in water with high salt content (Dunson and Travis 1994). The kidneys of certain forms of mice and birds living in salt marshes have enhanced abilities to concentrate salts and to process greater volumes of water (Goldstein forthcoming). Perhaps the most complex desalinization mechanism is found in those species with specialized nasal or lachrymal glands that concentrate and exude solutions that vary in their salt composition depending on the amount of salt intake in the diet. Among estuarine vertebrates, such glands are known for crocodilians, terrapins, and certain birds, most notably waterfowl, larids, and rails (Olson 1997). Where salt glands are found in both salt marsh and fresh marsh forms, the glands are larger in the salt marsh taxa. This difference has been shown to have both a genetic and a developmental basis in rails (Olson 1997).

Morphological adaptations.
The best-known "habitat rule" for morphological divergence of tidal marsh forms is the tendency toward a greater expression of grayish and black (eumelanin) over buff, ochre, and rust (phaeomelanin) colorations, particularly in the dorsal color of terrestrial vertebrates of tidal marshes (Grinnell 1913). A review (Greenberg and Droege 1990) suggests that eumelanin coloration is prevalent in sparrows, shrews, and voles, and noted for several other tidal marsh taxa, such as the Carolina water snake, the clapper rail (*Rallus longirostris,* in contrast with the king rail, *Rallus elegans*), and coastal subspecies of the marsh wren. The primary hypothesis for the adaptive value of grayer and blacker coloration is that it matches the background of the acid sulfate soils often associated with tidal marsh (Greenberg and Droege 1990).

Other examples of convergent or parallel evolution can be found among taxonomic subsets of tidal marsh specialists. The six species of emberizid sparrows found in tidal marshes probably represent multiple invasions of this habitat. The bills of tidal marsh sparrows are longer and narrower than those of closely related taxa (Grenier and Greenberg 2005): A comparison of bill dimensions of the 10 tidal marsh sparrows in North America with those of 26 taxa representing emberizids as a whole revealed that as body size increased, bill size increased at a faster rate in the tidal marsh sparrows than in the nontidal marsh birds (Grenier and Greenberg 2005). This phenomenon may be an adaptation for greater consumption of animal prey and less reliance on plant foods, such as seeds. This morphological difference is more pronounced in taxa that diverged further back in evolutionary time.

Life history of tidal marsh vertebrates

The tidal marsh environment has shaped the life history of populations of vertebrates. For example, tidal marsh sparrows have small clutches for birds of the temperate zone, ranging from 2 to 4, with an average of 3.4, for 15 populations of 7 species (Greenberg et al. forthcoming). Within-species comparisons of adjacent or nearby populations show a significant reduction in clutch size for song and swamp sparrows of the tidal marshes. Fewer comparative data are available for other taxa, but the clutch size of the clapper rail is substantially smaller than that of the closely related king rail of freshwater marshes. The smaller clutch sizes may be related to the reduced seasonality of resources in coastal marshes (Ashmole's hypothesis) or to the high levels of nest failure, which might select for reduced investment in any individual reproductive

attempt if energy is limited over a season for clutch production. Nest success appears to be quite low for tidal marsh sparrows as a whole, averaging 31% for 15 populations of tidal marsh sparrows, and was as low as 15% to 20% during long-term studies of song and swamp sparrows (Greenberg et al. forthcoming).

Adaptations for reproduction in the face of flooding and predation

Flooding is one of the greatest threats to reproductive success for tidal marsh–breeding species. Flooding can occur with normal tidal flow, but can also be unpredictable when rain, wind, and tides align to bring water into areas that are normally spared regular tidal inundations. Tidal marsh birds regularly elevate their nests, whereas their nontidal marsh relatives seldom do (Greenberg et al. forthcoming). However, the simplicity of the vegetation and the abundance of visual predators constrain the ability of animals to raise their structures. Nesting adaptations to flooding include the building of high platform structures bound to *Spartina* support stems, such as the clapper rail constructs (Reinert forthcoming). This species often uses vegetation cues to indicate safe nesting sites, and its eggs are resistant to submersion in salt water. The timing of nesting is thought to be affected by the probability of flooding. In certain songbirds, such as the saltmarsh sharp-tailed sparrow (Shriver 2002) and populations of the red-winged blackbird (*Agelaius phoeniceus;* Reinert forthcoming), the rapid resumption of nesting after the predictable flooding caused by extreme high tides allows a nesting cycle to occur between the two high summer tides that characterize New England marshes (Shriver 2002). There is far less information on mammal nests in tidal marshes, but anecdotal evidence suggests that they too are elevated, often placed in structures abandoned by birds (Greenberg et al. forthcoming).

Space use and social systems

The combination of high but variable productivity and simple structure in marshes has contributed to the formation of theories of social evolution, including the study of coloniality, polygyny, and interspecific territoriality, particularly in birds (Orians 1980). Tidal salt marshes share many of the attributes of freshwater marshes, but they have an additional ecological feature that shapes social organization. The area that provides refuge from nest loss due to flooding or predation is often much smaller than the area that can be used for foraging (Post 1974). In particular, the tendency to form aggregations is very well developed in tidal marsh vertebrates. Social tolerance and the tendency to flock or aggregate during normal high or flood tides is also a unique feature of tidal marsh vertebrates. Social aggregations have been reported even for normally solitary shrews (Hays and Lidicker 2000).

A high proportion of North American salt marsh–breeding bird species (7 out of 12) are reported to show highly patchy distribution, with separate nesting territories and feeding ranges, during the breeding season; this proportion is only 2 out of 10 for their closest relatives that do not breed in salt marshes (McDonald and Greenberg forthcoming). For example, Johnston (1956) reports that the territories of salt marsh–nesting song sparrows were clustered at an exceedingly high density of 20 to 25 pairs per hectare (ha) along the raised ground bordering narrow channels. Saltmarsh sharp-tailed sparrows, unlike many other sparrows that defend territories, have evolved a semicolonial spacing system associated with a polygynous mating system in which males compete directly for access to females. This system may have developed because females tend to concentrate to a point where they represent an undefendable resource and territoriality breaks down.

Threats to tidal marsh diversity

Given the enormous pressures on delicate coastal ecosystems, it should not be a surprise that the 25 species of vertebrates restricted to tidal marshes and the nearly 50 subspecies that they represent are disproportionately endangered, threatened, or otherwise of heightened conservation concern (table 2).

Conservation status of endemic taxa. One salt marsh–dwelling subspecies of ornate shrew from Baja California (*Sorex ornatus juncensis*) may already be extinct (Maldonado 1999). Federally endangered taxa include the salt marsh harvest mouse, three subspecies of the clapper rail, and the Florida meadow vole (*M. pennsylvanicus dukecampbelli*). The Atlantic coast subspecies of the salt marsh water snake (*Nerodia clarkii taeniata*) is listed as threatened by the US Fish and Wildlife Service.

Coastal 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 human population was found within 100 km of the coast (Cohen et al. 1997). At the same time, 42% of the US population lived in coastal counties along the Pacific, the Atlantic, and the Gulf of Mexico (NOAA 2005). The impact of human populations around major estuaries, where most tidal marsh is found, is undoubtedly higher than along random sections of coastline. The overall loss of coastal wetlands in North America has been estimated at 30% to 40% (Horwitz 1978). In particular, the filling and development of the shoreline of tidal estuaries such as the San Francisco and Chesapeake bays and the Río de la Plata has led to the direct loss of large areas of tidal marsh. The loss of over 80% of the original wetlands around San Francisco Bay is of special concern (Takekawa et al. forthcoming), because its three major embayments support more endemic tidal marsh taxa than any other single coastal locality.

Much of the tidal marsh loss in Asia and Europe may have occurred early in the history of human civilization. In an area where tidal marsh has been converted and exploited for many centuries, it may be difficult to estimate the amount of human-caused loss. It is suspected that at least 65% of the original tidal marshes of Europe have been developed, and 70% of the remaining marshes are heavily managed (Greenberg and

Maldonado forthcoming). These rates of loss add up to a global loss that is at least as high as 35% for mangroves along tropical estuaries (Valiela et al. 2001). And the loss of marshes continues: In China, tidal marsh area has declined by 50% since 1953 (Shuqing 2003).

Apart from draining and filling, tidal marshes are diked, grazed, harvested for fodder, and otherwise used for agriculture. Grazing has been a traditional use of coastal marshes, and continues to be the major threat to coastal marshes in South America. In some areas *Spartina* and other grasses were (and are) also harvested for hay production.

Along the coast of the Yellow Sea in China and the southern coast of North America, marshes were diked to form impoundments for rice production. In the coastal Carolinas and Georgia, these impoundments, created in the 18th century, dominated the coastal zone well after the crash of the rice-growing industry in the region. In some areas, most notably San Francisco Bay and the China coast, large areas of tidal marshes were converted into settling ponds for salt production, beginning (in the case of California) over 200 years ago.

Marshes have traditionally been managed for waterfowl and muskrat in the southeastern United States, where marshes are commonly burned to open up habitat and to favor the young growth of preferred forage. Burning is currently used, often in conjunction with herbicides, to control invasive stands of the common reed (*Phragmites australis*). In addition, ponds are often created within tidal marshes to create waterfowl habitat and to assist in the control of mosquitoes (Erwin et al. 1994). Although these management practices are widespread, few studies have attempted to rigorously assess their effects on either the target wildlife species or the endemic taxa of sparrows, small mammals, and rails (Mitchell et al. forthcoming). Other forms of management of unexploited marshes include ditching and reduction of tidal flow, both of which may profoundly influence the vegetation. In addition, reducing the tidal flow of a marsh greatly alters the marsh floristics (Zedler et al. 2001) and has an adverse effect on habitat quality for seaside and sharp-tailed sparrows (DiQuinzio et al. 2002) as well as clapper rails (Powell forthcoming).

Sea-level rise. The conversion of tidal marshes to dry land has been greatly reduced in recent decades in the United States. The greatest future threat is loss due to rising sea levels (Titus 1988, Church et al. 2001). Sea-level rise transforms tidal flat to estuary, low marsh to tidal flat, and high marsh to low marsh. Depending on the shape of the estuary and the nature of land use at the upper edge of the marsh, sea-level rise has resulted in a variable but significant reduction in the amount of coastal wetlands, with estimates of loss ranging from 0.5% to 1.5% per year for North America (Titus 1988). The specific rate of habitat loss depends on the rate of sedimentation and the geomorphology of the estuary. The mid-Atlantic estuaries of North America are showing particularly high rates of sea-level rise (4 to 8 millimeters per year) that are accompanied by a several-fold increase in late spring flooding events (Erwin et al. forthcoming). The latter events could seriously affect birds that are constrained in their reproductive success by flooding. Sea-level rise may bring greater saltwater intrusion and increased salinity (Titus 1988), which may affect species adapted to brackish conditions.

In addition, human-induced habitat alterations of the coastal landscape may prevent coastal organisms from shifting inland with the advance of sea level. For instance, rising sea levels have encroached on low-lying, highly populated areas of the southeastern United States. As a result of mainly nonclimatic influences, this region lost more than 13,000 ha of coastal tidal marsh between 1985 and 1995. Although sea-level rise caused some of this loss, the primary contributing factors were human development, groundwater pumping, and, in some places, natural subsidence (sinking) as coastal soils compact. In addition to sea-level rise, changes in climate could lead to more frequent or more intense storms, and are likely to result in more erosion, flooding of low-lying areas, intrusion of salt water, wetland destruction, and negative impacts on the biology and ecology of tidal marsh endemics. Other sources of wetland degradation, such as overgrazing caused by population increases in geese and snails, have been reported to have various impacts on tidal marshes in specific regions.

Invasive species. Tidal marshes appear to be particularly susceptible to shifts in dominant species of vegetation that come with the spread of invasive species. Along the coastlines of Asia, western North America, Tasmania, and New Zealand, and in parts of Northern Europe, low salt marsh and adjacent unvegetated mudflats are being invaded by *Spartina* species, mostly *S. alterniflora,* which often hybridizes with the local native species. At the upper edge of marshes along the Atlantic coast of North America, a strain of *Phragmites* (*P. australis*) is spreading into areas once dominated by *Juncus, Spartina,* and *Iva* shrubs. The effect of such invasions is poorly documented, but recent research has shown that *Phragmites* invasion favors certain generalist species over tidal marsh specialists (Benoit and Askins 1999). The invasive *Spartina* and *Phragmites* support the local increase in marsh wren populations, which may further affect endemic sparrows. Furthermore, *Spartina* that grows on what were formerly unvegetated mudflats may serve as a death trap, attracting low-nesting sparrows and rails to attempt breeding in areas that are too prone to flooding for successful reproduction (Guntenspergen and Nordby forthcoming). At low densities, *Phragmites* may create habitat heterogeneity, but when it spreads to form large single-species stands, resources for some marsh-nesting species disappear.

Toxins and pollutants. Tidal marshes are particularly vulnerable to the pollutants, fertilizers, and wastes that enter the watersheds that support them, as well as to the chemical spills and contaminants introduced from coastal marine waters. Contaminants bind to sediments, and some, including methyl mercury, selenium, PCBs (polychlori-

nated biphenyls), and trace metals, bioaccumulate up the estuary food chain (Takekawa et al. forthcoming). Mercury contamination can be a particularly severe problem (Novak et al. forthcoming), causing acute toxicity in fish, birds, and mammals. High-level exposure damages the central nervous system, while lower-level exposure affects reproduction in vertebrates (Wolfe et al. 1998). Furthermore, tidal marshes are often the recipient of broad-spectrum pesticides for mosquito control, a practice that may be exacerbated by the perception that the habitat is a source of vectors for emerging diseases, such as West Nile virus (Takekawa et al. forthcoming).

Future research needs

Understanding why reported endemism for tidal marsh species and subspecies is largely restricted to North America is a good starting point for a global research program on tidal marsh biota. Is this a real pattern, or an artifact of sampling bias? If it is indeed the result of biases in the way that subspecies are recognized and described, then a more global approach to research on the differentiation of tidal marsh taxa will provide a more complete inventory of endemic taxa. If, on the other hand, the phenomenon of greater differentiation in North America is real, then further work is required to determine whether historical or current ecological factors are responsible for the pattern. Along with this global inventory, scientists should encourage and expect more comparative work on physiological, trophic, life history, and social factors in shaping adaptations of tidal marsh taxa (vertebrate, invertebrate, and floristic) inhabiting the different coastal tidal marsh systems. This work should help determine factors that drive and inhibit divergence of tidal marsh populations from their inland source and sister populations. To do this, we need more research on the Quaternary history of tidal marshes, focusing on their extent, distribution, and floral composition through time.

Given the myriad threats to coastal ecosystems, researchers need to expand on both modeling and empirical monitoring approaches to determine how the distribution of different species will respond to regional habitat loss and fragmentation, as well as changes in the floristic composition, vegetative structure, and hydrology of tidal marshes. Given the seeming delicate balance of the species with respect to tidal flow and salinity levels, we need to develop predictive models for how changes in mean sea level and in the frequency or intensity of severe storms might influence flooding regimes, and how this will affect the survival and reproductive output of tidal marsh vertebrates in general. Tidal marshes are particularly prone to invasions by dominant species of plants. Given the low diversity of the tidal marsh flora, such invasions have a major impact on the structure and function of marsh ecosystems. With a detailed history of the invasion process as a backdrop, future research should focus more on how tidal marsh species adapt to the change in dominant vegetation caused by invasions. Similar studies should also be conducted on the impact of invasive

fauna such as rats, mice, nutrias, and opossums, as well as invasive mollusks and other nonnative invertebrates, on tidal marsh systems.

Conclusions

Tidal marshes support relatively few species of terrestrial vertebrates. However, in response to the sharp environmental gradient, many marsh-inhabiting vertebrate taxa have differentiated at the level of ecological race (subspecies), some differentiating to the point of becoming tidal marsh–endemic species. Characteristics associated with ecological races specific to tidal marshes include coloration, size and shape differences of the skull, and kidney structure and function. At present, almost all (24 out of 25) species that are wholly or partially restricted to tidal marshes are found along the North American coasts. This may be partly an artifact of unrepresentative taxonomic research concentration, but it may also be a real biogeographic phenomenon that calls for a general explanation. At this time, no single comprehensive theory can fully explain the phenomenon of North American endemism.

Coastal marshes are threatened by continued development, pollution and toxins, invasive species, changes in sea level and salinity, and fragmentation at the landscape level that is likely to increase the impact of invasives, predators, competitors, and diseases. The global impact of such threats has remained poorly understood, as tidal marsh ecology and conservation is usually approached on an estuary-by-estuary basis. Research with a more global approach on tidal marsh taxa may provide a more complete view of the factors responsible for the observed patterns of differentiation.

Acknowledgments

References cited

Adam P. 1990. Saltmarsh Ecology. Cambridge (United Kingdom): Cambridge University Press.

Avise JC. 1994. Molecular Markers, Natural History and Evolution. New York: Chapman and Hall.

Avise JC, Nelson WS. 1989. Molecular genetic relationships of the extinct dusky seaside sparrow. Science 243: 646–648.

Benoit L, Askins R. 1999. Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. Wetlands 19: 194–208.

Bertness MD. 1992. The ecology of a New England salt marsh. American Scientist 80: 260–268.

Chan YL, Hill CE, Maldonado JE, Fleischer RC. Evolution and conservation biology of tidal marsh vertebrates: Molecular approaches. In Green-

berg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Chapman VJ, ed. 1977. Wet Coastal Ecosystems. Ecosystems of the World, vol. 1. Amsterdam: Elsevier Scientific.

Church JA, Gregory JM, Huybrechts P, Kuhn M, Lambeck K, Nhuan MT, Qin D, Woodworth PL. 2001. Changes in sea level. Pages 639–694 in Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden P, Dai X, Maskell K, Johnson CI, eds. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (United Kingdom): Cambridge University Press.

Cohen JE, Small C, Mellinger A, Gallup J, Sachs J. 1997. Estimates of coastal populations. Science 278: 1209–1213.

Colman SM, Mixon RB. 1988. The record of major Quaternary sea-level changes in a large coastal plain estuary, Chesapeake Bay, eastern United States. Palaeogeography, Palaeoclimatology, and Palaeoecology 68: 99–116.

DiQuinzio DA, Paton PWC, Eddleman WR. 2002. Nesting ecology of salt-marsh sharp-tailed sparrows in a tidally restricted salt marsh. Wetlands 22: 179–185.

Dunson WA, Travis J. 1994. Patterns in the evolution and physiological specialization in salt-marsh animals. Estuaries 17: 102–110.

Erwin RM, Hatfield J, Howe M, Klugman S. 1994. Waterbird use of saltmarsh ponds created for open marsh water management. Journal of Wildlife Management 58: 516–524.

Erwin RM, Prosser D, Sanders G, Cahoone D. High tides and rising seas: Potential effects on estuarine birds. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Getz LL. 1965. Salt tolerance of salt marsh meadow voles. Journal of Mammalogy 47: 201–207.

Goldstein D. Osmoregulatory biology of saltmarsh passerines. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Greenberg R, Droege S. 1990. Adaptations to tidal marshes in breeding populations of the swamp sparrow. Condor 92: 393–404.

Greenberg RG, Maldonado JE. Diversity and endemism in tidal marsh vertebrates. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Greenberg RG, et al. Flooding and predation: Trade-offs in the nesting ecology of tidal-marsh sparrows. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Grenier JL, Greenberg R. 2005. A biogeographic pattern in sparrow bill morphology: Parallel adaptation to tidal marshes. Evolution 59: 1588–1595.

Grinnell J. 1913. The species of the mammalian genus *Sorex* of west-central California with a note on the vertebrate palustrine fauna of the region. University of California Publications in Zoology 20: 179–205.

Guntenspergen GR, Nordby JC. The impact of invasive plants on tidal marsh vertebrate species: *Phragmites australis* and *Spartina alterniflora* as case studies. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Hays WST, Lidicker WZ. 2000. Winter aggregations, Dehnel effect, and habitat relations in the Suisun shrew *Sorex ornatus sinuosus*. Acta Theriologica 45: 433–442.

Horwitz EL. 1978. Our Nation's Wetlands. Washington (DC): Council on Environmental Quality.

Isacch JP, Holz S, Ricci L, Martinez MM. 2004. Post-fire vegetation change and bird use of a salt marsh in coastal Argentina. Wetlands 24: 235–243.

Johnston RF. 1956. Population structure in salt marsh song sparrows, part 2: Density, age structure, and maintenance. Condor 58: 254–272.

Leck MA. 1989. Wetland seed banks. Pages 283–306 in Leck MA, Parker VT, Simpson RL, eds. Ecology of Soil Seed Banks. San Diego: Academic Press.

Lefebvre G, Poulin B. 2000. Determinants of avian diversity in neotropical mangrove forests. Pages 161–179 in Gopal B, Junk WJ, Davis JA, eds. Biodiversity in Wetlands: Assessment, Function and Conservation, vol. 1. Leiden (The Netherlands): Backhuys.

Levin PS, Ellis J, Petrik R, Hay ME. 2002. Indirect effects of feral horses on estuarine communities. Conservation Biology 16: 1364–1371.

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography. 3rd ed. Sunderland (MA): Sinauer.

Lopez-Laborde J. 1997. Geomorphological and geological setting of the Río de la Plata. Pages 1–16 in Wells PG, Daborn GR, eds. The Río de la Plata: An Environmental Overview. Halifax (Canada): Dalhousie University.

Malamud-Roam KP, Malamud-Roam FP, Watson EB, Collins JP, Ingram BL. The Quaternary geography and biogeography of tidal saltmarshes. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Maldonado JE. 1999. Family Soricidae. Pages 39–52 in Alvarez-Castañeda ST, Patton JL, eds. Mamíferos del Noroeste de México. La Paz (Mexico): Centro de Investigaciones Biológicas del Noroeste.

McDonald MV, Greenberg R. Mating and social systems of birds and mammals in tidal marshes. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Mitchell L, Gabrey S, Marra PP, Erwin RM. Impacts of marsh management on coastal marsh birds and their habitats in the southeastern United States. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Mitsch W, Gosselink JG. 2000. Wetlands. 3rd ed. New York: Van Norstrand Reinhold.

Neill WT. 1958. The occurrence of amphibians and reptiles in saltwater areas and a bibliography. Bulletin of Marine Science of the Gulf and Caribbean 8: 1–95.

[NOAA] National Oceanic and Atmospheric Administration. 2005. Population Trends along the Coastal United States: 1980–2008. (1 June 2006; *www.oceanservice.noaa.gov/programs/mb/pdfs/coastal_pop_trends_complete.pdf*)

Novak JM, Gaines KF Cumbee JC Jr, Mills GL, Rodriguez-Navarro A, Romanek CS. Clapper rails as indicator species of estuarine marsh health. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Odum WE. 1988. Comparative ecology of tidal freshwater and salt marshes. Annual Review of Ecology and Systematics 19: 147–176.

Olson S. 1997. Towards a less imperfect understanding of the systematics and biogeography of the Clapper and King rail complex (*Rallus longirostris* and *R. elegans*). Pages 93–111 in The Era of Allan R. Phillips: A Festschrift. Albuquerque (NM): Museum of Southwestern Biology.

Orians G. 1980. Some Adaptations of Marsh-nesting Blackbirds. Princeton (NJ): Princeton University Press. Princeton Monographs in Population Biology 14.

Pettus D. 1958. Water relationships in *Natrix sipedon*. Copeia 1959: 207–211.

Post W. 1974. Functional analysis of space-related behavior in the seaside sparrow. Ecology 55: 564–575.

Powell AN. Are southern California's fragmented saltmarshes capable of sustaining endemic bird populations? In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Reinert S. Avian nesting response to tidal-marsh flooding: Literature review and a case for adaptation in the red-winged blackbird. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Riddle BR, Hafner DJ, Alexander LF, Jaeger JR. 2000. Cryptic vicariance in the historical assembly of a Baja California peninsular desert biota. Proceedings of the National Academy of Sciences 97: 14438–14443.

Shriver WG. 2002. The conservation ecology of salt marsh birds in New England. PhD dissertation, State University of New York, Syracuse.

Shuqing AN. 2003. Ecological Engineering of Wetlands. Beijing (China): Chemical Industry Press.

Sillman BR, Bertness MD. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences 99: 10500–10505.

Takekawa JY, Woo I, Spautz H, Nur N, Grenier JL, Malamud-Roam K, Nordby JC, Cohen AN, Malamud-Roam F, Wainwright-De La Cruz SE. Environmental threats to tidal marsh vertebrates of the San Francisco Bay estuary. In Greenberg RG, Maldonado JE, Droege S, McDonald MV, eds. Terrestrial Vertebrates of Tidal Marshes: Ecology, Evolution, and Conservation. Studies in Avian Biology. Forthcoming.

Teal JM. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614–624.

Titus JG, ed. 1988. Greenhouse Effect, Sea Level Rise, and Coastal Wetlands. Washington (DC): US Environmental Protection Agency. EPA 230-05-86-013.

[USFWS] US Fish and Wildlife Service. 2002. Birds of Conservation Concern 2002. Arlington (VA): US Fish and Wildlife Service, Division of Migratory Birds.

Valiela I, Bowen JL, York JK. 2001. Mangrove forests: One of the world's threatened major tropical environments. BioScience 51: 807–815.

Wolfe MF, Schwarzbach S, Sulaiman RA. 1998. Effects of mercury on wildlife: A comprehensive review. Environmental Toxicology and Chemistry 17: 146–160.

Zedler JB, Callaway JC, Sullivan G. 2001. Declining biodiversity: Why species matter and how their functions might be restored in Californian tidal marshes. BioScience 51: 1005–1017.